

A THEORY OF THE REPRESENTATION,  
ORGANIZATION AND TIMING OF ACTION  
WITH IMPLICATIONS FOR SEQUENCING DISORDERS

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This paper develops a theory for explaining how the components of everyday actions are sequenced and timed (e.g., typing, hammering a nail). Under the theory, a hierarchy of content nodes represents the form of a pre-planned action, while an independently stored set of (sequence) nodes codes the serial order rules for the action and determines sequence in the final output. Another independently stored set of (timing) nodes determines when and how rapidly these action components become activated. The theory also postulates a superordinate organization of content, sequence and timing nodes into systems. Each system has unique characteristics and rules of its own and is independently controllable, enabling thought of particular kinds without the occurrence of action. Four systems are discussed in detail: the muscle movement system, the movement concept system the action plan system and the pragmatic system implications of the theory for several related issues are discussed: the physiological bases for action, errors in action of normals and apraxics, the nature of attention and intention, and the relations between knowledge, memory, action and speech.

The present chapter examines the question of how everyday behaviors are planned, represented in the brain and executed as sequences of movement. It outlines a theory of the organizational principles underlying skilled behavior and then examines the predictions of this theory for the nature of errors in the behavior of normals and apraxics suffering from brain damage. The theory places special emphasis on the sequencing and timing of behavior and was developed originally to explain how words, syllables and phonemes are sequenced and timed in producing speech (see MacKay, 1982). The present study extends the theory by specifying possible neural mechanisms underlying the sequencing and timing of not just speech, but actions involving the arms, hands and fingers as well as the entire body.

The main emphasis of the chapter is the cognitive control of action. The goal of the theory is a detailed specification of the relations between cognition and action. The main problem confronting such a theory is the interaction paradox: In the past, cognition and action have been viewed to involve fundamentally different components and principles of operation, so that the interaction between the two is paradoxical. That is, most theories assume two fundamentally different types of knowledge: cognitive knowledge about actions e.g., lighting a candle and motor

knowledge; e.g., the timing, force and direction of particular muscle movements for lighting a particular candle in a particular position. The distinction between these two types of knowledge can be illustrated by the doubly dissociable symptoms of paralysis on the one hand and apraxia on the other (see Roy, 1982). A patient with apraxia can perform the movements for an action such as lighting a candle, but lacks the cognitive control mechanisms that enable the execution of the movements in the appropriate sequence and at the appropriate time. On the other hand, patients with paralysis know what to do and recognize the action when someone else performs it appropriately but cannot move their muscles to perform the action themselves.

Differences between motor and cognitive knowledge are also apparent to introspection. We are generally unaware of how we move our muscles but are usually conscious of what we are doing at a cognitive level. For example, in carrying out an action such as lighting a candle, we can express in words that we are lighting a match and applying it to the wick of the candle. Given these differences between cognitive and motor knowledge, then, how do the seemingly incompatible languages of action interact in the execution of behavior? The theory developed here is designed to resolve this interaction paradox by treating cognitive and motor knowledge within the same framework, with similar underlying components and principles of operation.

Other studies of the neural mechanisms underlying sequencing have concentrated on the locus of the mechanisms for sequencing and timing. For example, Kolb and Whishaw (1980) point to the left cerebral cortex as the usual locus for constructing sequences of voluntary movements. The present study attempts to be precise not so much on the issue of where the processes of sequencing and timing take place, but more on exactly how timed sequences of voluntary movement are represented and executed and the neural principles underlying these execution processes.

We illustrate the theory initially by means of examples from the skill of Morse code and then apply the theory to data on everyday skills such as typing and driving a car.

#### Why Morse code?

Although there have been many first class studies of Morse code, extending from Bryan and Harter (1899) to Klapp and Wyatt (1979), the experimental literature on piano playing is much more extensive. Moreover, typing is a much more common skill than Morse code, which seems destined to become extinct as a natural skill in the not too distant future. We therefore wish to justify our choice of Morse code rather than typing or piano playing as an initial source of examples for a theory of the control of skilled manual behavior.

Morse code has advantages over both typing and piano playing for anyone with a general interest in the timing and sequencing of behavior. First, Morse code shares formal similarities with both typing and piano playing that neither shares with the other. Like typing, the goal in sending Morse code is to maximize speed and minimize errors, but like piano playing, the motor components (*dit*, *dah* and pause) must be precisely timed, an important consideration for anyone interested in the timing of behavior.

