AD-A013 616

BIOLOGICAL CORRELATES OF COGNITIVE, SENSORY AND MOTOR ABILITIES

John M. Talbot

Federation of American Societies for Experimental Biology

Prepared for:

Air Force Office of Scientific Research
Defense Advanced Research Projects Agency

April 1975

AFOSR - TR - 75 - 1124

237099

ADA013616

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Prepared for

Human Resources Research Office
Defense Advanced Research Projects Agency
Arlington, Virginia 22209

by

John M. Talbot, M. D.

This research was supported by the Advanced Research Projects Agency of the Department of Defense and was monitored by the Air Force Office of Scientific Research under Contract No. F44620-74-C-0077 (ARPA Order No. 2808; Program Code 4D20).

Life Sciences Research Office
Federation of American Societies
for Experimental Biology
9650 Rockville Pike
Bethesda, Maryland 20014

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UNCLASSIFIED

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

REPORT DOCUMENTATION PAGE		READ INSTRUCTIONS BEFORE COMPLETING FORM
1. REPORT NUMBER AFOSR - TR - 75 - 1124	2. GOVT ACCESSION NO.	3. RECIPIENT'S CATALOG NUMBER
4. TITLE (and Subtitle) Biological Correlates of Cognitive, Sensory and Motor Abilities		5. TYPE OF REPORT & PERIOD COVERED Technical
		6. PERFORMING ORG. REPORT NUMBER
7. AUTHOR(s) John M. Talbot		8. CONTRACT OR GRANT NUMBER(s) F44620-74-C-0077
9. PERFORMING ORGANIZATION NAME AND ADDRESS Federation of American Societies for Experimental Biology* 9650 Rockville Pike, Bethesda, Maryland		10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS 61101E ARPA Order # 2808 681312
11. CONTROLLING OFFICE NAME AND ADDRESS Defense Advanced Research Projects Agency Arlington, Virginia 22209 **		12. REPORT DATE April 1975
		13. NUMBER OF PAGES 33
14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office) DEPARTMENT OF THE AIR FORCE AIR Force Office of Scientific Research (AFSC) 1400 Wilson Boulevard Arlington, Virginia 22209		15. SECURITY CLASS. (of this report) Unclassified
		15a. DECLASSIFICATION/DOWNGRADING SCHEDULE

16. DISTRIBUTION STATEMENT (of this Report)

Approved for public release; distribution unlimited.

17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)

18. SUPPLEMENTARY NOTES

*Life Sciences Research Office **Human Resources Research Office

19. KEY WORDS (Continue on reverse side if necessary and identify by block number)

20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

This review of somaesthesis attempts to highlight its biological correlates and to relate somatic sensory processes to behavior. Current knowledge of the somaesthetic systems is summarized and significant gaps are noted. Exciting disclosures in the anatomy, physiology, biochemistry and biophysics of somaesthetic systems are surfacing with increasing frequency as a result of modern research approaches. Progress has been rapid in the electrophysiological "mapping" of afferent systems from the peripheral

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FOREWORD

The Life Sciences Research Office (LSRO), Federation of American Societies for Experimental Biology (FASEB), provides scientific assessments of topics in the biomedical sciences. Reports are based upon comprehensive literature reviews and the scientific opinions of knowledgeable investigators engaged in research in specific areas of biology and medicine. In addition, LSRO utilizes consultants to prepare reports on special topics where their expertise is applicable to particular needs for review and analysis.

This technical report was prepared for the Human Resources Research Office, Defense Advanced Research Projects Agency (DARPA), Department of Defense, under contract number F44620-74-C-0077 monitored by the Air Force Office of Scientific Research.

Under terms of this contract, LSRO agreed to assess recent developments in research on certain aspects of biological correlates of cognitive, sensory and motor abilities. This report was written by John M. Talbot, M.D., who served as a special consultant to the LSRO for this study.

The report was reviewed and approved by the LSRO Advisory Committee (which consists of representatives of each constituent society of FASEB) under authority delegated by the Executive Committee of the Federation Board. Upon completion of these review procedures, the report has been approved and transmitted to DARPA by the Executive Director, FASEB.

While this is a report of the Federation of American Societies for Experimental Biology, it does not necessarily reflect the opinion of all of the individual members of its constituent societies.

C. Jelleff Carr, Ph. D.
Director
Life Sciences Research Office

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SUMMARY AND CONCLUSIONS

In the broad fields of neurophysiology and physiological psychology, this review has focused on somaesthesis, with an attempt to highlight its biological correlates and to relate somatic sensory processes to behavior. In this report, somaesthesis refers essentially to all the sensory systems except the "special senses." Current knowledge of the somaesthetic systems is summarized and significant gaps in knowledge are noted. Exciting disclosures in the anatomy, physiology, biochemistry and biophysics of somaesthetic systems are surfacing with increasing frequency as a result of modern research approaches (e.g., the neurochemical transmitters, the neural coding of sensory information, the mechanisms of stimulus transduction, the molecular biology, biochemistry and biophysics of action potentials and transmission of sensory information via the afferent fibers and associated synapses). Progress has been rapid in the electrophysiological "mapping" of afferent systems from the peripheral receptors into the sensorimotor cortex and in identifying in other parts of the brain and brain stem, neurons and groups of cells which respond to somaesthetic stimulation. Sensory feedback and control are under investigation, and important revelations of perceptual processes, especially in vision and hearing, are being published.

