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Memorial Paper in Honor of Jerzy Konorski

# CONSCIOUSNESS FROM NEURONS [1]

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*Abstract.* Consciousness derives from a neural process that requires unceasing metabolic support, and probably involves only a select population of neocortical elements. The essential process must operate for roughly more than 100 msec for sensorial registration (Libet). It is highly unlikely that the essence of the process lies in its computational logic and hence it can never be produced by inanimate machines. Since the process is thus unique to neurons, and since the consciousness of the left hemisphere normally communicates with that of the right (and probably vice versa) via the forebrain commissures, at least some portion of the nerve impulse traffic across the commissures must possess a wholly mysterious property enabling its transcendent compilation into a unified conscious experience. Comprehending the nature of this property which couples ionic fluxions into mentality is the quintessential problem of science. The forebrain commissures may ultimately provide the clues for its solution.

The mystery of consciousness unites all humankind as does no other experience or phenomenon. The deepest aspirations of religion are to enhance or to preserve it. For science it is the ultimate solipsism, so far wholly inaccessible, yet undeniable. The thesis of this essay is that the

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[1] To the memory of Jerzy Konorski, brave pilot of the waters skirted here. I can vividly imagine the zest and skill with which he would have responded, to elaborate, to clarify, to refute, to immerse himself vigorously in the arguments I now present. May the verve, the devout honesty and ceaseless creativity he brought to neuroscience remain forever with its practitioners.

neurophysiological analysis of consciousness is perhaps not as hopeless as it presently seems. What more challenging quest than to learn how the multimillioned shuttling of damp sparks can weave a comprehending self within the fatty fabric of the brain!

Man has pondered his consciousness throughout recorded history, but the first dim clue as to where the focus should be placed came at the end of the sixth century B.C. This was somehow a remarkable period that saw from one end of the civilized world to the other an intellectual revolt against the follies of religion as well as the materialism of the State. Zoroaster (born ca. 628 B.C.), Ezekiel (exiled from Jerusalem to Babylon ca. 597 B. C.), Mahāvīra Vardhamāna, he last of the 24 Tirthankaras (born ca. 599 B.C.), Siddhartha Gautama the Buddha (born ca. 563 B.C.), K'ung-fu-tzu (Confucius, born ca. 551 B.C.) and Pythagoras (in Kroton ca. 525 B.C.) each strove mightily to alter man's concepts. All founded or were associated with great religions or philosophical systems; all but that of Pythagoras surviving until today, albeit in wildly distorted forms. Yet with Pythagoras somehow went the more certain light. Perhaps it was the mathematics. Perhaps it was a rumor from the Orient. Whatever, it was the pupil of Pythagoras, Alkmaion, who at Kroton ca 500 B.C. first discerned and left recorded the fact that mind originates in brain (5). From here on within the Western world consciousness was perceived as focused, as requiring a physical vehicle.

The Doric experimenters must also have known the other cardinal fact about the physical requirements for consciousness, that the brain needs blood. Since the circulation of the blood and its oxygenation were to go unrecognized for another 2,100 years, the full significance of the observation undoubtedly escaped them, yet the word "carotid", from *ϰαϱουν* (to stupefy), unequivocally indicates they knew the quick consequence of pressure on these arteries (see 30).

Each of the 1,500 mitochondria within a large neuron needs 10 atoms of oxygen each microsecond for normal function (28). If oxygen is cut off, consciousness is lost within 10 sec, and most of the latency can be attributed to the circulation time. Consciousness thus cannot be created without a ceaseless flame of chemistry.

Yet it is the process not the material which produces the conscious state. The basic physical materials can confidently be considered as immutable. As I write these lines my thoughts depend upon oxygen atoms once exhaled by great belugas, white ghosts beneath the arctic sea, by the Pithecanthropoid cannibals of Chou-k'ou-tien, by Gautama the Buddha, perhaps even the atoms that passed through his cerebral mitochondria on that night of the full moon in May when he attained knowledge of all his former existences. Here is an atomic transmigration beyond even the wildest dreams of the prophets of karman. With each breath my neurons imbibe about 400,000 atoms of oxygen once used by neurons of the Buddha, of Pythagoras, of Ashurbanipal, of Lavoisier; by neurons of all creatures whose brain required a total of $4 \times 10^{28}$ molecules of oxygen throughout their lifetime[2]. But use imparts nought to the atoms, Teilhard de Chardin (36) notwithstanding. This transmigration has no imprint of the past, and Christ's atoms nourish equally the fires of Nero as corrode the steel of the Khanate hordes, the bark of the sequoia as the suffering of the saints.