Movements for Morse code are readily quantified and involve specifiable muscles, whereas typing movements involve complex distributions of work by the many interacting muscles which control the dynamic links between the arm, elbow, wrist

and hands. Only difficult-to-measure, high-speed films can currently capture the movements themselves, let alone the underlying pattern of muscular activation (see Norman and Rumelhart, 1983). Typewriting movements are also variable across individuals and surprisingly large in number: if any pair of the 48 keys of the standard typewriter, taken in either order, allowed only a single movement, there are millions of possible movements. To complicate matters further, each of these movements can both overlap and interact with upcoming movements in the sequence. The result is a cacophonous flow of fingers moving in many directions at once, a phenomenon best described metaphorically as resembling "sea grass weaving in the waves, bending this way and that, all in motion at the same time." (Norman and Rumelhart, 1983, p.47). In contrast, Morse code movements are few in number, discrete in space and time, and virtually invariant across repetitions and between individuals. Such constancy and simplicity is a major advantage for anyone interested in either the muscle movements themselves or, as in our case, the mechanisms responsible for the cognitive control of the skill.

Even so we will see that Morse code is surprisingly complex. It raises issues which concern not just the representation, sequencing and timing of skilled behavior but the nature of memory and cognition in general. Indeed, what follows is not a theory of Morse code. Our treatment of this seemingly simple skill is not meant to be exhaustive. For example, we largely ignore certain aspects of the code (e.g. nonalphabetic punctuation and numerals), and we ignore the mechanisms involved in the actual muscle movements, in the perceptual encoding of the letters to be sent and in the perception of input strings, including the perceptual monitoring that occurs during output. What follows is instead a general theory of the cognitive control mechanisms underlying the timing and sequencing of skilled behavior, using examples from the skill of Morse code for purposes of illustration.

### The Theory

A viable theory of action must account for three basic aspects of skilled behavior. First what are the components for organizing actions and how do they combine to allow an infinity of possible sequences. Second, what processes enable these components to become activated in the proper sequence and at the proper time in producing an action. And third, what mechanisms are responsible for the temporal organization of the action, its overall rate and the relative timing of its components. The present chapter deals with each of these aspects in turn, beginning with the components and how they interact.

The basic components for organizing actions in the theory are nodes. Each node consists of one or more neurons but we will forego discussion of the possible neural instantiation of nodes until the end of the chapter. We focus here on the abstract or theoretical properties of nodes. Nodes have three general properties which are relevant to the organization and execution of behavior: activation, priming and linkage strength.

#### Activation

Activation of a node is all-or-none in degree and is self sustained, continuing for a specifiable period of time, independently of the state of the source that led originally to activation. Activation is initiated by means of a special activating mechanism and is terminated by inhibition, usually a process of self-inhibition.

Behavior occurs if and only if the lowest level nodes within the muscle movement system become activated. Activation of most nodes is serial in nature and the

special activating mechanism determines when and in what order the nodes controlling an action become activated. During its period of self-sustained activation, a node strongly and simultaneously primes or readies for activation all nodes connected directly to it.