However, the rate of progress has lagged somewhat in locating and understanding the higher-level central nervous system mechanisms of sensory information processing involved in the integration, storage, and use in learning, thinking, decision making, and sensorimotor coordination and control of "voluntary" as well as "automatic" activities. The human nervous system is immense when viewed in terms of its astronomical numbers of neurons and their seemingly endless variety of interconnections. It is not surprising that successful scientific penetration of the mysteries of cognitive functions has been limited. Thus, in examining the relatively restricted field of somatic sensory biology, one finds areas laden with scientific challenges and rich in potential for improving human effectiveness and well-being. A wide scope of new scientific information is needed to build a comprehensive understanding of somatic sensory biology and its influence on human behavior and performance capabilities. The identification of specific research of critical importance will require a deeper examination of selected areas of the neurobiological literature.

Despite the existence of great stores of knowledge of the neurophysiology and physiological psychology of somaesthesis and its role in perception, major research opportunities exist for contributing to an understanding of the mechanisms of sensory function throughout the spectrum from stimulus to organized, conscious, behavioral response. The breakthroughs that reasonably can be expected from adequately supported studies of somaesthesis would have practical applications of great significance to military personnel effectiveness.

TABLE OF CONTENTS

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I. INTRODUCTION

Numerous advances have resulted from developments in the human engineering of displays and controls of man-machine systems based upon scientific knowledge of human perceptive and performance abilities. The behavioral knowledge that has been most useful in these advances has come from studies of the performance level of human perceptual and motor abilities. Important progress in understanding behavior and improving performance may be anticipated from additional knowldege of sensory mechanisms and the processing of sensory information.

The somaesthetic systems, that is, the sensory apparatus exclusive of the "special senses," were selected from the broad field of sensory biology to limit this review and because the role of somaesthesis in perception, learning, and the development of skilled behavior perhaps is less understood than in more intensively studied sensory systems such as the visual, auditory and vestibular. To moderate the size of the report, several closely related and exceedingly important fields such as neuroendocrinology and neuropharmacology were not included.

This brief review assesses some of the current ideas in the field of somaesthesis, identifies some significant gaps in knowledge, and considers promising areas of research that should be exploited.

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II. SOMAESTHESIS IN PERCEPTION, COGNITION AND BEHAVIOR

A thorough understanding of how the somatosensory systems influence perception, cognition and action could lead to significant improvements in training methodology and operator effectiveness. It appears that not much is known about how information received in the central nervous system (CNS) from the somaesthetic receptors affects these higher neural functions. However, an appraisal of what is known and what is lacking should assist in estimating where to place research emphasis.

In this report, perception refers primarily to the development of meaning based on current sensation input; it should not be confused with sensation. Cognition is considered a manifold aggregate of concepts, none well defined but involved in conscious activities of knowing, decision making, and purposeful action. Behavior is used in its broad sense and, more restrictedly, as the responses to somaesthetic input as manifested by the effector organs and organ systems. A summary of developments in the fields of somaesthesis in perception, cognition and behavior is presented.

A. SOMAESTHETIC RECEPTORS

The somaesthetic receptors may be divided into the exteroceptors, which interact with stimuli of the external environment, and the interoceptors, which respond to stimuli arising within the organism. Somaesthetic exteroceptors are stimulated by touch-pressure, vibration, pain, heat and cold. The interoceptors include a variety of mechanoreceptors and chemoreceptors such as the skeletal muscle spindles, tendon end organs, end organs in joint capsules, the visceral stretch receptors of the alimentary canal and urinary bladder, and the chemical and pressure receptors of the cardiovascular system. Free sensory nerve endings not possessing special end organ morphology richly supply the skin and mucous membranes as well as joints, muscle, vessels, connective tissue and the viscera. They are responsive to nociceptive (pain), mechanical and probably other stimuli.

The functional characteristics of a number of specialized, encapsulated sensory end organs such as Meissner's corpuscles, Krause's end bulbs, Pacinian corpuscles, Ruffini's end organs, and Golgi tendon organs are fairly well known. The receptors in most cutaneous sense organs are specialized, histologically modified ends of sensory nerve fibers. The receptors are designed to respond to a particular form of energy at a much lower threshold than other receptors respond to the same energy. The form of energy to which a receptor is most sensitive is called its "adequate stimulus."

Altman and Dittmer (1973) list the anatomical and functional characteristics of 39 different primary receptor units (with afferent dorsal root fibers) divided into cutaneous, subcutaneous somatic, somatic articular, and visceral, with subgroups for mechanical, thermal and noxious stimuli. It is likely that other somatic sensory receptors remain to be identified. The question of sensory modality specificity of some of the somaesthetic receptors is only partially answered. Their electrophysiological and behavioral responses to stimulation have been studied abundantly, and there seems to be no question that functionally specific receptors exist for each of the sensory modalities. However, the specificity of certain receptors remains in doubt (Ganong, 1973; Uttal, 1969). According to modern concepts, sensory specificity as defined by the Law of Specific Nerve Energies still applies to the major sensory modalities, but not to specific subqualities (micromodalities) of sensory reception, i.e., most sensory receptors appear to be broadly tuned.

Spector *et al.* (1974) studied the responses of individual claustral* neurons in the cat to somatic sensory mechanical stimuli, clicks and flashes. Of 397 neurons measured, 31 percent were unresponsive. The 275 responsive neurons were located throughout the claustrum and were heterogeneous. Ninety percent of these were activated by the somatic sensory stimulation, 48 percent by clicks and 5 percent by flashes. Eighteen percent of the somatic sensory cells had restricted or greatly restricted receptive fields; 38 percent had widespread fields; and 44 percent were sensitive to more than one sensory modality. Seventeen percent of the auditory neurons responded only to click, and 83 percent were multisensory. Seventy-five percent of the responsive cells were heterotrophic or heterosensory; 25 percent were specific. These experiments demonstrated that the majority of neurons measured in the cat's claustrum were not modality specific; they possessed multiple sensory information processing capabilities, suggesting common modes of sensory communication.

