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exhibit HD tuning (so the input is focused on the correct flank of the attractor bump) and a turning preference. Blair and Sharp (1995) called these turn-modulated head direction (TMHD) cells. TMHD cells with a clockwise turning preference should make excitatory projections onto attractor HD cells with preferred directions slightly to the right of their own; TMHD cells with a counterclockwise turning preference should project to attractor HD cells slightly to the left. When the animal is still, both populations of TMHD cells should fire at the same rate, supplying identical input to both flanks of the attractor bump. When the animal is in a clockwise turn, the clockwise TMHD population should increase its firing rate, while the counterclockwise population should decrease its rate, in proportion to the angular velocity. Hence the bump would receive more input on its right flank, and begin shifting to the right. The opposite would occur for counterclockwise turns.

Cells in LMN seem to meet all the requirements for the hypothesized TMHD population: they show normal HD tuning, velocity modulation, and a turning preference. In the Goodridge and Touretzky (2000) model, the clockwise and counterclockwise LMN populations both project to AD. Since AD does not appear to have recurrent connections, it cannot function as an attractor network, and thus cannot exhibit all the stability properties of such a network. But AD HD cells integrate information from LMN, PoS, and perhaps retrosplenial HD cells, and AD projects to PoS. The attractor network is located in PoS, which does have recurrent connections. This model explains why the firing of PoS HD cells is independent of angular velocity, while AD HD cells are influenced by velocity.

In a complementary attractor model by Sharp et al. (2001), DTN cells make inhibitory projections onto LMN cells, which in turn make excitatory projections back onto the DTN population. DTN cells also receive angular velocity information from vestibular nuclei. HD cells in LMN and DTN have different tuning properties, but their interaction is hypothesized to produce the attractor dynamics required to integrate angular velocity.

HD cells in other areas, such as retrosplenial cortex and caudate nucleus, could also contribute to the functioning of the "core" HD system. Further work may explain why there are so many HD areas, and why the difference in ATI values for PoS, AD, and LMN cells is so much greater than can be accounted for by synaptic delays alone.

Road Map: Mammalian Motor Control
Related Reading: Dynamic Remapping; Hippocampus: Spatial Models; Vestibulo-Ocular Reflex

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Schema Theory

Michael A. Arbib

Introduction

Schema theory complements neuroscience's well-established terminology for levels of *structural* analysis (brain region, neuron, synapse) with a *functional* vocabulary, a framework for analysis of behavior with no necessary commitment to hypotheses on the localization of each *schema* (unit of functional analysis), but which can be linked to a structural analysis whenever appropriate. Schemas provide a high-level vocabulary that can be shared by brain theorists, cognitive scientists, connectionists, ethologists, and even kinesiologists, even though the implementation of the schemas may differ from domain to domain. This article presents a general perspective, notes but does not emphasize learning models for schemas, and focuses on two issues: structuring perceptual and motor schemas to provide an action-oriented account of behavior and cognition (as relevant to the roboticist as the ethologist); and how schemas describing animal behavior may be mapped to interacting regions of the brain. Schema-based modeling becomes part of neuroscience when constrained by data provided by, for example, human brain mapping, studies of the effects of brain lesions, or neu-

rophysiology. The resulting model may constitute an adequate explanation in itself or may provide the framework for modeling at the level of neural networks or below. Such a *neural* schema theory provides a functional/structural decomposition, in strong contrast with models that employ learning rules to train a single, otherwise undifferentiated, neural network to respond as specified by some training set.

Schemas: History and Comparisons

Central to our approach is the notion of the "active organism," which seeks from the world the information it needs to pursue its chosen course of action. In *action-oriented perception*, current sensory input is itself a function of the subject's active exploration of the world, which is directed by *anticipatory schemas*, which Neisser (1976) defines as plans for perceptual action as well as readiness for particular kinds of sensory structure. This view has resonances with that of Piaget (1971, pp. 6–7): "Any piece of knowledge is connected with an action . . . [T]o know an object or a happening is to make use of it by assimilation into an action schema . . . [namely] whatever there is in common between various repetitions or superpositions of the same action." Acting on the basis of an action schema usually entails the *expectation* of certain consequences. Piaget talks of *assimilation*, the ability to make sense of a situation in terms of a stock of schemas, and *accommodation*, whereby the stock of schemas may change over time as the expectations based on assimilation to current schemas are not met. Piaget traces the cognitive development of the child from reflexive schemas through eye-hand coordination and object permanence all the way to schemas for language and abstract thought.