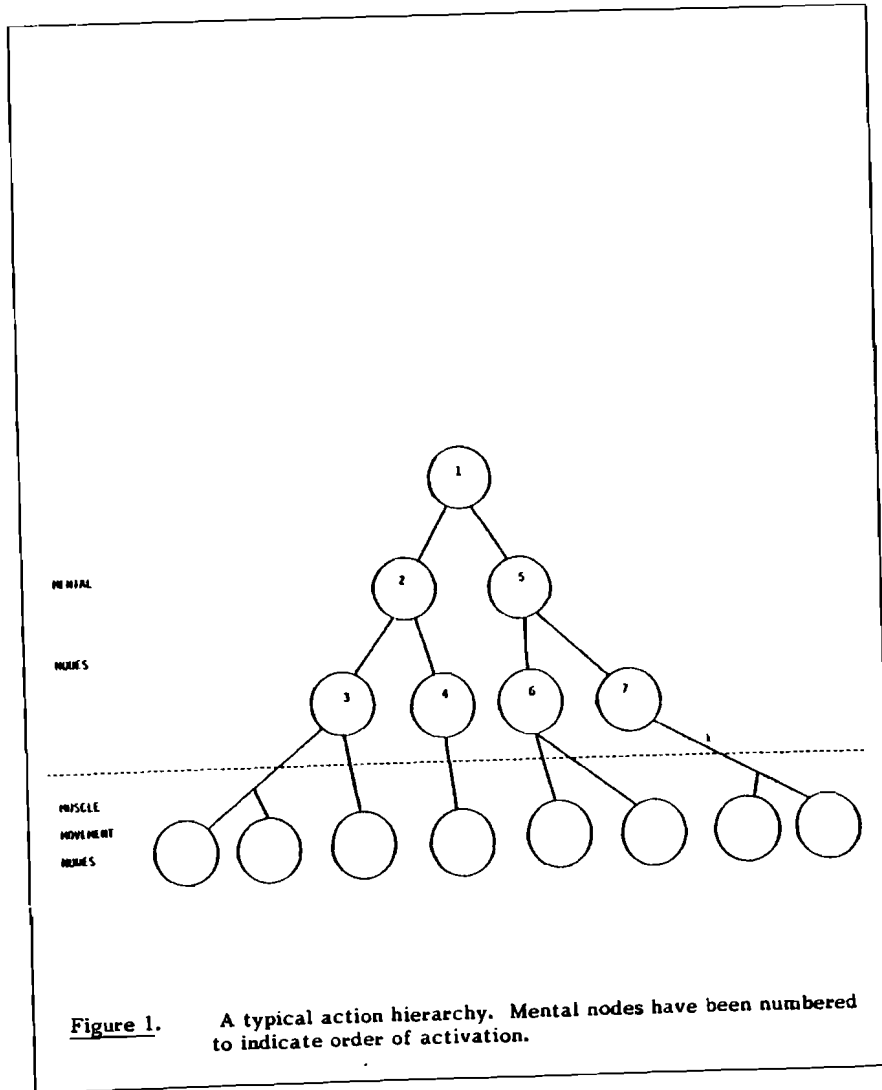
**Priming.** Priming refers to transmission across a connection which readies a connected node for activation. The level of priming of a node varies in degree from a spontaneous level up to asymptotic level. The level increases via spatial summation (across all simultaneously active connections) and via temporal summation (during the period that any given connection remains active). Each node has hundreds of connections and continually receives some relatively constant degree of priming from these connected nodes. This contextual or background priming constitutes the spontaneous or resting level of the node and remains relatively constant, varying mainly with the arousal and anxiety of a subject at any point in time.

Priming arrives in two degrees: first-order and second-order. A node receives first-order priming from an activated node and second-order priming from a node which is receiving first-order priming but has not itself become activated. Second-order priming summates to a lower asymptotic level and at a slower rate than first-order priming.

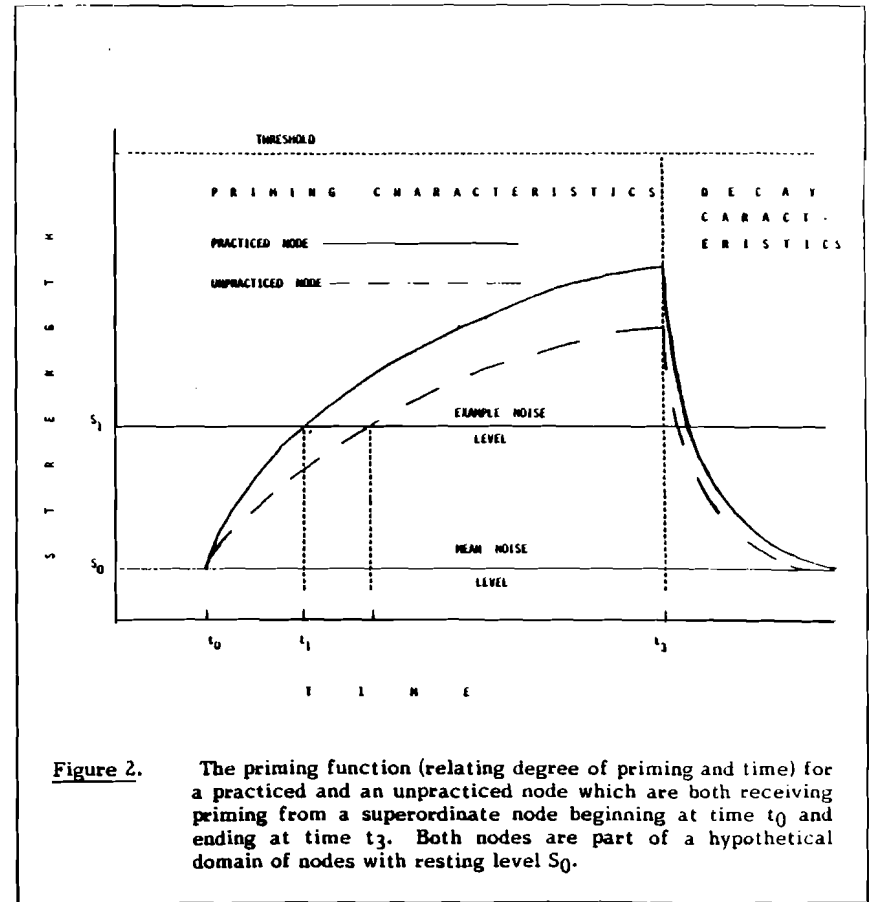
Connections between nodes are both many-to-one and one-to-many. For a many-to-one connection from say Nodes A,B,C,D,... to Node Z, Node Z receives first and second order priming in direct proportion to the activity of A,B,C,D,... However, priming from any number of other nodes over any length of time only summates to some subthreshold, asymptotic level and cannot directly cause activation of a connected node: As already noted, a special activating mechanism is required for activation.