The trophic functions of sensory nerves in inducing and maintaining the differentiation of their receptor organs are of great interest in a comprehensive understanding of sensory systems (Harris, 1974). Taste buds disappear following denervation and are induced again from the germinal epithelium after reinnervation. Muscle spindles, which are induced from myoblasts by sensory neurons, fail to develop if the sensory innervation to muscle is interrupted during a critical phase of development. There is good evidence that most nerve terminal proteins move from the cell body to the terminals by axoplasmic transport, about one-third being carried by the fast transport system (e.g., 400 mm per day) and two-thirds by the slow component. Harris (1974) in reviewing the subject, emphasized that a very

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*The claustrum is a thin plate of subcortical gray substance located between the lenticular nucleus and the cerebral cortical structure known as the island of Reil.

important recent scientific advance was the finding that the fast transport component of axoplasmic flow is an essential part of the mechanism by which sensory nerves maintain some of their trophic functions.

Recent progress in characterizing the somatic mechanoreceptors involved identification of rapidly adapting and slowly adapting receptors in the human hand and measurement of their receptive field sizes (Hahn, 1974). Mechanical stimuli sufficient to evoke 1 or 2 action potentials in the fiber of a rapidly adapting receptor appear to be at the threshold of sensation. A single action potential from a human hair mechanoreceptor is sufficient for sensation. Differential human sensations from vibrating stimuli of various frequencies have been partially described and correlated with cutaneous receptors, and it was established that human Pacinian corpuscles are among the mechanoreceptors that can mediate vibrating stimuli in terms of discriminable sensations. According to Deutsch and Deutsch (1973), Pacinian corpuscles adapt rapidly to vibrating stimuli and are insensitive to temperature changes. However, in some studies of the response characteristics of cutaneous mechanoreceptors, evidence for perception of the transmitted information was lacking.

Progress in understanding the functioning of temperature receptors has been achieved, particularly the cold receptors; however, the correlation of electrophysiologic with behavioral manifestations remains difficult. For example, cutaneous receptors in some body loci signal warm stimuli, without apparent behavioral effects, whereas stimulation of warm receptors at other loci results in definite behavior. Several types of mechanoreceptors have shown responsiveness to cooling.

Thus, the vertebrate nervous system has at least 39 somatic sensory receptors for touch-pressure, temperature, pain, chemical stimuli, and submodalities of these, located in the skin, subcutaneous and deeper tissues, and more somatic sensory receptors will probably be discovered. Some receptors appear to be modality specific; others heterosensory. The trophic functions of primary sensory nerves for maintaining receptor differentiation and the functional integrity of the tissues they innervate are partially understood. However, despite excellent progress in identifying and characterizing the somaesthetic receptors, there are important gaps of information including questions of specificity, adaptability, conduction velocity, terminal morphology and peripheral anatomic distribution.

B. SOMAESTHETIC SYSTEMS

As used in this report, somaesthetic systems refers to the complete afferent neural chain for a given receptor, through the spinal cord, brainstem and sensorimotor cortex connections and the associated feedback control connections. Recent progress in somatic sensory biology is described in reviews by Handler (1970) and Ganong (1973). Despite major information gaps, published data in the field are prolific. Knowledge of the neural pathways of somatic afferent fibers has been refined by modern research methods such as single cell biochemical analysis and electrical recording; recording of slow wave events in higher level sensory cell populations and areas, aided by computer control and analysis; and synaptic biochemical and biophysical techniques. Numerous somatosensory pathways from the receptor organs through the spinal cord, brain stem, thalamus and into the sensorimotor cortex have been described anatomically and electrophysiologically and their synaptic biochemistry partially characterized. The lemniscal parts of the somaesthetic systems maintain modality specificity and the spatial features of the stimulus and the anterolateral systems appear to be concerned with pain and other affective qualities of stimuli.

At least two types of functional organization at the cortical level of the lemniscal system have been described: the gross topographic arrangement corresponding to parts of the body, and the columnar substructures of this topographic mosaic, specialized to process information related to a specific sensory submodality. However, the functional pathways beyond the sensorimotor cortex and the modes of interaction of the higher centers for perception, integration, storage and behavioral responses remain largely unknown.

Various views of how the somaesthetic systems work were reviewed by Deutsch and Deutsch (1973). One concept regards the "total sensory picture" as a sum of the different types of sensory information arriving at various central analyzers from a number of separate transmission systems. This concept includes provisions for sensory interactions. Another view considers the entire cutaneous sensory apparatus as a single, massive transmission system which relies on spatial and temporal patterning of neural activity for differentiation of sensory information; information about different sensory modalities may be transmitted by the same fiber by different temporal patterns. It is known that some afferent fibers transmit after receptor stimulation by more than one stimulus modality, for example both touch and cold. Whether or not this means that the fiber relays differential information about each modality or responds to each as if they were the same appears an open question. For pain sensitivity, there is increasing evidence that a chemical mediator is involved in the initial receptor events. Whether or not there are fibers exclusively for pain stimuli and their ability to relay all pain impulses are essentially unknown.

