

The Orienting Reaction: Key to Brain Re-presentational Mechanisms

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INTRODUCTION

Psychology as a science has shown several seemingly incompatible faces. In the beginning psychology was defined in terms of intentionality: the ability of people to discern the difference between intent and act and between perceiver and what is perceived (Brentano, 1967). The problems addressed by psychology were thought (e.g., Külpe, 1893) and feeling (e.g., Wundt, 1874, Freud, 1954), sensation and movement were explored by physiologists (e.g., Mach, 1914; and Helmholtz, 1867). But soon it became clear that the boundaries between sensation and perception and between movement and action could not be so sharply delineated. Even feelings had their physiological roots in the instincts (Woodworth, 1940). Thus psychology became physiological either overtly (Pavlov, 1927; Wundt, 1874) or covertly (Freud, 1950; Pribram & Gill, 1976).

A new departure was signaled by Watson (1919) when, in the tradition of a growing positivism, he declared that psychology must be rooted in observation and that what could be observed was the behavior of organisms. Watson himself remained oriented to physiology as did his eminent student Karl Lashley. But in the hands of others—Tolman (1932), Hull (1951), Spence (1956), and, more explicitly, Skinner (1938)—psychology as a strictly behavioral science flowered.

The older views continued to develop, however. Psychophysics (e.g., Fechner, 1860; Stevens, 1975; Werner & Mountcastle, 1965; De Valois, 1960; De Valois, Albrecht, & Thorell, in press) honed the relationship between introspection, physical specification, and physiological inquiry to a fine edge. Gestalt psychology (e.g., Köhler, 1964) also followed this tradition, using the data from illusions as anchors for theoretical construction.

Clinical and social psychology often reflected the more basic developments by enunciating therapies of various persuasions (e. g., analytic, behavioral, Gestalt, etc.). However, the importance of the social (as contrasted to the physical) environment became a paramount concern in these disciplines, which led them in directions that appeared to be only remotely related to introspection, physiology, and physics.

Into this history was injected another development that has proved to be as seminal as Watson's behaviorism (1919). During the late 1950's Eugene Sokolov (1960) demonstrated that the habituation of the orienting reaction (OR) could not be explained on the basis of a fatiguing or simple decremting adaptation of neurons. Any change in a repetitive stimulus situation—even a diminution of sound or light—could call forth dishabituation of the OR. A neuronal model, a re-presentation of the stimulating environment must have been formed in the nervous system against which every change is tested. Sokolov's experimental demonstration consolidated trends that had been initiated by Sharpless and Jasper's (1956) physiological work on the OR; MacKay's (1956) description of self-organizing systems; Bruner's (1957) detailing of perception as a match-mismatch process; and Miller, Galanter, and Pribram's (1960) treatment of psychology as an information process based on feedback mechanisms and the list structures of computer programming.

The Nature of Re-presentation

Central to all these developments is the conception that a representation of the organism's environment becomes organized in the brain by either genetic evolution or individual experience and that behavior is guided by a process in which a comparison is made between current input and the relevant brain re-presentation. The generality of this principle has been challenged by both experimental data and by theory. Despite this, there is no question but that current experimental "cognitive" psychology is based on the principle of "re-presentation" and that it has had a unifying effect on a field of inquiry that had been on the point of disintegrating. The importance of brain re-presentational processes to the very fabric of psychology makes it imperative that we carefully examine its validity.

Let us therefore begin with some definitions. Re-presentation implies that a presentation exists and that this presentation is replicated in some form or other in another system. Presentations are descriptions. When the presentation (description) of a form with reference to its entirety is simpler than a reference to its parts, a level of presentation is discerned. Systems encompass levels of presentation, their forms related by transformations, that is, transfer functions. Each level of presentation is thus re-presented by virtue of the transformations, the transfer functions that describe the relationship between levels of the system.

Systems of interest to psychologists consist of biological organisms immersed in physical and social environments. Behavioral descriptions are presentations of the relationship between organisms and their environment. Brain re-presentations must therefore represent such *relationships*, not simply some environmental form.

Two problems can be distinguished. One concerns the existence of re-presentations in the sense defined above. The other involves the specification of the transfer functions that describe the transformation of behavioral presentations into neural presentations. Considerable progress has been made with regard to the first of these problems, the existence of re-presentations. The second problem is the more difficult, but here also some headway can be discerned.