Head and Holmes introduced the term schema to neurology in 1911, speaking of the *body schema* (Frederiks, 1969, reviews relevant literature): "Anything which participates in the conscious movement of our bodies is added to the model of ourselves and becomes part of those schemata: a woman's power of localization may extend to the feather of her hat." A woman with unilateral damage to the parietal lobe may lose awareness that the body on the opposite side actually belongs to her—not only ignoring painful stimuli but even neglecting to dress that half of the body. Damage to the thalamus and the somatosensory system may also produce disorders of the body schema.

Bartlett (1932) carried the schema idea into cognitive psychology, with a schema being "an active organization of past reactions [or] experiences, which must always be supposed to be operating in any well-adapted organic response." He stressed the constructive character of remembering. When people try to recall a story, they reconstitute it in their own terms—relating what they experience to a familiar set of schemas—rather than by rote memorization of details. Instead of thinking of ideas as impressions of sense data, schema theory posits an active and selective process of schema formation (cf. Piaget's notion of assimilation), which in some sense constructs reality as much as it embodies it. More generally, cognitive psychology views schemas as cognitive structures built up in the course of interaction with the environment to organize experience. Not only is sensory input coded by instantiating certain schemas (we say a schema is instantiated when active copies are running, and refer to these copies as "schema instances"), as seeing a chair instantiates an instance of the "chair schema," but the current stock of schema instances may also instantiate related action schemas such as "sitting" and general schemas such as "furniture" while inhibiting other competing schemas. Shallice (1988, p. 308n) stresses that the schema "not only has the function of being an efficient description of a state of affairs—as in, say, Bartlett's usage—but also is held to produce an output that provides the immediate control of the mechanisms required

in one cognitive or action operation. The usage is thus more analogous to Piaget's view than to Bartlett's original concept." In a connectionist vein, Rumelhart et al. (1986) suggest how schemas may be seen as emergent properties of adaptive, connectionist networks, but they neither relate schemas to action nor show how schemas may be combined to form assemblages (see discussion later in this article).

Schmidt (1976) offered a schema theory of discrete motor skill learning. Through experience, the subject builds up a *recall schema* that pairs the response specifications of a movement with the actual outcome. Later, this recall schema can be consulted to infer, from a desired outcome, the response specification that will produce it. Similarly, a *recognition schema* pairs the desired outcome with the expected sensory consequences of each movement. The recall schema is what is now known in the literature of motor control as an "inverse model" (SENSORIMOTOR LEARNING)—it goes from a desired response to a pattern of commands that achieves it, rather than the "direct" causal path from commands to action; while the recognition schema corresponds to Neisser's anticipatory schema.

Arbib (1981; Arbib, Érdi, and Szenthágothai, 1998, Chapter 3 for an exposition) offered a schema theory more tightly constrained by the need to explain the neural basis of behavior, stressing that a schema expresses a function that need not be co-extensive with the activity of a single neuronal circuit. (This view was foreshadowed in the work of Kilmer, McCulloch, and Blum (1969) who posed the general question of how the nervous system could set the organism's "overall mode of behavior" through the cooperative computation [no executive control] of modules, each of which aggregates the activity of many neurons.) A *schema* is what is learned about some aspect of the world, combining knowledge with the processes for applying it; a *schema instance* is an active deployment of these processes. A *perceptual schema* not only determines whether a given "domain of interaction" (an action-oriented generalization of the notion of object) is present in the environment, but can also provide parameters concerning the current relationship of the organism with that domain. Each schema instance has an *activity level* that indicates its current salience for the ongoing computation. The activity level of a perceptual schema signals the credibility of the hypothesis that what the schema represents is indeed present, whereas other schema parameters represent other salient properties such as size, location, and motion of the perceived object. Given a perceptual schema, we may need several schema instances, each suitably tuned, to subserve our perception of several instances of its domain. *Motor schemas* provide the control systems that can be coordinated to effect a wide variety of actions. The *activity level* of a motor schema instance may signal its "degree of readiness" to control some course of action (thus enriching somewhat the related notion of motor pattern generators; see MOTOR PATTERN GENERATION).