Reflex arcs, the basic units of integrated neural activity, have been elucidated in some biologic systems for many somatosensory-motor connections such as the myotatic reflex arc of the muscle spindles and certain more complex, multisynaptic connections as in the flexion reflexes. For example, in the crayfish, a single "command interneuron" in the reflex arc can excite flexor neurons, override the peripheral inhibitor of flexion, and cause inhibition of extension. The single command interneuron influences as many as 120 motoneurons and governs the full tail flexion response. A number of higher-level reflex mechanisms are known in other species including the so-called "vital reflexes" for maintaining certain homeostatic parameters such as blood pressure, respiration and the circulatory and postural reflexes.

During the past decade a number of important concepts have been established concerning the somatosensory systems. It appears that there are afferent systems which, though not directly involved in sensation, disseminate the meaning of sensory information to nonsensory elements of the CNS for storage and subsequent motor action. A significant amount of sensory information is transformed peripherally as a result of lateral interactions among adjacent afferent elements. In excitatory modes, the effect is facilitation; when inhibitory, spatial contrast is enhanced. A single sensory stimulus may activate multiple sensory interneurons, resulting in parallel representation of a given sensory area in varying spatial combinations with other areas (Handler, 1970). The inhibition process apparently does not occur at the level of sensory end organs and the role of the primary afferent fiber is evidently solely excitatory. However, Davidoff *et al.* (1974) and others have found evidence suggesting presynaptic inhibition in primary afferent sensory neurons. The afferent input of sensory systems is widely distributed in various parts of the CNS.

The role of sensory feedback is partially understood, and some of the associated neural pathways have been identified. However, a large void exists regarding the higher level CNS mechanisms of sensory feedback and control. More information is needed on the somatosensory systems, emphasizing such problems as how quality and intensity of sensation are coded, how the somatosensory systems interact with each other and with the visual, auditory and vestibular systems, and how sensory information is processed at the integrative levels beyond the primary reception areas of the cerebral cortex. Additional biological correlates of somaesthetic activity are necessary for all levels of the CNS and, if possible, noninterfering methods of measurement should be devised.

C. TRANSDUCTION, TRANSMISSION AND CODING OF SOMAESTHETIC STIMULUS INFORMATION

This section briefly reviews mechanisms of stimulus reception, transduction and information transmission. The basic mechanisms of nerve impulse propagation and synaptic transmission are generally applicable and should not be regarded as being restricted to the somatic sensory systems.

Transduction refers to the conversion of sensory stimuli into action potentials at the receptor end organs and to the interactions of the action potentials with neurochemical transmitters in the process of nerve impulse transmission at the chemical synapses. Coding relates to sensory information processing symbols and the rules for their combination, which can be used to represent a pattern of information in a manner different from that of the original signal. Uttal (1969) considered sensory coding as a multidimensional process, with overlapping and redundant codes at all levels, and that an information pattern represented by impulse frequency at one level may be represented by some other coding dimension at a higher level. He referred to codes generated at the receptor level as stimulus codes, or, if introduced during transmission at a higher level, as systemic codes.

Important coding dimensions include not only mean nerve impulse frequency, but also impulse interval statistics, nerve impulse count as distinct from mean impulse frequency; neural response amplitude, and several temporal and spatial parameters of common sensory dimensions. Much of the information processing that has classically been associated with complex higher level perceptual events actually occurs peripherally in the sensory receptors and their first order neurons. Physical stimulus information is transduced in the receptor into graded fluctuations of the receptor membrane potential, that is, the generator potential. This is the precursor of the spike action potential. The information contained in the graded generator potential is reflected by the frequency characteristics of the ensuing spike action potentials.

The exact mechanisms of conversion of adequate somaesthetic stimuli at the sensory receptor into nerve action potentials are among the elusive problems of neurobiologists. The prevailing concept is that the stimulus is detected by a specific protein receptor in the excitable end organ membrane. This induces conformational changes in the receptor which, in turn, changes the permeability of the membrane to Na^+ and K^+ ions. The process is reversible so that the receptor returns to its resting or excitable state. For example, in the Pacinian corpuscle, the generator potential resulting from mechanical pressure originates in the nonmyelinated nerve terminal; removal of the onion shaped connective tissue layers surrounding the nerve end does not abolish the sensitivity of the nerve end to mechanical stimuli. Relationships between stimulus intensity and action potential frequency have been characterized in a number of somaesthetic receptors. The immediate effect of an adequate stimulus appears to be the depolarization of the sensory ending membrane. It is believed that the depolarization of the receptor end membrane occurs as a result of an increase in its permeability to Na^+, but exactly how this works is unknown. The absolute and relative refractory periods of neuronal membrane reactivity are significant dimensions in defining an adequate stimulus at any given moment.

Klett *et al.* (1973) used an ingenious approach to the study of excitable membrane permeability. They investigated the postsynaptic acetylcholine receptors in the electroplaxes of electric eels by measuring the binding efficiency of the receptor for certain neurotoxins such as cobratoxin. The neurotoxin was labeled with ^{125}iodine, thus marking the receptor with a radioactive label, an aid in subsequent identification of the specific receptor protein.

Transmission refers to electrical or chemical events associated with the propagation of nerve impulses. Progress has occurred in understanding nerve transmission, but a comprehensive explanation of nerve action, that is, a complete molecular, biochemical, electrochemical and mathematically defined picture of nerve signal conduction is still lacking. Three examples of recent concepts are mentioned here.