Unlike activation, priming is automatic and parallel in nature, requiring no special mechanism to determine when and in what order it occurs. Also unlike activation, priming never results in behavior: no movement occurs when the lowest muscle movement nodes become primed. Again unlike activation, priming is neither self-sustaining nor terminated via inhibition. For example, consider a one-to-many connection between an arbitrary Node X to its connected Nodes (E,F,G,H,...): when X becomes activated, it starts priming its connected nodes (E,F,G,H,...) but if X ceases its activity, priming of E,F,G,H,... stops accumulating and begins to decay to its resting level.

The way that priming summates has important implications for the theory. One is a faster potential rate of output for the later components of a pre-planned output sequence. By way of general example, consider the nodes in Figure 1 (from MacKay, 1981) which illustrate a typical action hierarchy (the set of mental and muscle movement nodes directly controlling an output sequence). The appropriate order for the lowest level output components corresponds to the left to right axis in the figure and the mental nodes controlling the action must be activated in the order shown so that these components can be executed in proper sequence. Activating Node 1 simultaneously primes Node 2 and 5, but since 5 can only be activated after 2, 3 and 4 have been activated, the priming of 5 constitutes "anticipatory priming" which summates during the interval that Nodes 2, 3 and 4 are being activated. Anticipatory priming makes it easier to activate the later components in a pre-planned output sequence, thereby speeding up the potential rate of output. Anticipatory priming likewise reduces the probability of error for these later components, since as discussed below, increased potential rate and reduced probability of error derive from the same underlying mechanism and are therefore coreferential in the present theory (see MacKay, 1982).



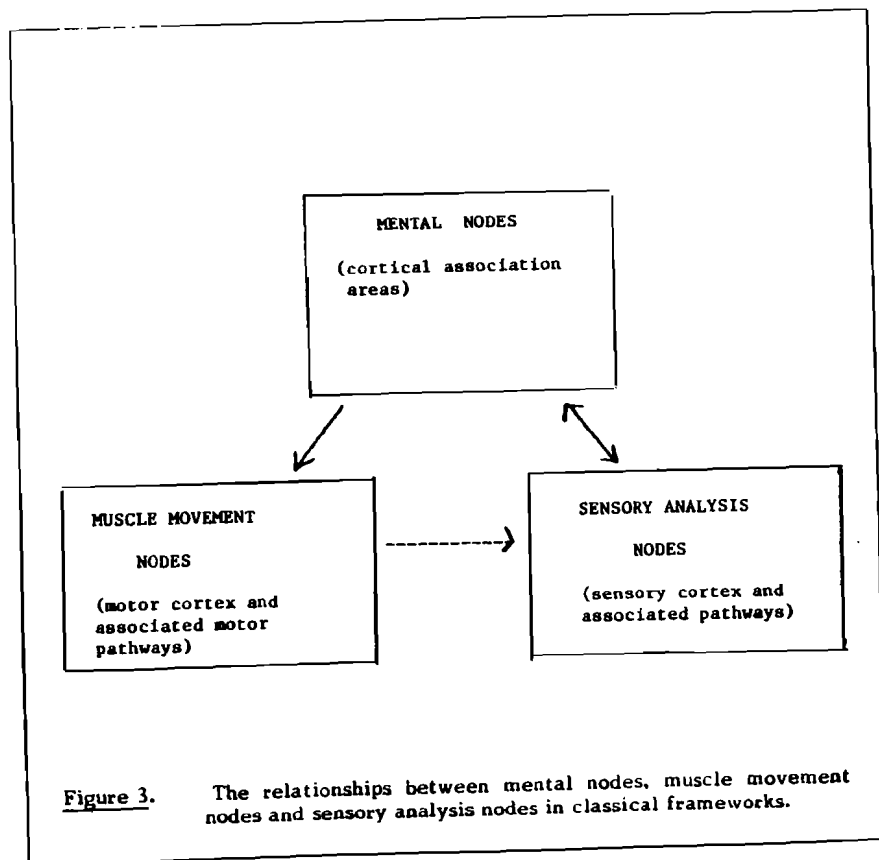
**Linkage strength** The priming function in Figure 2 illustrates how the level of priming of a node summates over time from onset of priming up to asymptotic level. As discussed above, the asymptotic level varies with the degree of activity and number of connections simultaneously contributing priming. However, the asymptotic level and the rate of summation per unit time across any one connection (represented by the slope of the priming function) also vary with practice, i.e., the frequency with which the node has been activated via that particular connection in the past. Thus, repeated activation increases linkage strength, reflected in a higher