Schema instances may be combined (possibly with those of more abstract schemas, including coordinating schemas) to form *schema assemblages*. For example, an assemblage of perceptual schema instances may combine an estimate of environmental state with a representation of goals and needs. A *coordinated control program* is a schema assemblage that processes input via perceptual schemas and delivers its output via motor schemas, interweaving the activations of these schemas in accordance with the current task and sensory environment to mediate more complex behaviors. Figure 1 shows the original coordinated control program. As the hand moves to grasp an object, it is *preshaped* so that when it has almost reached the ball, it is of the right shape and orientation to enclose some part of the object prior to gripping it firmly. Moreover (to a first approximation), the movement can be broken into a fast initial movement and a slow approach movement, with the transition from the fast to the slow phase of trans-

Figure 1. Hypothetical coordinated control program for reaching and grasping. Note that different perceptual schemas (at the top) are required to provide parameters for the motor schemas (at the bottom) for the control of "reaching" (arm transport ≈ hand reaching) and "grasping" (controlling the hand to conform to the object). Note too the timing relations posited here within the "Hand Reaching" motor schema and between the motor schemas for "Reaching" and "Grasping." Dashed lines—activation signals; solid lines—transfer of data. (Adapted from Arbib, 1981.)
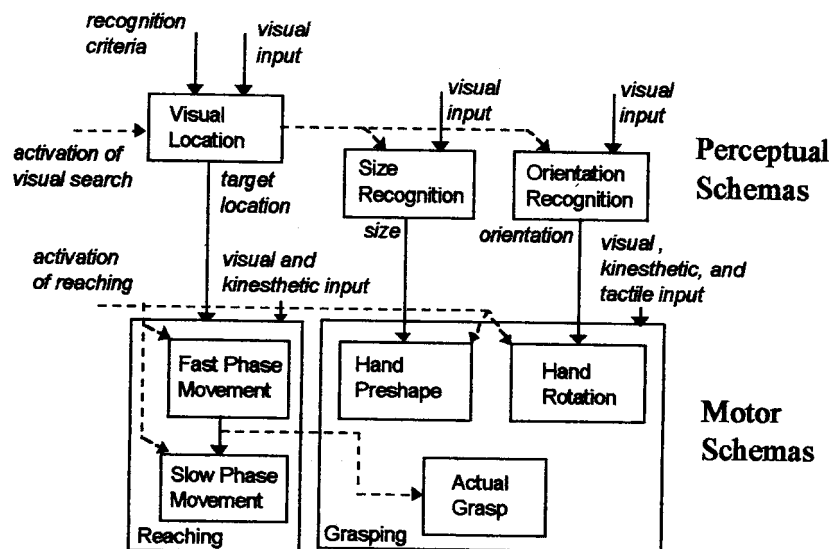
port coming just before closing of the fingers from the preshape so that touch may take over in controlling the final grasp. The top half of Figure 1 shows three perceptual schemas: successful location of the object activates the schemas for recognizing the size and orientation of the object. The outputs of these perceptual schemas are available for the control of the hand movement by concurrent activation of two motor schemas, one controlling the arm to transport the hand toward the object and the other preshaping the hand, with finger separation and orientation guided by the output of the appropriate perceptual schemas. Once the hand is preshaped, it is only the completion of the fast phase of hand transport that "wakes up" the final stage of the grasping schema to shape the fingers under control of tactile feedback. (This model anticipates the much later discovery of perceptual schemas for grasping in a localized area [AIP] of parietal cortex and motor schemas for grasping in a localized area [F5] of premotor cortex. See GRASPING MOVEMENTS: VISUOMOTOR TRANSFORMATIONS.)