Nachmansohn and Neumann (1974) presented a model of nerve excitation in which basic excitation units are formed by a "gateway" surrounded by membrane protein assemblies which are capable of processing acetylcholine. The excitation units are distributed throughout the membrane. The concept holds that acetylcholine is not a neurohumoral transmitter, but is released and acts within the membrane as the signal which, on excitation, initiates a series of events that lead to increased permeability. Operation of the model depends in part on conformational changes in membrane biopolymers resulting from electrical impulses of 20kV/cm; the drop in potential is assumed to result in a conformational change of the storage protein, release of acetylcholine, and its movement to the receptor. A conformational change occurs in the receptor, releasing calcium ions. If the number of acetylcholine ions released reaches a critical value, the local response may lead to the all-or-none response or action potential. The authors stated, "Today a vast amount of evidence exists which documents the unified concept of the role of acetylcholine as the signal that initiates the reactions that change ion permeability in all excitable membranes."

Wei (1974) presented a dipole model that defines some of the macroscopic phenomena (electrical, optical and thermal) observed in nerve action, in terms of flip-flops between the quantum states at the membrane surface. As a result of stimulation, the dipole flips alter the outer barrier potential which, on amplification, appears as the nerve impulse. When the dipoles flop down, infrared radiation may be emitted in the membrane. Field changes and dipole energy changes give rise to the positive and negative heats of the nerve impulse. The dipole theory is versatile and could account for many other phenomena of nerve action.

Brewer and Passwater (1974) postulated mechanisms to define the action potential and axon conduction based on the nature of the neuronal membrane and the electron physics of the P=O functional group in the membrane lipoproteins. One of their models, which accommodates the essential temporal and spatial dimensions of action potential propagation, depicts a positive ion band moving rapidly along the axon wall. The initial exciting event raises the P=O bonds to a high energy level in the singlet state. Within the time frame required, many of these bonds return to ground state with emission of electromagnetic radiation in the short ultraviolet range. This radiation excites electrons in adjacent P=O bonds, resulting in repetition of the process further along the axon wall. The excitation of these bonds changes them to strong electron donors, which causes extracellular cations, in particular Na^+, to enter the membrane ahead of the excitation area. Under the influence of the strong potential gradient (approaching 10^7 V/cm during the excited state) between the outer and inner axon membrane walls, these cations accelerate to the inner wall where they are stopped by a strong negative intrinsic field.

A detailed treatment of the neurotransmitter substances is beyond the scope of this review; however, a brief summary of current concepts is presented. The passage of nerve impulses through synapses is apparently in two modes or a mixture of these: direct, "electrical" transmission at synaptic junctions where presynaptic and postsynaptic structures are in contact over relatively large areas, and by chemical transmitters in synapses with synaptic clefts. It is generally accepted that chemical transmitter molecules, stored in vesicles in the presynaptic membrane, move into the synaptic cleft following arrival of action potentials, then progress rapidly across the cleft to interact with specific receptor molecules in the postsynaptic membrane and to be inactivated. A transduction of energy results, leading to an action potential in the postsynaptic neuron. Acetylcholine is recognized as the synaptic transmitter between preganglionic and postganglionic nerves of the autonomic nervous system, at the myoneural junction, and at some postganglionic sympathetic endings. Norephinephrine is the neurotransmitter at most postganglionic sympathetic endings. Evidence for their probable role as neurotransmitters is accumulating for γ-aminobutyric acid (GABA), dopamine, glutamic acid, serotonin, glycine, taurine, histamine and the prostaglandins.

Flock and Lam (1974), in biosynthesis and electrophysiological studies of the inner ear in frogs and the lateral line sense organs in toadfish and skates, reported evidence suggesting that GABA may be the neurotransmitter at the excitatory synapse between the hair cells of these organs and the afferent fiber. This is of special interest because previous studies have identified GABA with an inhibitory role.

Grossman and his colleagues (1973) observed an intracellular control phenomenon when stimulation of the proximal axon in the spiny lobster led to complete block of spike propagation into a large axonal branch while the impulse into the smaller branch was not altered. Evidently, differential channeling of information can occur at points of axonal branching and, after stimulation, if not before, the membrane properties of the two branches must differ. These observations may have special significance for elucidating mechanisms of inhibition and facilitation in information processing by neurons.

Interest continues in the influence of age on mental processes. Vernadakis (1975), noting that neuronal intercommunication is mediated via neurotransmitters, pointed out that possible shifts from excitatory to inhibitory and vice versa may occur in some CNS areas with advancing age. Because some neurotransmitter processes decline and mental functions, including memory, may become retarded with age, this subject deserves additional study.

Important areas which are not adequately understood include the exact mechanisms by which sensory receptors transduce stimulus energy into action potentials. A precise picture of the biophysics and biochemistry of action potential propagation in nerves is needed as is the identification of all chemical synaptic transmitters, their postsynaptic membrane receptors, and the associated control enzymes or other control substances. Knowledge of neural coding and sensory information processing from neuron to neuron in the sensory pathways and particularly above the level of the thalamus is very limited.

D. PERCEPTION OF SOMAESTHETIC INFORMATION

Teuber (1960) found no adequate definition of perception and no neurophysiologic theory for it despite a vast literature on the subject. He felt that most investigators reduced all perception to discriminatory responses and did not account adequately for some of the other aspects of perception such as patterning, selectivity, ratios or relations of stimuli, reaction to similarity, apprehension of serial order and equivalent reactions to certain spatial and temporal sequences. A suitable theory of perception should consider the nervous system as more than a passive receiver of sensory information and should not arbitrarily separate sensation and perception. It should be based partially on studies of the effects of temporally and spatially realistic patterns of sensory stimuli rather than on the traditional "pure" experimental stimuli such as punctate pressure. It should clarify intrinsic and acquired tendencies and how they interact.