Emphasizing then, that consciousness is a process and not derivative from the past history of the participating atoms, it becomes necessary to identify the essential features of this process. It has been a popular pseudoscientific pastime to claim that consciousness could be attributed to computers were they but sufficiently complex. Were this true, the significant process would perforce be merely one of computational logic. While it might be preferable before deciding the question to await the building of a computer that would properly scan its sonnets and artfully argue its philosophy, a gedanken experiment may adumbrate the outcome, and significantly shorten the wait. The appeal of the computer, of course, is that its processes, like those of brains, are digital, and exquisitely rapid. However, it is the logic not the speed which is the essence of the computational process. Babbage's "analytical engine" though mechanical would yield the same answer as its electronic counterpart. Suppose, then, that knowing all the computational events that occur in retina and central nervous system upon the perception of "red", the nations of the world set about constructing a vast clockwork which, with its gears and cables, would exactly duplicate the millions of digital escapements and transmissions which occur for the eye and brain. Obviously, the temporal domain must be expanded many thousand fold, but the intervals can all be precisely and proportionately preserved, as could any of the analog retinal processes required. The system is set in motion to tick away the idle interval of darkness, great armies of atom-driven steam engines applying power at the appropriately designated moments. Now shines the light,

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[2] The calculations are as follows. In man at rest 250 ml $0_2$/min are required of which 1/5 is utilized by brain (19). In $26.28 \times 10^6$ min (50 years) this $= 6 \times 10^6$ liters $0_2 = 3 \times 10^5$ moles $= 18 \times 10^{28}$ molecules of $0_2$ per "lifetime". At a respiratory rate of 12/min the brain will obtain 4 ml $0_2$/breath $= 1.2 \times 10^{20}$ molecules $0_2$. The atmosphere contains $11.8 \times 10^{20}$ grams $0_2$ (23) $= 22 \times 10^{42}$ molecules $0_2$. Each lifetime thus uses $2 \times 10^{-15}$ of the total atmosphere and each breath $5 \times 10^{-24}$. Assuming total mixing and ignoring fixation in nonatmospheric forms, each breath will include from the fraction utilized by each former "lifetime" in the atmosphere pool 220,000 molecules $0_2$ [$(5 \times 10^{-24})$ $(2 \times 10^{-15})$ $(22 \times 10^{42}$ molecules $0_2)$].

a great pure red. The "retinal" network shifts, cables transmit; minutes, hours, days or years later the million "lateral geniculate" gears turn a new pattern, that which conforms to red in the corresponding million human neurons. These cables in turn transmit, the cortical gears respond, the surface of the earth shudders as mile upon mile the cogwheels churn throughout the mountainous machine, pursuing their ponderous, ineluctable logic. But despite the accuracy of its imitation of the human computational state can anyone really believe that this fantastic contraption experiences a sensation of "red"!? Yet if not, why not?

Is it the millisecond timing, an element of randomness, the compactness, the fluid medium, the lipoproteins, the electron exchange within the mitochondria that is essential to the human neuronal machine to yield the transcendent quality of "red"; where following equal logic pipe and gears or silicon wafers, however many billion byted, remain devoid of "sense"? The conclusion seems inescapable that the neuronal interchange exceeds manifestations of its logic because of some integrative process capable of concurrent evaluation of the state of the entire system. By their mere ability to construct the clockwork imitation of the visual system the designers, of necessity, knowing beforehand the state of the gears corresponding to "red", could incorporate a means of sampling the condition of their geared mechanism. This integrated read out informs an external observer when "red" occurs. However, no such external integrative mechanism is known for brain, and this is the heart of the problem: either to invent one, as in the dualist conception of an external soul that supernaturally scans and manipulates neurons, or to discover the true nature of the internal integration of neural activity which proceeds within the brain.