Neuroscience and cognitive psychology often view working memory as storing a single item (e.g., the location of a target, or a single phone number) for a short delay period between observation of the item and its use in some action, after which it is discarded. Here, we extend the notion to insist that working memory may hold a range of items relevant to upcoming actions, and these items may remain accessible for extended periods so long as they remain relevant. Schema-based modeling of action-oriented perception (VISUAL SCENE PERCEPTION) then views the *short-term memory* (STM) of an organism as a working memory that combines the schema instances encoding relevant aspects of, and plans for interaction with, the current environment. This assemblage is dynamic, as certain schema instances are discarded from memory ("de-instantiated") while others are added ("instantiated"). *Long-term memory* (LTM) is provided by the stock of schemas from which STM may be assembled. New sensory input as well as internal processes can update STM. The internal state is also updated by knowledge of the state of execution of current *plans* that specify a variety of coordinated control programs for possible execution. Jeannerod (1997) surveys the role of schemas and other constructs in the cognitive neuroscience of action.

Schemas for *Rana Computatrix*

A schema model becomes a neural model, as distinct from a purely functional model, when explicit hypotheses are offered as

to how the constituent schemas are played over particular regions of the brain. To exemplify this, consider approach and avoidance in the frog (VISUOMOTOR COORDINATION IN FROG AND TOAD; and see Arkin et al., 2000, for a related discussion of behavioral models of the praying mantis as a basis for robotic behavior). A frog surrounded by dead flies will starve to death, but the frog will snap with equal "enthusiasm" at a moving fly or a pencil tip wiggled in a fly-like way. On the other hand, a larger moving object can trigger an escape reaction. Thus, a highly simplified model of the functioning of the brain of the frog has signals from the eye routed to two basic perceptual schemas, one for recognizing small moving objects (foodlike stimuli) and one for recognizing large moving objects (enemylike stimuli). If the small-moving-object schema is activated, it will in turn trigger the motor schema that gets the animal to approach what is apparently its prey. If the perceptual schema for large-moving-object is activated, it will trigger the motor schema for avoidance, causing the animal to escape an apparent enemy.

The biological model relates these schemas to anatomy. Each eye of the frog projects to regions on the opposite side of the brain, including the important visual midbrain regions called the *tectum* and the *pretectum* (in front of the tectum). If we hypothesize that the small-moving-object schema is in the tectum, while the large-moving-object schema is in the pretectum, the model (Figure 2A) predicts that animals with a pretectal lesion would approach small moving objects, but would not respond at all to large moving objects. However, Peter Ewert in Kassell studied toads with the pretectum removed and found that they responded with approach behavior to both large and small moving objects. This observation leads to the new schema-level model shown in Figure 2B. We replace the perceptual schema for *small* moving objects of Figure 2A by a perceptual schema for *all* moving objects and leave the right-hand column the way it was. The inhibitory pathway from the large-moving-object perceptual schema (in the pretectum) to the all-moving-object schema ensures that the model yields the normal animal's response to small moving objects with approach but not avoidance. This model explains our small database on the behavior of both normal animals and those with a lesion of the pretectum.