THE FORM OF SENSORY AND MOTOR RE-PRESENTATIONS

Do re-presentations exist, and if so, what form do they take? Since Sokolov's seminal demonstration, other data have become available that can be interpreted only as evidence that the brain functions do re-present the organism's experience. Take, for instance, the classical argument as to whether muscles or movements are re-presented in the motor cortex. A great number of experiments, anatomical and neurophysiological, showed discrete one-to-one mapping of muscles and even parts of muscles onto the cerebral convexity (e.g., Chang, Ruch, & Ward, 1947). Penfield's well-known homunculus issued from such studies on humans (Penfield & Boldrey, 1937).

But other, more physiologically-oriented experiments, provided different results. These show that the same electrical stimulation at the same cortical locus produces *different* movements, depending on such other factors as position of the limb, the density of stimulation, and the state of the organism (e.g., respiratory rate, etc.). For the most part one could conceptualize the results as showing that the cortical re-presentation consists of movements centered on one or another joint (e.g., Phillips, 1965). The controversy was thus engaged—proponents of punctate muscle re-presentation vis à vis proponents of the re-presentation of movement.

I decided to repeat some of the classical experiments in order to see for myself which view to espouse (reviewed in Pribram, 1977a, chapters 12 and 13). Among the experiments performed was one in which the motor cortex was removed (unilaterally and bilaterally) in monkeys that had been trained to open a rather complex latch box to obtain a peanut reward (Pribram, Kruger, Robinson, & Berman, 1955–56). My results in this experiment were, as in all others, the replication of the findings of my predecessors. The latch box, was opened, but with such clumsiness as to prolong the time taken some two- to threefold.

But the interesting part of the study consisted in taking cinematographic pictures of the monkeys' hands as they performed the latch box task and moved about the cage. Viewing these films in slow motion we were able to establish to our satisfaction that no movement or even sequence of movements was specifically impaired by the motor cortex resections! The deficit appeared to be *task-specific* not muscle- or movement-specific.

Therefore, my conclusion was that, depending on the *level of analysis*, one could speak of the motor re-presentation in the cortex in three ways. Anatomically, the re-presentation was punctate and of *muscles*. Physiologically, it consisted of mapping the muscle re-presentation into *movements*, probably around joints as anchor points. But behavioral analysis showed that these views of the re-presentation were incomplete. No muscles were paralyzed, no movements precluded, by total resection of the re-presentation. It was *action*, defined as the environmental consequence of movements, that suffered when motor cortex was removed.

The realization that acts, not just movements or muscles, were re-presented in the motor systems of the brain accounted for the persistent puzzle of motor equivalences. We all know that we can, though perhaps clumsily, write with our left hands, our teeth, or, if necessary, our toes. These muscle systems may never have been exercised to perform such tasks yet immediately and without practice can accomplish at least the rudiment required. In a similar fashion, birds will build nests from a variety of materials, and the resulting structure is always a habitable facsimile of a nest.

The problem immediately arose of course as to the precise nature of a re-presentation of an act. Obviously there is no "image" of an action to be found in the brain if by "image" one means specific words or the recognizable configuration of nests. Yet some sort of re-presentation appears to be engaged that allows the generation of words and nests—an image of what is to be achieved, as it were.

The precise composition of images-of-achievement remained a puzzle for many years. The resolution of the problem came from experiments by Bernstein (1967), who made cinematographic records of people hammering nails and performing similar more or less repetitive acts. The films were taken against black backgrounds with the subjects dressed in black leotards. Only joints were made visible by placing white dots over them.

The resulting record was a continuous wave form. Bernstein performed a Fourier analysis on these wave forms and was invariably able to predict with a few centimeters the amplitude of the next in the series of movements.

Bernstein's analysis suggests that a Fourier analysis of the invariant components of motor patterns (and their change over time) is computable and that an image-of-achievement may consist of such computation. Electrophysiological data from unit recordings obtained from the motor cortex have provided

preliminary evidence that in fact such computations are performed (Everts, 1967, 1968).

The computation of exquisite timing relationships between organism and environment that characterize such performances raises an issue that has been clearly framed as a question by Michael Turvey (1973): Does such timing imply a complementation of organism to environment rather than the existence of a re-presentation? This point is both important and difficult. Complementation suggests something akin to a mirror image, whereas re-presentation suggests an image that is more a duplicate of the imaged. The essential point about complementation is that organism and environment mutually imply each other. Thus the acquisition of a motor skill is an attunement, the organism ordinarily tuning to the environment. Just as often, having a skill can result from the attunement of the environment to the organism: Musical instruments, toys, and tools provide common examples of artifacts involved in skilled performances.