There are, of course, many human beings who also will never experience "red" by reason of their lacking the requisite receptor or neuronal machinery. This, however, is but another example of the fact that without neural processes subjective experience is impossible. The "blind spot" of the visual field does not betray its presence, since without neurons to represent the corresponding portion of the world nothing exists therein. When a scintillating scotoma migrates slowly across my field of view, objects which pass into it enter the same state of nonexistence as objects behind me. The neurons of my striate cortex that should register the presence of the object are otherwise occupied in creating a nonsensical, flickering cloud. The neurons are there, but the process is awry. So too is it with the unseeing eye of sleep. The neurons of the sleeping visual cortex fire as often as they do awake, yet their pattern differs (11). They have slipped out of control by the eye and are instead given into the command of some other system, perchance to dream (Fig. 1 and 2).

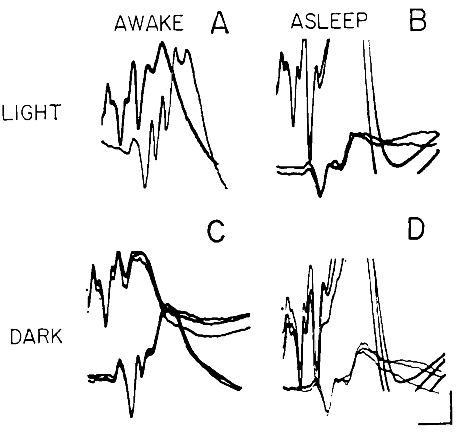

Fig. 1. "Release" of striate cortex in the macaque during sleep. All records from same point in striate cortex, monitoring its excitability directly to electrical stimulation of optic radiation (upper traces) and, 250 msec later (lower traces), indirectly to excitation of optic tract. In the alert state in the light (*A*) the response is greatest to input arriving from optic tract, i.e., lateral geniculate nucleus is "on". Excitability is diminished in darkness (*C*, "Chang effect"). In slow wave sleep, in the light or dark (eyes closed; *B*, *D*) the lateral geniculate nucleus is "off" but striate cortex is highly excitable (compare upper with lower traces). Calibration: 200 $\mu$v; 4 msec. From Bartlett et al. (3)

The transition in control of the striate cortex with sleep, so clearly seen in blind monkeys (Fig. 2), is probably attributable to action of the centrencephalic system (see 37). Penfield (27) conceived this system to be "that system within the diencephalon, mesencephalon and probably rhombencephalon which has bilateral functional connections with the

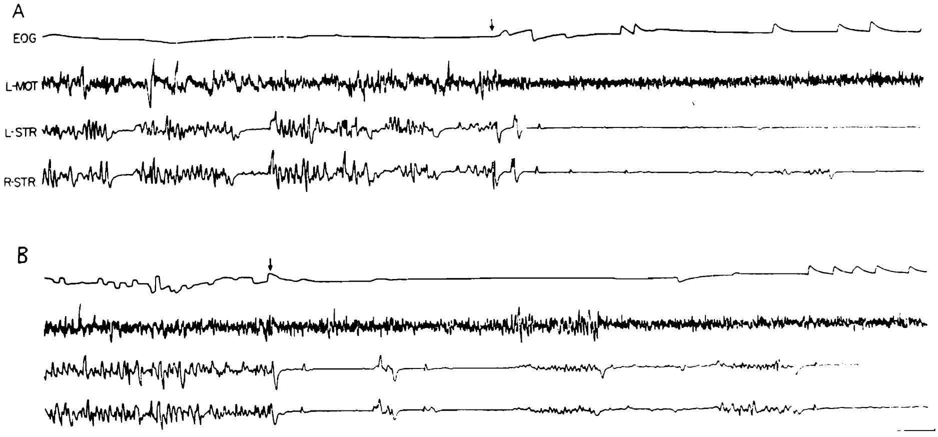

Fig. 2. Transition from sleep to wakefulness (arrows) in squirrel monkey 53 days after blinding by increased intraocular pressure. The EEG of striate cortex (lower two traces) is isoelectric for long periods in the alert state, as is usual in the blind monkey. In both slow wave (*A*) and REM (*B*, note electroculogram, upper trace) sleep, however, the pattern in striate cortex is very similar to that in these states in normal monkey except that amplitude is greater. Monkey aroused by had clap at arrows. Calibration: 200 $\mu$v, precentral cortex (L-MOT); 400 $\mu$v, striate cortex. From H. Sakakura and R. W. Doty (unpublished).