We have thus shown how hypotheses about neural localization of subschemas may be tested and refined by lesion experiments. The important point is that models expressed at the level of a network of interacting schemas can really be testable biological
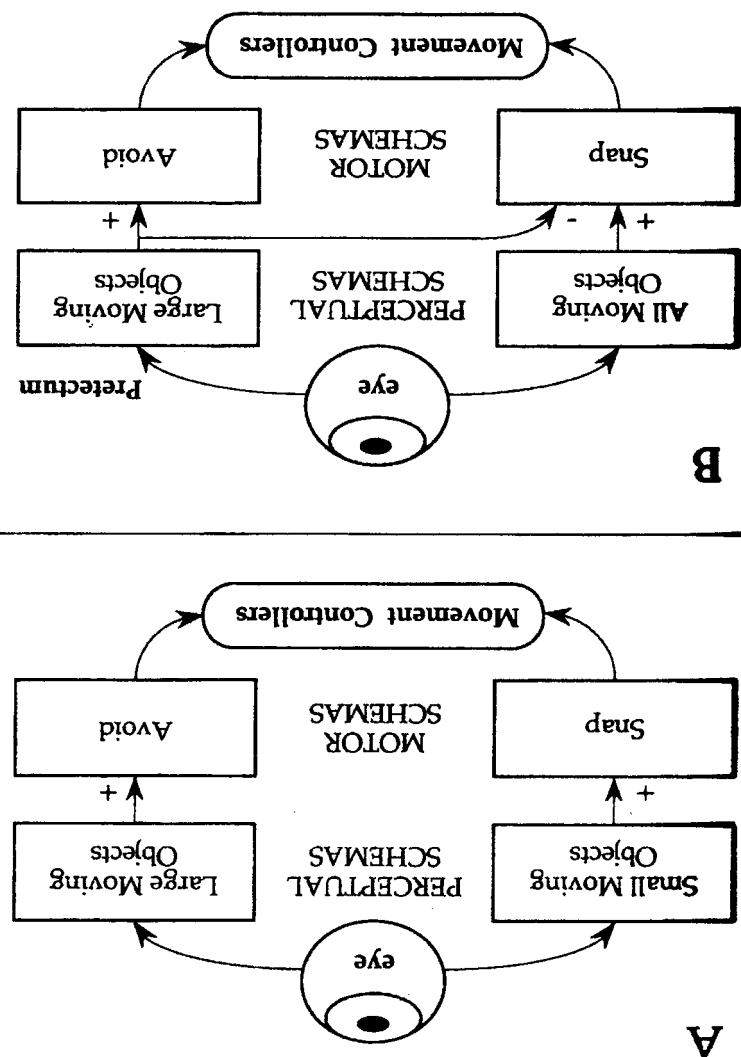
Coordinated Control Programs and Motor Schemas

We have seen that schemas can be combined to form *coordinated control programs* that control the phasing in and out of patterns of schema co-activation and the passing of control parameters from perceptual to motor schemas. The notion of schema is thus *recursive*—a schema defined functionally may later be analyzed as a coordinated control program of finer schemas, and so on until such time as a secure foundation of neural localization is attained.

Subsequent work has extended work on *Rana computatrix* ("the frog that computes"; Arbib et al., 1998, for a partial review) at the level of both schemas and neural networks for phenomena such as detours and path planning, avoidance behavior sensitive to the trajectories of predators, and details of snapping behavior that link neural control to biomechanics. The work constitutes a grounding example of work in modeling neural mechanisms in overall animal behavior (NEUROETHOLOGY, COMPUTATIONAL).

The model of Figure 1 distinguished two phases of arm movement—a fast phase controlled by a ballistic schema (i.e., one that moves rapidly to completion, unaffected by feedback), followed by a slow phase controlled by a schema that does admit error-correction by use of sensory feedback. However, Jeannerod et al. (1992) showed that reaching is subject to modification by sensory input even during the fast phase. If the target of a pointing task was perturbed at movement onset, the subject did not complete a ballistic movement toward the initial target before moving on to the new target. Rather, a smooth adjustment was made about 100 msec after target perturbation to a new trajectory terminating at the new target, without loss of accuracy. To address such data (and more), Hoff and Arbib (1993) extended the use of OPTIMIZATION PRINCIPLES IN MOTOR CONTROL (q.v.) by showing how to embed an optimality principle for arm trajectories into a controller that can use feedback to resist noise and compensate for target perturbations, and a predictor element to compensate for delays from the periphery. The result is a feedback system that can act like a feedforward system described by the optimality principle in "familiar" situations, where the conditions of the desired behavior and accuracy requirements are such that "normal" errors in execution may be ignored. However, when perturbations must be corrected for or when great precision is required, feedback plays a crucial role in keeping the behavior close to that desired, taking account of delays in putting feedback into effect.

Another claim embodied in Figure 1 is that the transition from preshaping to enclosing is controlled by, but does not influence,

A

eye

PERCEPTUAL SCHEMAS
Small Moving Objects | Large Moving Objects

MOTOR SCHEMAS
Snap | Avoid

Movement Controllers

B

eye — Pretectum

PERCEPTUAL SCHEMAS
All Moving Objects | Large Moving Objects

MOTOR SCHEMAS
Snap | Avoid

Movement Controllers

Figure 2. *A,* A "naïve" schema program that represents the perceptual and motor schemas for frog approach behavior (snap at prey) as completely separated from those for small moving objects. *B,* A schema program for approach and avoidance that takes into account data on the effect of lesioning the pretectum. In particular, the "approach schema" is *not* localized in the tectum alone since it depends on pretectal inhibition for its integrity.