Such artifacts are of course "re-presentations" of the organism's intent, even though they complement that intent. In similar fashion the evidence reviewed above indicates that the motor cortex does in fact operate as a re-presentation of the environment, albeit a complementary one.

By "motor image" therefore we mean a re-presentation that is composed of a punctate muscle-brain connectivity that is mapped into movements over joints in order to process environmental invariants generated by or resulting from those movements. This three-level definition of the motor re-presentation can be helpful in resolving the problems that have become associated with the term *image* in perceptual systems.

There is by now a considerable body of evidence that the visual system also computes its representation in the Fourier or some similar domain (see Pribram, 1977a, chapter 8; Pribram, Nuwer, & Baron, 1974). This evidence has accrued in the laboratories of Cambridge University (Campbell & Robson, 1968; Movshon, Thompson, & Tolhurst, a, b, c, in press), Harvard University (Pollen & Ronner, 1975; Pollen & Taylor, 1974), Massachusetts Institute of Technology (Schiller, Finlay, & Volman, 1976a, 1976b, 1976c), the University of California (De Valois, et al., in press), our own at Stanford (Pribram, Lassonde, & Ptito, in press), and from many other institutions, such as The University of Pisa (Maffei & Fiorentini, 1973) and the University of Leningrad (Glezer, Ivanoff, & Tscherbach, 1972, 1973). All this evidence shows that the visual system operates as a frequency analyzer. For pattern vision, overlapping neural channels have been demonstrated to be composed of single neurons each of which is tuned to a band width of from $\frac{1}{2}$ to $1\frac{1}{2}$ octaves of spatial frequency. The conception held for almost two decades that these cells act as bar or edge detectors has been shown wanting: The cells are not very responsive to changes in bar width, and they change their orientation selectivity when presented with a checkerboard or a plaid to the exact amount predicted by the Fourier transform of the pattern. There

is little doubt but that these cells operate as a spatial filter and that the filtering performs a frequency analysis on visual patterns.

In audition and somesthesia (and perhaps to some extent in chemical senses) as well as in vision, there is a punctate connectivity between receptor surface and cortical representation over which sensory signals are relayed. At the physiological level of analysis, however, there occurs a mapping of the punctate elements of the array into functions. This is accomplished in part by convergences and divergences of pathways but even more powerfully by networks of lateral interconnectivities, most of which operate by way of slow-graded dendritic potentials rather than by nerve impulses propagated in long axons. Thus in the retina, for instance, no nerve impulses can be recorded from receptors, bipolar, or horizontal cells. It is only in the ganglion cell layer, the last stage of retinal processing, that the nerve impulses are generated to be conducted in the optic nerve to the brain (reviewed by Pribram, 1977a, chapters 1, 6, and 8). These lateral networks of neurons operating by means of slow-graded potentials thus map the punctate receptor-brain connectivities into functional *ambiences*.

By analogy to the motor system, this characterization of the perceptual process is incomplete. Behavioral analysis discerns perceptual constancies just as it had to account for motor equivalences. In short, *invariances* are processed over time, and these invariances constitute the behaviorally derived aspects of the re-presentation (e.g., Pribram, 1974). Ordinarily an organism's re-presentational processes are called *images*, and there is no good reason not to use this term. But it must be clearly kept in mind that the perceptual image, just as the motor image, is more akin to a computation than to a photograph.

The perceptual image so defined is therefore a re-presentation, a mechanism based on the precise anatomical punctate receptor-cortical connectivity that composes an *array*. This array is operated upon by lateral interconnections that provide the *ambiences* which process the *invariances* in the organism's input. Thus the cortical re-presentation of the percepts go therefore beyond the anatomical re-presentations of the receptor surfaces just as the cortical re-presentation of actions goes beyond the mere anatomical re-presentations of muscles.