cerebral hemispheres" (note the pronounced symmetry in the EEG of right and left striate cortex in Fig. 2). He tentatively proposed that the centrencephalic system might represent the highest level of cerebral activity. There are also suggestions that it functions principally in the control of sensory input (e.g., 2, 3, 7), thus relating it to attentive mechanisms. In any event, it was tempting to look upon this system as providing the unifying, integrative internal monitoring which, as noted above, is an essential feature of the mechanism of consciousness. As is well known, relatively small lesions within the mesencephalic portion of this system in animals or man produce a permanent loss of consciousness (e.g., 17). However, there are a number of facts which now indicate that the centrencephalic system is not the primary focus of consciousness. First, in 19 patients undergoing angiography of the vertebro-basilar arterial system Alemà et al. (1) were able to affect mesencephalic activity directly and quite exclusively by injecting amobarbital into the vertebral artery without altering consciousness. The pupils dilated, corneal and pupillomotor reflexes disappeared, horizontal nystagmus occurred, all indicating a profound, localized curtailment of mesencephalically controlled activity, yet consciousness and memory for the procedure were unimpaired. The converse observation, by Obrador (25) is that injecting amobarbital into the carotid artery ipsilateral to the surviving hemisphere in two cases of hemispherectomy produced an immediate loss of consciousness. All this strongly suggests that the forebrain rather than the midbrain is the more critical structure for consciousness. Indeed, for the cat the activity of the mesencephalic reticular formation is itself dependent on input from the forebrain, for it essentially ceases when these connections are interrupted (38). The decisive evidence, however, for a cortical seat of consciousness, is provided in the analysis by Sperry and his colleagues (24, 32–34) of patients in whom the forebrain commissures have been transected. Here the centrencephalic system is intact (except for the massa intermedia) but fails to integrate the conscious experience of the two hemispheres.

The deleterious effect of midbrain lesions must thus be tentatively assigned to interruption of trophic influences which derive from the prodigious ramification of the brain stem monoaminergic systems (12, 18, 22, 26). In this regard it should be noted that Ingvar and Sourander (17) observed a striking atrophy of the cerebral cortex in a patient surviving 3 years after a midbrain lesion; and, correlating with the data in Fig. 2, the atrophy was largely confined to the occipital lobes.

This seems to leave the unity of consciousness to be arranged by the forebrain commissures. There is, of course, the possibility that the unity might arise only because of the restrictions on motor activity. If the conscious mechanism consists largely in the flow of sensory information into motor output, it is readily apparent that the latter is unified by its very nature; movement can proceed in only one direction at a time. There are, however, several reasons for believing that the motor system is not the primary focus of consciousness. First is the maintenance of learned posture or movement in the absence of consciousness, as in the common instance of patients preserving the position of an arm with an intravenous catheter while they sleep; or the case, with better documentation of the true depth of sleep, where human subjects can continue pressing a switch upon a given signal even though fast asleep (15).

Performance is thus not equivalent to consciousness nor is consciousness always required for performance. Indeed, the motor system is, to a large degree, served by an extensive sensory system exclusively its own which operates wholly at the subconscious level. Afferents from the muscle spindles produce no sensation in man (13, but see 16) nor, apparently, in cats (35). Similarly, stimulation of the cerebellum, whose primary function is the organization of movement and its control by proprioceptive and other sensory input, has no immediate conscious effects in man (31, and R. S. Snider, personal communication), and in cats cannot be used as a conditional stimulus for the performance of a learned behavior (4). The latter inability to support effects available from all other sensory systems is seen as well for electrical excitation of nucleus ventralis lateralis in the thalamus of the cat (J. E. Swett, personal communication). Large potentials can be evoked in the sensorimotor cortex, thus having a demonstrable neural effect, yet as a signal for performance by the cat it remains undetected; and the same feature appears in man (Fig. 3).