the transition in the transport phase. However, data show that when the hand has unexpectedly to open wider (if object size is increased during reach) transport slows by about 200 msec, but if target location is perturbed, the hand temporarily closes so that maximum aperture is delayed as transport takes longer to reach the new target. Hoff & Arbib (1993) designed a controller for the preshape schema to tradeoff an optimality criterion needed to prevent discontinuous "jumps" in the preshape and a "cost" for having the hand open more than a certain amount. The latter yields the partial reclosing of the hand during prolonged movement caused by location perturbation. Their strategy for coordinating the motor schemas is set forth in Figure 3. Here, the Enclose schema is a replica of the Preshape schema with the only exception that its starting point is the maximum aperture achieved by the preshape schema (there seems to be a linear relation between the actual object size and the maximum aperture achieved). The coordinating schema receives from each of the constituent schemas—Transport, Preshape, Enclose—an estimate of the time that it needs to move for execution. Then, whichever schema is going to take longer, Transport or Grasp (Preshape + Enclose), is given the full time it needs, while the other schema will be slowed down to apply its optimality criterion over the longer time base. This yields a satisfactory match between data and simulation.

The implication (a truth better known in motor control than in other areas of neurophysiology) is that much is to be learned at the level of schema analysis prior to, or in concert with, the "lower level" analysis of neural circuitry. Although the hypotheses developed in this section allow us to gain insight into the interaction of a number of different processes, they also pose major challenges for further neurophysiological investigation.

Discussion

Perceptual and Motor Schemas

We have suggested that schemas provide some sort of action-oriented memory, yet have made a distinction between perceptual schemas and motor schemas. Why not combine these two constructs into a single notion of schema that integrates sensory analysis with motor control, as suggested in the earlier quote from Shallice? Indeed, there are cases in which such a combination makes sense. However, recognizing an object (an apple, say) may be linked to many different courses of action (to place the apple in one's shopping basket; to place the apple in the bowl at home; to pick up the apple; to peel the apple; to cook with the apple; to eat the apple; to discard a rotten apple, etc.). Of course, once one has decided on a particular course of action, then specific perceptual and motor subschemas may be invoked. But note that, in the list just given, some items are apple-specific whereas other invoke generic schemas for reaching and grasping. It was considerations like this that led me to separate perceptual and motor schemas—a given action may be invoked in a wide variety of circumstances; a given perception may, as part of a larger assemblage, precede many courses of action. Putting it another way, there is no one "grand apple schema" that links all "apple perception strategies" to "every act that involves an apple." At the same time, however, note that, in the schema-theoretic approach, "apple perception" is not mere categorization—"this is an apple"—but may provide access to a range of parameters relevant to interaction with the apple at hand. The *Rana* example shows this in simplest form. In Figure 2A, the two schemas at left may be combined into a single unitary prey schema and the two at right into a single unitary predator schema. However, the lesion study suggested splitting perception from action since it is recognition of the large moving object that inhibits the prey-catching schema—based on the view that tectum and pretectum are "more perceptual" and the brainstem to which they project is "more motor."