It is, of course, a well-known tenet of Gestalt psychology that the percept is not the equivalent of the retinal (or other receptor) image. This tenet is based on the facts of constancy (e.g., size) and the observations of illusions. Neurophysiologists, however, have only recently begun seriously to investigate this problem. Thus Horn (Horn, Stechler, & Hill, 1972) showed that certain cells in the brainstem (superior colliculus) maintained their firing pattern to an environmental stimulus despite changes in body orientation; in my laboratory, Spinelli (1970) and Bridgeman (1972), using somewhat different techniques, demonstrated constancy in the firing pattern of cortical neurons over a range of body and environmental manipulations. Further, neurobehavioral studies have shown that

size constancy is impaired when perivisual and inferior temporal cortex are removed (Humphrey & Weiskrantz, 1969; Ungerleider, Ganz, & Pribram, 1977).

The fact that the cortex becomes tuned to invariances in the organism-environment relationship rather than just to the retinal image is borne out dramatically by a hitherto unexplained discrepancy in the results of two experiments. In both experiments a successful attempt was made to modify the orientation selectivity of the cortical neurons of cats by raising them from birth in environments restricted to either horizontal or vertical stripes. In one experiment (Blakemore, 1974) the kittens were raised in a large cylinder appropriately striped. A collar prevented the animals from seeing parts of their bodies—so they were exposed only to the stripes. However—and this turns out to be critical—the kittens could observe the stripes from a variety of head and eye positions. By contrast, in the other experiment, which was performed in my laboratory (Hirsch & Spinelli, 1970, head- and eye-turning were prevented from influencing the experiment by goggles onto which the stripes were painted. In both experiments cortical neurons were found to be predominantly tuned to the horizontal or vertical, depending on the kittens' environment, although the tuning in Blakemore's experiments appeared to be somewhat more effective. The discrepancy arose when behavioral testing was instituted. Blakemore's kittens were consistently and completely deficient in their ability to follow a bar moving perpendicular to the orientation of the horizontally or vertically striped environment in which they had been raised. In our experiment, Hirsch, despite years of effort using a great number of quantitative tests, could never demonstrate *any* change in visual behavior! The tuning of the cortical cells to the environmental situation that remained invariant across transformations of head and eye turning was behaviorally effective; the tuning of cortical cells to consistent retinal stimulation had no behavioral consequences.

These results are consonant with those obtained in other sensory modes and help to provide some understanding of how brain processing produces perception of an objective world separated from the receptor surfaces that interface the organism with the environment.

Von Bekesy (1967) has performed a large series of experiments on both auditory and somatosensory perceptions to clarify the conditions that produce projection and other perceptual effects. For example, he has shown that a series of vibrators placed on the forearm will produce a point perception when the phases of the vibrations are appropriately adjusted. Once again, in our laboratory we found that the cortical response to the type of somatosensory stimulation used by Bekesy was consonant with the perception not with the pattern of physical stimulation of the receptor surface (Dewson, 1964; Lynch, 1971). Further, Bekesy showed that when such vibrators are applied to both forearms and the subject wears them for a while, the point perception suddenly leaps into the space between the arms.

Other evidence for projection comes from the clinic. An amputated leg can still be perceived as a phantom for years after it has been severed and pickled in a pathologist's jar. A more ordinary experience comes daily to artisans and surgeons who "feel" the environment at the ends of their tools and instruments.

When validation is lacking or incomplete, we tend to call the perception an illusion and pursue a search for the physical events that may be responsible for the illusion.

There is thus incontrovertible evidence that re-presentations of prior experience with the environment are involved in the processing of sensory input. Such re-presentations are often complementary in nature—that is, the organism and environment are joined in a finely tuned and resonating couplet. What then is the role in this process of the OR with which our knowledge of re-presentational mechanisms began?

THE OR AND NEURAL RE-PRESENTATION

Sokolov's demonstration that a neuronal model, a re-presentation of experience, is constructed by repetitious input must be the starting point of any analysis of the relationship between brain re-presentational mechanisms and the OR. The first question a scientist asks therefore is whether or not the data on which Sokolov based his inference are reliable. Koepke and Pribram (1966, 1967) undertook to answer this question and with only minor reservations were able to replicate the essentials of Sokolov's findings.