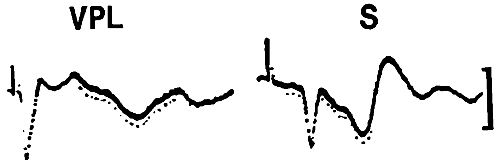

Fig. 3. Average of 250 responses to electrical stimulation of ventral posterolateral nucleus of the thalamus (VPL) and skin (S) at 1.8/sec recorded from somatosensory cortex in locally anesthetized human patient. None of the stimuli to VPL were felt even though each was six times the threshold strength for detection of a train of stimuli at 60 Hz. Each of the stimuli to the skin were twice threshold for detection of single pulses. Note that in the stimuli which were not detected the primary evoked potential (first downward deflection, VPL) is larger than for those which were (S), and that the detected stimuli produced a much larger "late" response. Calibration, 50 $\mu$v; total trace, 125 msec. From Libet et al. (21).

Thus, not only in sleep but in wakefulness as well certain forms of neural activity, even at cortical levels (see also below), are not necessarily reflected in consciousness. There is a peculiar dichotomy here in data for monkey vs. man. A macaque can detect the application of electrical excitation at about the same level of current at any neocortical locus and can perform a learned act in response thereto (6, 8, 9). The data suggest that it is the most excitable cortical elements (and definitely not trigeminal afferents) whose stimulation constitutes the signal. Yet in man application of much stronger currents through implanted electrodes at numerous loci yields no subjective sensation. There is thus either: a) a radical and hence unlikely difference in the basic properties of the neocortical systems in man versus macaque, b) an automatism in the monkey such that the learned response is made consequent to processing of the cortical signal without its ever attaining a level of awareness, or c) in monkey as well as man an initial "subjective silence" to unnatural direct excitation of cortical elements, which only enters awareness as a consequence of learning. There is, of course, the possibility that a human subject, trained as is the macaque to electrical excitation of a cortical locus which initially yields no report of subjective experience, might learn to press a lever for reward each time this locus was stimulated, and still be unable to report why the response was made. Such an outcome would be but another example of a learned motor response that could proceed in the absence of consciousness.

Libet and his colleagues (20, 21) are unique in having most carefully and ingeniously examined these questions of the relation of cortical neural activity to human conscious experience. Working with the sensorimotor cortex of unanesthetized patients undergoing various neurosurgical procedures, they have clearly demonstrated that only certain components of the potential evoked by peripheral or central stimuli are associated with conscious perception (Fig. 3). The concept of consciousness as a process here receives direct support since a certain "utilization time" is required before stimuli, demonstrably effective in exciting neurons, produce sensation. In other words, single or slowly repeated stimuli applied directly to the cortex, each of which evokes an electrical response, may remain ineffective until delivered within a span of time where their action can summate to attain the threshold for consciousness. Furthermore, activity initiated by stimuli which would ordinarily yield a conscious experience can be interrupted ("masked") at any time up to roughly 200 msec after its onset, thereby aborting both the process and the experience. As Libet (20) remarks, the process of consciousness appears to behave in an all or none fashion. This can also be perceived in ordinary life. It is a common experience for me, lying abed in the morning, to begin counting the strokes of our chiming clock only to awaken as the echo of the last stroke dies away, realizing that I have fallen asleep between the strokes five and seven (or was it five and eight!). In other words, consciousness can be turned off and on within a second or two, deleting or reinstating the registratoin of iterative, identical sensorial events. This fact, combined with the data in Fig. 3 on the critical electrical events at a cortical locus, and knowledge that these critical events must develop for ~125–500 msec (20) to reach consciousness, clearly point to the possibility that the neural activity specifically associated with conscious perception can be identified.

There is, however, a perplexing complication in the idea of a "threshold"; for the threshold for conscious perception is by no means conceptually identical with that for consciousness per se. While some might argue that "consciousness per se" is meaningless (consciousness devoid of content; lacking immediate or recalled sensation!?), there are conditions ("lost in thought" or the claims made for "meditation" by certain cults) which suggest that the phenomenon of consciousness is not entirely related to sensorial processing. The "threshold" for a "pure" consciousness independent of sensation then becomes a difficult neurophysiological problem. What are the conscious concomitants of increasing the relevant neural activity beyond the threshold level? There are, perhaps, degrees of consciousness, but their quantification in relation to the numbers of participating neurons is indefinable. The same problem is faced with the phylogenetic and ontogenetic evolution of consciousness. At what point in the development of the nervous system is the threshold of consciousness attained? Even if it is agreed that consciousness arises in association with the action of only certain classes of neurons, how many such neurons are required? Suppose in one's present state these neurons necessary for consciousness suddenly began to behave like radioactive nuclei and, with a short half life, started to disappear one by one. At what point would consciousness be lost? Would certain qualities of consciousness, e.g., the appreciation of color, of odor, etc. be lost more rapidly than others? Or, perhaps, in such circumstances the threshold for consciousness would prove to be a myth, and the level of awareness would simply deteriorate gradually.