During the past 15 years, considerable progress has been made in identifying and characterizing some of the neural mechanisms involved in perception, especially in vision and audition. For instance, among the factors that influence visually mediated perception, Krech *et al.* (1969)

emphasize assimilation, contrast, figure and ground, contour, closure, grouping, learning, frame of reference and perceptual set. One of the bases of perception may be a system for matching incoming information from environmental stimuli with preprogrammed "feature detectors" and some basic sensory perceptive functions are innate but require repeated sensory experience not only to develop properly, but also for maintenance and elaboration. A further study of this approach may yield information useful in developing concepts to investigate the somaesthetic system.

An understanding of the ways single neurons in animals' brains react to sensory input aids in devising models for sensory information processing and for extrapolating to human perceptual processes. Regan (1975) described some of the advantages of evoked brain potential recording in studying the sequential processing of sensory information. He regarded the recording of evoked potentials from the brain as an important tool for bridging the gap between subjective and quantitative data on conscious perception from human subjects and the recording from individual sensory cells of experimental animals. Some degree of correspondence has been found between the forms of evoked brain potentials and patterned stimuli such as visual presentations with edge features. Similar possibilities should be explored for patterned somatosensory information.

The tissue-ablation approach has aided in understanding perceptual mechanisms. Removal of the vertical lobe system of the octopus brain results in loss of ability to discriminate certain shapes which had been previously learned. Subhuman primates lose the ability to discriminate shapes after visual cortex removal. However, it is very difficult to define the minimal disruptive lesion in the somatosensory system where loss of reactions to tactile patterns after restricted cortical removal has not been demonstrated experimentally (Handler, 1970).

Modification of certain perceptual processes might have practical uses if better understood. For instance, in Balint's syndrome, the subject perceives whatever he fixates, but nothing else; lateral interaction effects are probably involved. Possible analogs exist such as the cross-sensory masking of pain in one part of the body by counterirritation in another, and in the use of sound during dental procedures to reduce or abolish dental pain sensation.

Normal spatial perception is based partially upon a "learned" relationship between the physical environment and the sensory input. Evidently, the learning exposures must occur during a certain period in the maturation of the organism for perceptual ability to develop properly. If a customary, learned relationship is artifically changed by having a subject wear inverting or displacing prism spectacles, adaptation to the new spatial situation can be fairly rapid. However, if the subject is relatively immobilized while moving about in the "new" environment, as by being confined to a wheelchair, his adjustment rate is retarded.

Most studies of perception have involved vision and hearing. There seems to be a general consensus that mechanisms of visual and auditory perception have analogs in somaesthetic perception. The limited knowledge of the role of the association areas of the cerebral cortex suggests that they are involved in processing sensory information into percepts. While a great deal has been learned about perception and the factors that influence it, more significant information has yet to be revealed. The higher neuronal projections that are engaged during somatic sensory information processing and their functional significance in perception are but partially established, and the influence of interactions of somatic sensory systems with other sensory input on perception is only vaguely understood.

A better understanding of intersensory processes should lead to practical applications in terms of improved human effectiveness in a broad range of endeavors. It may be possible to mask thermal sensation by nondestructive sensory techniques so as to alleviate the perceived discomfort of otherwise tolerable cold or heat. Learning may be improved by certain manipulations of somaesthetic systems in relation to training procedures. With a better understanding of the processes it may be possible to use sensory facilitation to increase sensitivity to a modality of special importance in specific tasks.

E. THE INFLUENCE OF SOMAESTHETIC INFORMATION ON BEHAVIOR

Much is known about both ends of the spectrum from stimulation to response in lower organisms and man. Sensory information processing at the monosynaptic reflex arc level seems reasonably well understood, and there has been progress in elaborating some of the polysynaptic, multisegmental reflex systems and the higher level reflexes. Studies of classical and operant conditioning as well as the mass of common knowledge about the overt manifestations of learning experiences have permitted some appreciation of the significance of sensory information in adapting the organism to its environment. There is substantial knowledge of sensory pathways into the sensorimotor cortex and about the response characteristics of individual sensory neurons and populations of cells at most levels in the CNS hierarchy. Nevertheless, we have very limited knowledge of how the sensory input influences conscious, purposeful behavior and autonomic behavior. We do not know how "voluntary" movements are initiated, patterned into sequences, and developed to the level of skilled performance or how the neural mechanisms of efferent control of somatic sensory systems function, particularly at the higher CNS levels.

One approach to the study of these and corollary problems is to use animal models with relatively small nervous systems. This permits detailed exploration of neural systems which, using only one or a very few sensory neurons, provide the total input of a given sensory modality. The relative simplicity of such systems aids in tracing sensory input, transmission, central processing and output through to behavioral response. An important aspect of sensorimotor coordination is the relationship between self-produced movement and changes in stimulation patterns of somatosensory organs resulting from the movements (re-afference) (Deutsch and Deutsch, 1973). Further research on animal models should yield valuable data about the effects of somatosensory information on behavior. Fundamental new approaches may be required to develop this subject and bring it to man's complex level.

F. THE MYSTERY OF COGNITION

Cognition appears to involve the highest form of neural activity, and includes such scientific and philosophic categories as imagery, logical thinking, reasoning, judgment, creativity, linguistic performance, concept formation and problem solving. Most of these words have a high order of abstraction, and have different meanings for different people. While the subject is a broad one for investigation by several scientific disciplines, it is clear we do not have even the most elementary understanding of the neurophysiological correlates. After reviewing the recent literature, Neimark and Santu (1975) concluded that the field is diffuse, parochially compartmentalized, and lacking a comprehensive theory. They remarked that the varied use of the term "cognition" included any activity involving the CNS, between initiation and completion of a response. Hetherington and McIntyre (1975) observed that the need is for a careful analysis, synthesis and evaluation of the information we now have. An attempt should be made to evolve theories that will result in more systematic and fruitful strategies of research, according to these reviewers.