The next question of interest to us as physiological psychologists had to do with locating the brain mechanisms involved in constructing the neuronal model. We had already demonstrated that resections of the amygdala and of frontal cortex interfered with an organism's behavioral habituation to repeated input (Davis, 1951; Schwartzbaum, Wilson & Morrissette, 1961). It seemed only a simple step to show that the visceromotor components used by Sokolov would also fail to habituate. Much to our surprise we found these components to be severely disrupted by the lesions; most often they were completely absent. A series of carefully carried out studies on rhesus monkeys resulted in the following findings:

1. Resection of the amygdala or frontal cortex essentially deleted the visceromotor components of the OR although reflex visceromotor activity remained intact as did behavioral orienting (Bagshaw & Benzies, 1968; Bagshaw, Kimble, & Pribram, 1965; Kimble, Bagshaw, & Pribram, 1965; Pribram, Reitz, McNeil, & Spevack, 1974.)

2. Behavioral orienting failed to habituate (Schwartzbaum, et al., 1961).

3. Resection of the hippocampus enhanced the visceromotor components of orienting and reduced the susceptibility of the habituated monkeys to

dishabituation—i.e. to distraction and orienting (Douglas & Pribram, 1969; Pribram & McGuinness, 1975).

These results made two things evident: The visceromotor components of the OR are important and perhaps essential to the occurrence of habituation. What therefore is their role and that of habituation in the formation of the neuronal model? Further, the frontolimbic forebrain is somehow involved in the production of habituation and therefore of the neuronal model, the brain re-presentation of experience. How?

To answer the last question first, we removed a large portion of the limbic forebrain in order to assess the extent and nature of the nonlimbic learning (Pribram, Douglas, & Pribram, 1969). Not too surprisingly we found it to be excellent in our instrumental situation. When classical conditioning was tested, however, deficiencies were shown to occur when visceromotor behavior was measured. But, in the same classical conditioning situation a motor response was spared (Bagshaw & Coppock, 1968; Pribram, Reitz, McNeil, & Spevak, 1974).

Our interpretation of these results has been that when skills (motor and perceptual) are acquired without any visceromotor participation a greater number of repetitions is necessary to produce adequate performance (Vinogradova, 1970). Experiments are needed to address this issue.

Support for the interpretation comes, however, from work on humans. Removal of amygdala and hippocampus produces a peculiar "memory" deficiency (Milner, 1968) that can be overcome by providing sufficient context (Weiskrantz & Warrington, 1975) and is totally absent when the subject is tested instrumentally (Sidman, Stoddard, & Mohr, 1968). There appears to be a major difference between learning and remembering an instrumental motor or perceptual skill that becomes automatic and is apparently retained for the lifetime of the organism and a totally different sort of learning that demands control over attention and is specific to a particular context. I have elsewhere provided additional evidence for the distinction between context-dependent and context-free mnemonic processes (e.g., Pribram, 1977a). In human cognitive psychology a similar distinction has been made between terms of episodic and semantic memory (Tulving, 1970) and, more recently, between controlled and automatic processing (Schneider & Shiffrin, 1977). There is good evidence to believe that all of these distinctions refer to the same two types of learning mechanism: the controlled, context-dependent, episodic, which is a manifestation of frontolimbic function, and the automatic, context-free, semantic, which has reference to the functions of the posterolateral cerebral convexity (Pribram, 1978).

MODES OF CENTRAL PROCESSING

A series of experiments has clarified the neural mechanisms that separate controlled, context-dependent processing from the more automatic mode.

Orienting always occurs within the context of ongoing behavior and experience. The OR therefore indicates that dishabituation has taken place. The immediate response of the organism is phasic, as indicated by a galvanic skin response and perhaps a brief cardiac acceleration (see, e.g., Bagshaw & Benzie, 1968; Graham & Clifton, 1966). Pribram and McGuinness (1975) labeled such phasic responses "arousal" and distinguished them from longer lasting tonic responses which they called "activation."

Activation is signaled by a heart rate deceleration and indicates, according to the work of Lacey and Lacey (1970, 1974), that the organism is actively engaged in central processing operations. Their suggestion is based on the correlation between heart rate deceleration, behavioral readiness, and the appearance of a negative brain potential that has been called an "expectancy" or "readiness" potential (Donchin, Otto, Gerbrandt, & Pribram, 1971; Tecce, 1972; Walter, 1967).