While the foregoing questions may appear futile, the fact that they can be specifically phrased in terms of neurons and consciousness suggests that the problem is not wholly intractable. There may, however, be a more direct means of access to it. Sperry (32) has astutely remarked that the only way one brain can communicate directly with the consciousness of another is through the corpus callosum; meaning, of course, that the separate consciousness exhibited by right and left hemispheres in man after section of the forebrain commissures must, in the intact individual, intercommunicate. The argument obviously centers on the finding that the aphasic, illiterate right hemisphere of split brain man is conscious. Eccles (10) has vigorously argued that it is not, but rather that the linguistically skilled hemisphere is the unique and exclusive source of human consciousness, indeed that this consciousness is focused in activity in the temporal lobe area of Wernicke that is so enlarged in the "dominant" hemisphere (14). He states: "It is demonstrated that the minor cerebral hemisphere with its on-going activities that can be categorized as displaying memory, understanding even at a primitive verbal level, and concepts of spatial relations does not give any conscious experiences to the subject, who remains in conscious liaison only with neural events in the dominant hemisphere" (10).

Obviously there is something very special about the left, linguistic hemisphere; but need Descartes be followed from the pineal gland into the left temporal lobe? Eccles himself shows (10) the picture from Nebes and Sperry (24) of a commissurotomy patient, in whom language processes were well developed in both hemispheres, writing the word "book" with his left hand, correctly recording what his right hemisphere had seen, while the left, speaking hemisphere reports that "cup" is being written. His remark is "that the conscious subject was completely unaware of events in the right hemisphere" (10); leaving the implication that the correctly written response to the perceived word "book" was being accomplished by an unconscious subject! Surely the remarkable specialization of the left hemisphere for linguistic manipulation, on which rests almost the entire edifice of human accomplishment, can be conceded without at the same time insisting that consciousness does not exist without language. Indeed, from what is presently known (e.g., 34) one would not wish to enter a more mundane edifice in which the architect had not had the ability to utilize the nonlinguistic skills of his right hemisphere in the analysis of its spatial relations. There is also the likelihood that for languages like Chinese and Japanese which are written in complex characters requiring highly sophisticated analysis of spatial relations for their interpretation, the right hemisphere is dominant for reading and writing these characters (29). Nor are aphasic patients considered to be unconscious, nor would a physiologically normal, alinguistic human being who had been nurtured to adulthood wtihout benefit of human contact. It seems, clear therefore, that language is not the sine qua non of consciousness, and that the right hemisphere in split brain man lives a separate conscious existence.

This being true, is it not likely that for intact man also the two hemispheres have separate experiences that are unified by mutual commissural interchange? When a red light flashes in my left visual field, does not my right hemisphere experience the "red", as it would without the commissures, even though it is the left that speaks the word?

Throughout this essay I have refrained from defining "consciousness", as it is a futile task; those who lack it are beyond such explication, and those who possess it need no further definition. But there is an additional inference that now needs stipulation. If consciousness arises from neural processes, then it will be present wherever those neural processes exist. In my opinion the brains of all mammals have a sufficient similarity that some type of consciousness must be inferred for all; at least to date no fundamental qualitative distinction can be made in the neuroanatomy and neurophysiology of animals and man.

Proceeding then on this assumption, I can ask significant questions concerning "the monkey's consciousness" in the following situation (9). All of the forebrain commissures are severed save the splenium, the right optic tract is cut to render that hemisphere "physically" blind, and the left amygdala is removed to make the other hemisphere "emotionally" blind. So long as the splenium is intact, the monkey is normally fearful of man, since the left hemisphere communicates with the right across the splenium to interpret the significance of the input over the left optic tract. When the splenium is cut, such interpretation can no longer be made. Now, when the splenium is present, is it only the right hemisphere that experiences the fear? Would it not "know" something of the image cast into the left hemisphere? And does the left hemisphere while the splenium is intact have knowledge of the fear? Is there a "whole monkey" in the conscious state of this neural system, or is it fragmented? Certainly the behavior is not fragmented and it seems a reasonable assumption that the traffic of nerve impulses across the splenium is somehow unifying the conscious experience of this animal as it does within ourselves. Of course the experience of the monkey is forever outside our own, but the traffic across its splenium may present a reasonable approximation to that in man, to that which conveys consciousness from one hemisphere to another.