A detailed example of how schema theory extends to more "cognitive" realms than basic patterns of sensorimotor coordination is offered by the schema-based interpretation in the VISIONS computer vision system (see VISUAL SCENE PERCEPTION for references). This system shows the importance of schema theory within artificial intelligence (i.e., even when there is no claim to model the brain). Similarly, schemas have played an important role in the development of behavior-based robots (REACTIVE ROBOTIC SYSTEMS).
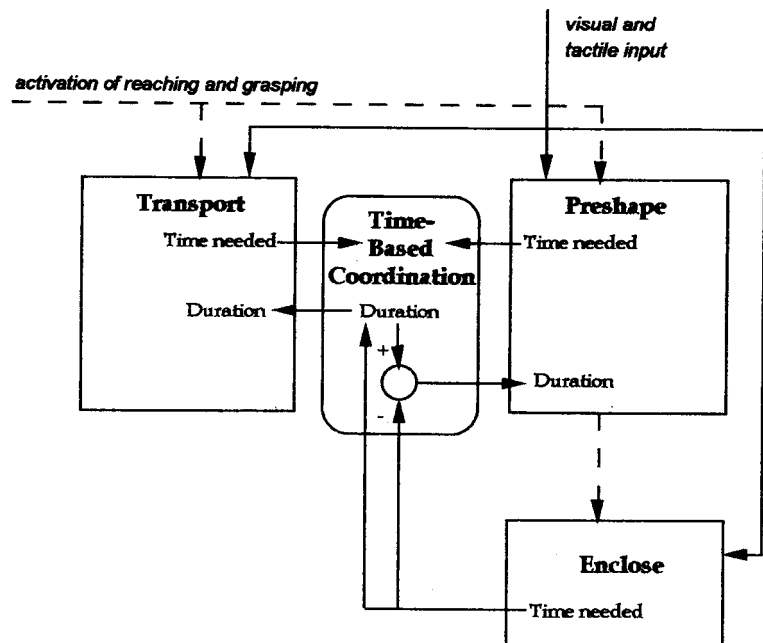

Figure 3. Feedback controllers for transport and preshape. "Co-operative computation" between subprograms is mediated by a coordinating schema ensuring that both reaching and grasping have adequate movement time (Hoff and Arbib, 1993).

Schemas and Their Assemblages Are Adaptable

Head himself considered schemas as plastic entities, which are subject to constant change, and adaptation is at the heart of Piaget's account of assimilation and accommodation. Although the examples of schemas given in the three figures above are fairly stable—as we explored the way in which schemas could be combined into coordinated control programs, and ways in which the psychological or neural correlates of such schema assemblages could be tested—it must be emphasized that schemas, and their connections with each other, change through the processes of accommodation. These processes adjust the network of schemas so that over time they may well be able to better handle a wide range of situations.

Work on HYBRID CONNECTIONIST/SYMBOLIC SYSTEMS (q.v.; see also Sun, 1995) has somewhat similar motivations to schema theory: In decomposing a cognitive model into a network of interacting processes, one may find at a given state of knowledge that quite different models will be appropriate for different components: some cognitive processes are best captured by symbolic models, some by connectionist models, and some by biologically realistic neural models. This leads to the development of hybrid systems. Schema theory is consistent with this in that it allows the schemas in an "assemblage" to be implemented in different ways so long as the input and output codes are compatible on any connection. However, it adds that what may appear to be disjoint schemas when implemented at one level may turn out to involve overlapping networks of subschemas when involved at a more detailed level (a simple example is given in Figure 2*B*). On the other hand, if we agree to the schema decomposition offered by high-level analysis, we may apply connectionist training procedures to adapt the initial schema structures if these are encoded by (artificial) neural networks.

Beyond Action and Perception

Through learning, a complex schema network arises that can mediate first the child's, and then the adult's, reality. Through being rooted in such a network, schemas are interdependent, so that each finds meaning only in relation to others. For example, a house is defined in terms of parts such as a roof, yet a roof may be recognized because it is part of a house that is recognized on the basis of other criteria such as "people live there." Each schema enriches and is defined by the others (and may change when a formal linguistic system allows explicit, though partial, definition). Though processes of schema change may affect only a few schemas at any time, such changes may "cohere" to yield dramatic changes in the overall pattern of mental organization. There is change yet continuity, with many schemas held in common, yet changed because they must now be used in the context of the new network. Arbib and Hesse (1986) offer an epistemology rooted in this view of schema theory, and show how it may be expanded to link "schemas in the head" with the "social schemas" that form the collective representations (to use Durkheim's phrase) shared by a community. Schemas have also been used in a "computational, neo-Piagetian" approach to language acquisition and may also be used in modeling language processing with special attention to the links between action, action and object recognition, and language (see LANGUAGE EVOLUTION: THE MIRROR SYSTEM HYPOTHESIS) and in relating these processes to neural schemas.

Road Maps: Artificial Intelligence; Psychology
Related Reading: Artificial Intelligence and Neural Networks; Compositionality in Neural Systems; Hybrid Connectionist/Symbolic Systems; Multiagent Systems

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