Both arousal and activation are two-component processes, however. Recall that, after amygdectomy or frontal cortex resection, the behavioral OR remains intact, but its visceromotoric components are absent. This absence is coupled with a failure of behavioral orienting to habituate. Thus the amygdala and frontal cortex and the visceromotoric responses they regulate are necessary for habituation to occur. Unless the OR becomes registered by virtue of the visceromotoric "booster," a neuronal model of the episode is not constructed. Registration, episodic memory, is thus dependent on the frontoamygdala brain system and the visceromotoric responses that it controls. It is this episodic memory function, the registration of the OR, not the behavioral OR itself that is controlled by this brain system.

In like manner two components can be discerned for activation. Ordinarily much of behavior proceeds relatively automatically. Postural and perceptual sets are continuously operating on the basis of prior experience. As reviewed elsewhere, the basal ganglia of the forebrain are critically involved in such processing (Pribram, 1977b; Pribram & McGuinness, 1975). As noted in these reviews, the evidence from the recording of readiness and expectancy potentials indicates that these and related parts of the brain are actively involved in "what's to be done" mechanisms. It is during such processing that heart rate deceleration is manifest.

But expected occurrences do not always occur as expected, and what the organism readies itself to do is often interrupted by some distraction (dishabituation). Thus another mechanism must be invoked that computes the consequences of maintaining set in the face of distraction or of allowing the distraction to control behavior. Recall that experimental evidence was obtained to show that the hippocampal formation is critically involved in such computations. On the basis of the fact that heart rate accelerates, Pribram and McGuinness (1975) suggested that this computation takes effort, and evidence was reviewed to show that both peripheral muscular work (anaerobic) and central processing work

(cerebral blood flow changes indicating changes in brain states) are involved when vigilant organisms "pay" attention. Thus the hippocampal formation, not the readiness mechanism, is directly involved in the effort.

CENTRAL PROCESSING AND NEURAL RE-PRESENTATIONS

It must be clear from what has been reviewed thus far that work on the neural mechanisms involved in the OR and its habituation has contributed a great deal to our understanding of the nature of central processing but has yielded little information regarding neural re-presentations per se. Another line of research on orienting and habituation has, however, filled this gap. Working with micro-electrodes, Richard Thompson (see Groves & Thompson, 1970, for review) has carefully teased apart the neural machinery that responds selectively throughout the neuraxis to repetitious excitation. He has shown that even in the spinal cord, interneurons (neurons other than input and output neurons) display these characteristics. Three groups of such neurons were identified: One type responds briskly to stimulation and then decrements when the stimulation becomes repetitious. Another type takes longer to respond to a series of repetitive excitations and monitors any change in stimulus parameters. Finally, there is a type of neuron that apparently sums the output of the first two types and shows essentially the characteristics of the behavioral OR and its habituation. Interestingly, the brisk type of neurons are laterally placed in the dorsal horn, whereas the monitoring type are more medially placed in the region of the column of Clark, where visceromotoric functions are represented.

Similar types of neurons have been identified in the brainstem—for example, the colliculi (Bures & Buresova, 1970; Horn, 1970; Lettvin, Maturana, Pitts, & McCulloch, 1961; for review see Horn & Hinde, 1970). These results suggest that orienting and habituation are ubiquitous in the mammalian nervous system and, as has been shown by Kandel (see Kandel & Gardner, 1972; Kandel & Kupfermann, 1970), in invertebrate nervous systems as well.

Does this mean that neuronal models, or re-presentations, are formed everywhere in the nervous system? Yes and no. Recall from the first part of this chapter that the power of a frequency-encoded representation is in part its ability to account for the evidence that storage in the nervous system apparently becomes widely distributed. The ubiquitous property of the interneurons to habituate could furnish the substrate for a distributed store. However, there is no evidence as yet that frequency encoding is involved in the simple types of habituation and, therefore, in the re-presentation described here. But evidence to the contrary is also lacking; the question has thus far not been posed.

Equally critical has been the lack of evidence for the existence at the spinal and brainstem levels of a neuronal model of the kind Sokolov's behavioral

evidence demands. Decrementing to repetitious stimulation, and only decrementing, has been observed. And although dishabituation is produced by changes in stimulus parameters, these cannot include the critical ones used by Sokolov: diminution of stimulus intensity. Horn and Hindé (1970) have developed a model whereby the simple habituations and dishabituations at the spinal and brainstem levels could be combined to produce the Sokolovian neuronal model, but the fact remains that at spinal and brainstem levels no evidence for such a model exists.