asymptotic level of priming and a faster accrual of priming per unit time across that one particular connection. Linkage strength is a long-term characteristic of a connection and must be contrasted with the degree of priming, which is a short-term characteristic of a node, reflecting the extent to which input from any number of connections has summated on that node at any particular point in time.

**The Representation of Actions: Content Nodes**

Content nodes are the theoretical units representing the form or components of an action and have traditionally been divided into the three categories illustrated in Figure 3: muscle movement nodes, sensory analysis nodes and mental or association nodes. Muscle movement nodes represent patterns of muscle movement and are located in the motor cortex and associated motor pathways.



Sensory analysis nodes represent patterns of sensory experience and are located in the sensory cortex and associated sensory pathways. Mental nodes are located within the classical association areas and represent neither muscle movements nor sensory experience but concepts such as 'I lift hammer'. Such concepts are neither sensory nor motoric but play a role in both input and output processes. For example, a node representing the concept 'I lift hammer' constitutes not only the instigator of such an action, but also the highest level perceptual representation of one's own behavior of lifting a hammer. That is, nodes within the visual system (representing e.g., the visual appearance of the arm and hammer) and within other sensory systems (representing e.g., the felt position of the arm) all contribute input to the 'lift hammer' node. However, this node is not responsible for initiating a verbal expression such as 'I am lifting a hammer' or for comprehending such an expression via auditory or other sensory channels. As discussed below, verbal systems are functionally independent of the action systems.

Only the lowest level muscle movement nodes represent specific actions. All other content nodes represent classes of action. For example, the content node representing the concept of lifting a hammer becomes activated whenever a ham-

mer is lifted, whether quickly or slowly, a long distance or a short distance, with the wrist locked or unlocked. These and other ways of lifting a hammer constitute the class of actions the node represents, and the higher the node in the action hierarchy, the larger this class of potential actions.

To illustrate how content nodes are connected to one another, consider the generation of a Morse code dit by a complete beginner. The content node *dit* (send) represents the entire action and is connected with two other mental nodes, say *key down* (press) and *key up* (release) (see Figure 4). These in turn are connected with muscle movement nodes for flexing and extending the muscles of say the right index finger and wrist. These muscle movement nodes are responsible for the actual press and release of the key and are the only truly necessary components for the action. However, without a 'dit' node, the actions of pressing and releasing a telegraph key cannot be represented or understood as a unitary behavioral component with its own characteristic temporal and sequential properties (discussed below).