In speculating on how the hundreds of millions of nerve impulses traversing the commissures each second are compiled into the flow of being which each man experiences, it seems inescapable that Nature's most profound secret lies hidden here. Some wholly unsuspected process must be at work, coupling the prosaic flux of ions into a domain far beyond our present ken. Science, however, advances in direct relation to the precision of the questions which it can formulate. The discovery that the processes of consciousness traverse the forebrain commissures should significantly sharpen the question as to how neurons fashion the miracle of mind.

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## REFERENCES

1. ALEMÀ, G., PERRIA, L., ROSADINI, G., ROSSI, G. F. and ZATTONI, J. 1966. Functional inactivation of the human brain stem related to the level of consciousness. J. Neurosurgery 24: 629–639.
2. BARTLETT, J. R. and DOTY, R. W. 1974. Influence of mesencephalic stimulation on unit activity in striate cortex of squirrel monkeys. J. Neurophysiol. 37: 642–652.
3. BARTLETT, J. R., DOTY, R. W., PECCI-SAAVEDRA, J. and WILSON, P. D. 1973. Mesencephalic control of lateral geniculate nucleus in primates. III. Modifications with state of alertness. Exp. Brain Res. 18: 214–224.
4. DONHOFFER, H. 1966. The role of the cerebellum in the instrumental conditional reflex. Acta Physiol. Acad. Sci. Hung. 29: 247–251.
5. DOTY, R. W. 1965. Philosophy and the brain. Persp. Biol. Med. 9: 23–34.
6. DOTY, R. W. 1965. Conditioned reflexes elicited by electrical stimulation of the brain in macaques. J. Neurophysiol. 28: 623–640.
7. DOTY, R. W. 1965. Some neural facts relevant to attention, motivation and learning. *In* E. R. Caianiello (ed.), Cybernetics of neural processes. Consiglio Nazionale delle Richerche, Rome, p. 95–116.
8. DOTY, R. W. 1970. On butterflies in the brain. *In* V. S. Rusinov (ed.), Electrophysiology of the central nervous system. Plenum, New York, p. 97–106.
9. DOTY, R. W., NEGRÃO, N. and YAMAGA, K. 1973. The unilateral engram. Acta Neurobiol. Exp. 33: 711–728.
10. ECCLES, J. C. 1973. Brain, speech and consciousness. Naturwissenschaften 60: 167–176.
11. EVARTS, E. V. 1965. Neuronal activity in visual and motor cortex during sleep and waking. *In* Aspects anatomofonctionnels de la physiologie du sommeil. Colloque Inter. du Centre National de la Recherche Scientifique No. 127, Paris, p. 189–212.
12. FELTEN, D. L., LATIES, A. M. and CARPENTER, M. B. 1974. Monoamine-containing cell bodies in the squirrel monkey brain. Amer. J. Anat. 139: 153–166.
13. GELFAN, S. and CARTER, S. 1967. Muscle sense in man. Exp. Neurol. 18: 469–473.
14. GESCHWIND, N. and LEVITSKY, W. 1968. Human brain: Left–right asymmetries in temporal speech region. Science 161: 186–187.
15. GRANDA, A. and HAMMACK, J. 1961. Operant behavior during sleep. Science 133: 1485–1486.
16. GRANIT, R. 1972. Constant errors in the execution and appreciation of movement. Brain 95: 649–660.