The situation is entirely different for cortex, however. Vinogradova (1970, 1976) has conclusively demonstrated the presence of neurons in hippocampal cortex that increment to repetitions of stimulation—as well as the usual decrementing types. In our laboratory, also, using small macroelectrodes, we have found regions of visual cortex where incrementing rather than decrementing accompanies stimulus repetition. During dishabituation such regions decrement in contrast to surrounding regions that increment, and dishabituation can be produced by lowering the intensity of the stimulation as in Sokolov's experiment (Dawson, 1975; Grandstaff & Pribram, 1972).

There is thus good evidence that a neuronal model in Sokolov's sense—a patterned brain re-presentation sensitive to all parameters of repetitious stimulation—is constructed in cortex.

What remains to be understood are the operations of the central processing mechanisms upon the representational stores. Cortico-subcortical connectivities especially with the basal ganglia are clearly involved in automatic context-free processing (Lassonde & Ptito, in press; Pribram, 1977). The operation of controlled, context-dependent processing mechanisms appears to be more complex. Inhibitory influences originating in the frontoamygdaloid system range downward into the reticular formation of the brainstem (Sauerland & Clemente, 1973; Skinner & Lindsley, 1973), which, in turn, activates cortical formations, including hippocampus (Vinogradova, 1976). Just what enables this circuit to encode episode-specific information remains to be investigated.

CONCLUSION

This chapter has reviewed some of the evidence bearing directly on Sokolov's seminal work on the OR, its habituations, and dishabituation. Sokolov concluded from the fact that dishabituation results from the diminution of the intensity of stimulation as well as from changes in its other parameters that a neuronal model of repetitious stimulation forms in the brain. With this demonstration, the importance of brain re-presentations was signaled and their nature investigated. Furthermore, a tool was provided that allowed probing of the central processing mechanisms involved in generating the brain re-presentations and in usefully addressing them.

Evidence was detailed to show that the nature of cortical re-presentations was to encode in the frequency domain. Evidence was also presented to show that the substrate for simple re-presentations was ubiquitous in the neuraxis. The question remained to be asked experimentally as to whether or not such simple re-presentations were also essentially encoding in the frequency domain—a question made reasonable by the fact that stimulus repetition is involved in habituation.

Re-presentations must become organized and addressed if they are to be effective guides to experience and behavior. Automatic and controlled modes of processing re-presentations were distinguished by evidence from neurobehavioral experiments. The brain mechanisms operating during these modes of processing were further delineated by neurobehavioral and psychophysiological techniques. Phasic and tonic processes were identified and each of these shown to be composed of an automatic and a controlled component. Control of the phasic component leads to registration of the OR by virtue of a visceromotor booster that acts to shorten the number of repetitions necessary for encoding; control of the tonic component leads to effortful, vigilant readiness to compute the consequences of continuing an experience or behavior or of allowing it to be guided by distracting interruptions. These functional and structural interrelationships are summarized in Fig. 1.1.

Almost all of the work recorded here has been accomplished in the past 25 years. The results have changed the face of psychology. The extreme behaviorist view of the organism as a kind of stimulus-response robot has given way to one in which the cognitive processes of sentient beings are as determining of their experience and behavior as is the environment in which these organisms develop and live. The pursuit of the OR and its habituation in all of our laboratories has not been in vain. Let us hope that the next quarter of a century will prove as fruitful.

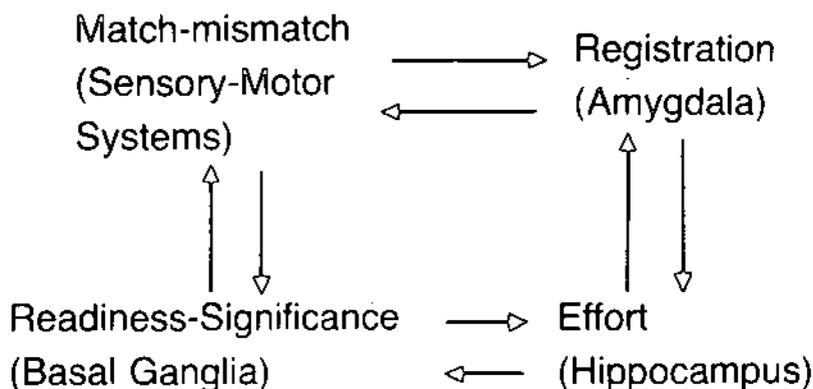


FIG. 1.1. Components of the orienting reaction.

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