Apparently not enough is known about how sensory input influences the cognitive processes to make a meaningful review at this time. Nevertheless, the extreme importance of a successful penetration of cognition is obvious. Any clues to improving effective learning, skill acquisition, or memory offer approaches to a better understanding and exploitation of cognitive processes. Even modest knowledge of these mechanisms improves our attempt to evolve models or theories. The biological correlates, especially neurophysiological and biochemical, seem to be the most fruitful fields to explore currently.

III. COMPARATIVE STUDIES

To further the understanding of sensation and perception and the processing of perceived information in terms of behavioral responses, some investigators consider the comparative approach as having rich potential. It is believed to be the only currently available means of definitely establishing mechanisms of neuronal action free from the bias of such experimental variables as drug effects and artifically induced deprivations and surgical ablations (Kupferman, 1975). Consequently, many species of animals are useful, from "lowest" invertebrates through the subhuman primates. Several examples are cited.

Crayfish, sea hares and the octopus are very useful in neurophysiology. The latter learns readily to differentiate objects with vertical or horizontal, but not oblique features. A possible interpretation is that the visually mediated spatial orientation of the octopus is "tuned to gravity" and that the animal is unable to adjust or compensate for tilt in visual stimuli. Decerebrate insects are able to carry out various behavioral patterns and certain insects have large neurons which lend themselves to intracellular manipulation. The decerebrate cockroach preparation is a widely used model for the study of reflex mechanisms, for, even without its head, it can be "trained" to withdraw a leg from a noxious stimulus.

Ingenious experiments with homing pigeons and other birds are yielding support for the notion that a component of their orientation and navigation system may be based on detection and interpretation of the earth's geomagnetic lines of force. Homing pigeons return from distant release points when alternate guidance aids such as visual reference to the sun are obsructed by heavy weather overcast. However, homing pigeons seem to use other, as yet undiscovered means for their orientation and navigation (Keton, 1974).

Brown *et al.* (1974) measured the responses of neurons of the electroreceptor apparatus of the lateral line of Black Sea skates to electrical stimulation and to changing magnetic fluxes. Changing magnetic fields evoked responses whereas constant fields did not, and the neuronal response was influenced by the direction of the magnetic field. Comparison between the neuronal responses to the experimental magnetic flux changes with the estimated effects of the magnetic field changes which could be expected from movements of the fish in their normal environments indicated the possibility of perception of the earth's magnetic field by these animals.

A very controversial subject is the biochemical transfer of memory as reported in such species as planaria, goldfish and rodents (Chapouthier, 1973; Deutsch and Deutsch, 1973; Handler, 1970). Mice injected with brain and liver homogenates of donors which were shocked or rolled in a glass container, performed better in avoidance tasks in the shuttle box. It appeared that something was transferred which improved performance during learning. Goldfish recipients of an intracranial injection of 1 μg of extract in 10 μl saline of nucleic acids extracted from the brains of donor goldfish which had learned an electric shock avoidance task, showed superior avoidance learning over the controls (Bisping *et al.*, 1974). These results supported the hypothesis that the extract contained chemically coded, specific information which facilitated or inhibited performance, depending on whether the donors had had positive or negative type response conditioning. Studies of this type have not been widely accepted as demonstrating memory transfer.

A better understanding of the comparative anatomy and neurophysiology of the echolocation systems of certain birds, bats and marine animals, and of the perception of polarized light by bees, offers potential for development of new or improved detection, identification, ranging and location devices to augment human performance.

From these comparative neurophysiological studies, we may reasonably expect progress toward the solution of problems of theoretical and practical importance, and perhaps, motivation to continue the search for possible latent, hitherto unknown sensory capabilities in man.

IV. SUGGESTIONS FOR FUTURE RESEARCH

Scientific knowledge is severly limited in the broad field of sensory biology, as related to perception, feedback, and the integration, storage and use of sensory information in cognitive functions. When one considers the scope and complexity of the areas, the opportunities for productive basic and applied research are essentially unlimited.

As a result of this review of somaesthesis and related topics, research emphasis on problems in the following areas would be justified for the ultimate improvement of human effectiveness. These are but a few suggestions that come to mind from this introductory overview:

- Studies should be done to extend the anatomical and functional classification of the somatic sensory receptors and to determine their sensory specificity. Refinement of knowledge in this area could lead to practical applications for personal environmental control methods and the use of somatic sensory systems to supplement the visual, auditory and vestibular systems of man.

- Mechanisms of sensory feedback have not been biologically and functionally defined and mapped. Aspects of sensory feedback and control in some peripheral parts of the nervous system are understood, but very little is known about this subject at the higher central nervous system levels.

- The interaction modes of the somatosensory inputs with each other and with those of the visual, auditory and vestibular organs and the chemical senses are poorly defined. Adequate knowledge of sensory interactions could open the way to dramatic improvement in discrimination and perception.

- Better-defined biological correlates of somaesthetic activity are needed for all levels of the central nervous system.

- The biophysics and biochemistry of stimulus transduction by the sensory receptors need added emphasis in research.

- The exact mechanisms for the generation and propagation of nerve action potentials must be defined and their interactions at the pre- and postsynaptic phases of impulse transmission understood.

- Equally significant are questions of the identity of the neurochemical transmitters; their sites of synthesis; and the mechanisms of liberation, reception in the postsynaptic membrane and deactivation after performing their role in information transmission.

- The transformation of sensory inputs into coded information and the modifications of sensory transformations at successive ascending levels of the central nervous system pose numerous challenging questions.