17. INGVAR, D. H. and SOURANDER, P. 1970. Destruction of the reticular core of the brain stem. Arch. Neurol. 23: 1–8.
18. IVERSEN, L. L. and SCHON, F. E. 1973. The use of autoradiographic techniques for the identification and mapping of transmitter specific neurons in CNS. *In* A. J. Manoul (ed.), Symposium on Drug Abuse and Metabolic Regulation of Neurotransmitters (La Jolla, California, 1972). New concepts in neurotransmitter regulation. Plenum, New York, p. 153–193.
19. KETY, S. S. 1967. Relationship between energy metabolism of the brain and functional activity. *In* S. S. Kety, E. V. Evarts and H. L. Williams (ed.), Sleep and altered states of consciousness. Assoc. Res. Nerv. Ment. Dis. 44. Williams and Wilkins, Baltimore, p. 39–47.
20. LIBET, B. 1973. Electrical stimulation of cortex in human subjects, and conscious sensory aspects. *In* A. Iggo (ed.), Handbook of sensory physiology, Vol. II. Somatosensory system. Springer Verlag, Berlin, p. 743–790.
21. LIBET, B., ALBERTS, W. W., WRIGHT, E. W., Jr. and FEINSTEIN, B. 1967. Responses of human somatosensory cortex to stimuli below threshold for conscious sensation. Science 158: 1597–1600.
22. MAEDA, T., PIN, C., SALVERT, D., LIGIER, M. and JOUVET, M. 1973. Les neurones contenant des catécholamines du tegmentun pontique et leurs voies de projection chez le chat. Brain Res. 57: 119–152.
23. MASON, B. H. 1974. Geochemical distribution of elements. *In* Encyclopedia Britannica, 15th ed. Vol. 6. Encyl. Brit., Chicago, p. 710.
24. NEBES, R. D. and SPERRY, R. W. 1971. Hemispheric deconnection syndrome with cerebral birth injury in the dominant arm area. Neuropsychologia 9: 247–259.
25. OBRADOR, S. 1964. Nervous integration after hemispherectomy in man. *In* G. Schaltenbrand and C. N. Woolsey (ed.), Cerebral localization and organization. Univ. Wisconsin Press, Madison, p. 133–154.
26. OLSON, L., NYSTRON, B. and SEIGER, A. 1973. Monoamine fluorescence histochemistry of human post mortem brain. Brain Res. 63: 231–247.
27. PENFIELD, W. 1952. Epileptic automatism and the centrencephalic integrating system. Ass. Res. Nerv. Ment. Dis. 30: 513–528.
28. SAMSON, F. R., Jr., BALFOUR, W. M. and JACOBS, R. J. 1960. Mitochondrial changes in developing rat brain. Amer. J. Physiol. 199: 693–696.
29. SASANUMA, S. and FUJIMURA, O. 1973. Selective impairment of phonetic and non-phonetic transcription of words in Japanese aphasic patients: Kana vs Kanji in visual recognition and writing. Cortex 7: 1–18.
30. SKINNER, H. A. 1970. The origin of medical terms. New York Hafner Publ. Co., Inc., New York. 438 p.
31. SNIDER, R. S. and WETZEL, N. 1965. Electroencephalographic changes induced by stimulation of the cerebellum of man. Electroenceph. Clin. Neurophysiol. 18: 176–183.
32. SPERRY, R. W. 1969. A modified concept of consciousness. Psychol. Rev. 76: 532–536.
33. SPERRY, R. W. 1970. An objective approach to subjective experience: Further explanation of a hypothesis. Psychol. Rev. 77: 585–590.
34. SPERRY, R. W. 1974. Lateral specialization in the surgically separated hemispheres. *In* F. O. Schmitt and F. G. Worden (ed.), The neurosciences: third study program. MIT Press, Cambridge, Mass., p. 5–19.
35. SWETT, J. E. and BOURASSA, C. M. 1967. Comparison of sensory discrimina-

tion thresholds with muscle and cutaneous nerve volleys in the cat. J. Neurophysiol. 30: 530–545.

36. TEILHARD dé CHARDIN. 1959. The phenomenon of man. Harper, New York.
37. VELIKAYA, R. R. and SYCHEVA, T. M. 1970. Role of the reticular formation of the brainstem in background activity of cortical neurons (in Russian). Neïrofizjologiya 2: 43–51. (Neurosci. Transl. 15: 11–18, 1971.)
38. ŻERNICKI, B., DOTY, R. W. and SANTIBAÑEZ-H., G. 1970. Isolated midbrain in cats. Electroenceph. Clin. Neurophysiol. 28: 221–235.

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