- When we understand the processes of somatosensory perception, we shall be at the threshold of practical applications for improving effectiveness in learning, skills acquisition, memory, and perhaps, methods for controlling excessive sensory input effects such as from heat and cold and the minimum sensory input for homeostasis.

- More definite research is required on cross-sensory masking. The possibility of employing sensory facilitation to increase sensitivity to a modality of special importance in certain tasks should be investigated.

- Sensorimotor coordination and the mechanisms of processing, storing and using sensory input in initiating and influencing "voluntary" and automatic motor activity are vaguely understood areas, laden with opportunities for productive research.

- We should remain alert to possibilities that human beings may possess undiscovered sensory abilities for which leads might come from further studies of comparative neurophysiology.

It seems logical that further, in-depth reviews would suggest specific, testable hypotheses and experimental approaches worthy of substantial research effort.

A fruitful endeavor might be to attempt an integration of the knowledge and concepts of the several fields reviewed in this study, with the objectives of gaining possible new insight into human behavior and of developing original hypotheses of how to explore the biological correlates of cognitive processes. To be meaningful, the scope of the study should embrace a comprehensive review and analysis of known facts associated with all neurobiological and behavioral events from reception of stimuli, through the processing of sensory inflow, to the ultimate response. The achievement of such a goal would require the participation of a variety of specialists from many disciplines but offers an unprecedented challenge.

V. BIBLIOGRAPHY

Altman, P.L. and D.S. Dittmer, compilers and editors. 1973. 138. Classification of afferent dorsal root fibers: mammals. Pages 1141-1149 *in* Biology data book, 2nd ed., vol. 2. Federation of American Societies for Experimental Biology, Bethesda, Md.

Bisping, R., U. Benz, P. Boxer and N. Lango. 1974. Chemical transfer of learned colour discrimination in goldfish. Nature 249: 771-773.

Brewer, K.A. and R. Passwater. 1974. Part III. Physics of the cell membrane: the mechanism of nerve action. Amer. Lab. 6(11): 49-62.

Brown, H.R., G.N. Andrionov and O.B. Ilyinsky. 1974. Magnetic field perception by electroreceptors in Black Sea skates. Nature 249: 178-179.

Chapouthier, G. 1973. Behavioral studies of the molecular bases of memory. Pages 1-17 *in* J.A. Deutsch, ed. The physiological basis of memory. Academic Press, Inc., New York, N.Y.

Davidoff, R.A., G.E. Silvey and R.L. Gulley. 1974. Observations on the frog dorsal column nucleus. Mt. Sinai J. Med. 41: 88-92.

Deutsch, J.A. and D. Deutsch. 1973. Pages 170-200 *in* Physiological psychology. The Dorsey Press, Homewood, Ill.

Flock, A. and D.M.K. Lam. 1974. Neurotransmitter synthesis in inner ear and lateral line sense organs. Nature 247: 142-144.

Ganong, W.F. 1973. Review of medical physiology, 6th ed. Lange Medical Publications, Los Altos, Calif.

Grossman, Y., M.E. Spira and I. Parnas. 1973. Differential flow of information into branches of a single axon. Brain Res. 64: 379-386.

Hahn, J.F. 1974. Somaesthesia. Annu. Rev. Psychol. 25: 233-246.

Handler, P., editor. 1970. Biology and the future of man. Oxford University Press, New York, N.Y.

Harris, A.J. 1974. Inductive functions of the nervous system. Annu. Rev. Physiol. 36: 251-306.

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Hetherington, E.M. and C.W. McIntyre. 1975. Developmental psychology. Annu. Rev. Psychol. 26: 97-136.

Keton, W.T. 1974. The mystery of the homing pigeon. Sci. Amer. 231: 96-107.

Klett, R.P., B.W. Fulpius, D. Cooper, M. Smith, E. Reich and L.D. Possani. 1973. The acetylcholine receptor. I. purification and characterization of a macromolecule isolated from *Electrophoros electricus*. J. Biol. Chem. 248: 6841-6853.

Krech, D., R.S. Crutchfield and N. Livson. 1969. Elements of psychology, 2nd ed. Alfred A. Knopf, New York, N.Y.

Kupferman, I. 1975. Neurophysiology of learning. Annu. Rev. Psychol. 26: 367.

Nachmansohn, D. and E. Neumann. 1974. Properties and functions of proteins in excitable membranes: an integral model of nerve excitability. Ann. N.Y. Acad. Sci. 227: 275-284.

Neimark, E.D. and J.L. Santu. 1975. Thinking and concept attainment. Annu. Rev. Psychol. 26: 173-206.

Regan, D. 1975. Recent advances in electrical recording from the human brain. Nature 263: 401-407.

Spector, I., J. Hassannova and D. Albe-Fessard. 1974. Sensory properties of single neurons of cat's claustrum. Brain Res. 66: 39-65.

Teuber, H.-L. 1960. Perception. Pages 1595-1668 *in* J. Field, editor-in-chief. Handbook of physiology, section 1: neurophysiology, vol. 3. American Physiological Society, Bethesda, Md.

Uttal, W.R. 1969. Emerging principles of sensory coding. Perspect. Biol. Med. 12: 344-368.

Vernadakis, A. 1975. Neuronal-glial interaction during development and aging. Fed. Proc. Fed. Amer. Soc. Exp. Biol. 34: 89-95.

Wei, L.Y. 1974. Dipole mechanisms of electrical, optical and thermal energy transduction in nerve membrane. Ann. N.Y. Acad. Sci. 227: 285-293.

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