#### The Sequencing of Action: Sequence Nodes

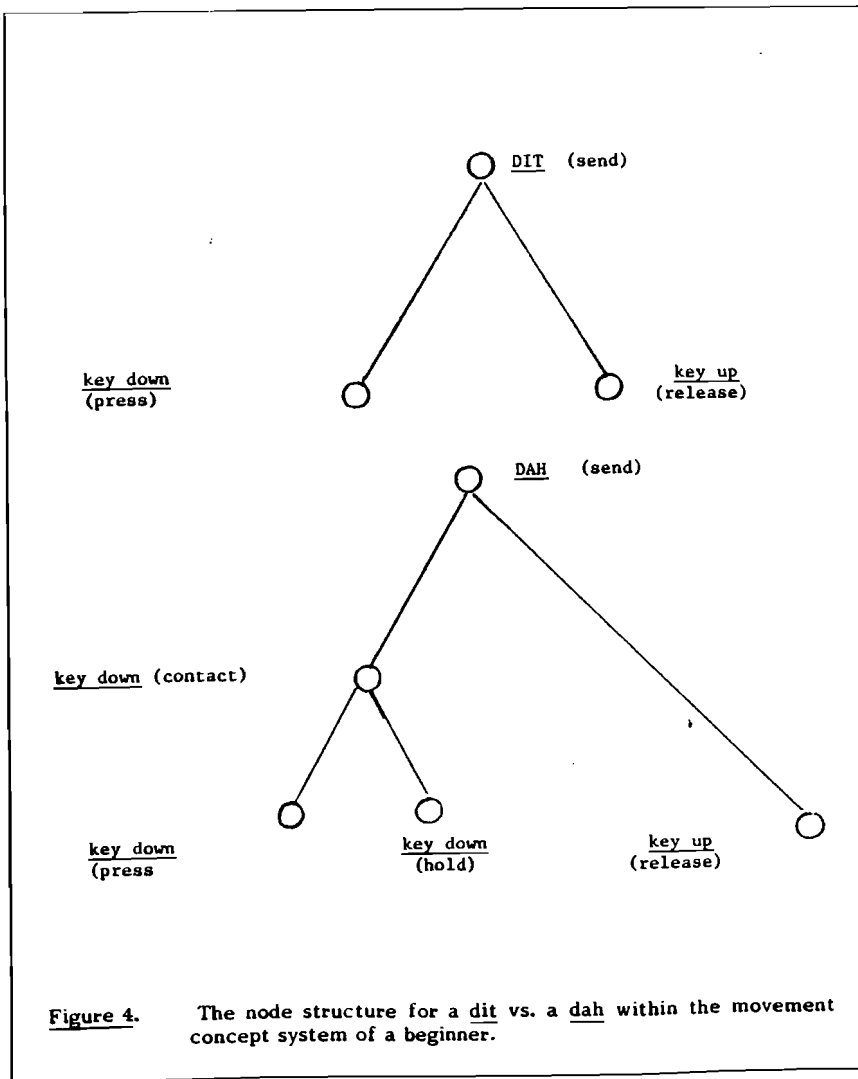
Sequence nodes are the special mechanisms for activating content nodes and are distinguished from content nodes by capitalization in the examples to follow. As discussed below, sequence nodes also organize the content nodes into sequential domains and determine the serial order in which the content nodes become activated.

**Sequential domains.** Each sequence node has a one-to-many connection with a domain of content nodes. By way of illustration, consider again the rank beginner who can send only a single dit or a single dah at any one time, unlike the expert who can send long strings of letters from memory. The content nodes representing the beginner's actions can be represented *dit* (send) and *dah* (send) where the class of actions the content node represents is indicated in italics and the domain they belong to in brackets. These content nodes both send and receive a connection from their sequence node SEND (see Figure 4).

*Dit* (send) is also connected to two content nodes, *press key* (press) and *release key* (release). Each of these content nodes have similar connections to and from their sequence nodes, PRESS and RELEASE (see Figure 4). These sequence nodes have much more extensive domains, however. The domain of PRESS, for example, includes nodes representing all the ways of pressing a key; with either hand, with the thumb, with the forefinger or middle and ring fingers in combination. Stated more generally, a sequential domain consists of the set of responses that are possible within a given sequential environment, here PRESS followed by RELEASE or by HOLD and then RELEASE, the only sequential relationships possible among these elements. Phrased in terms of nodes, a sequential domain consists of the set of content nodes serving the same sequential function and activated by the same sequence node.

As noted above, labels such as *press key* (press) are not intended to carry everyday English meaning or connotation but only to distinguish one node from another within the action system.

**Activation and the most-primed-wins principle.** When activated, a sequence node can be considered to deliver extremely strong priming to the domain of content nodes connected to it. This priming summates quickly over time with the level of existing priming in these nodes until one of them reaches threshold and becomes activated. This activated node will invariably be the one with the greatest degree of priming prior to receiving input from the sequence node, so that content nodes



can be said to become activated via a 'most-primed-wins' principle. As we will see, sequence nodes themselves become activated via this same principle in the case of automated behavior.

What nodes receive the most priming and become activated under the most-primed-wins principle? Normally, of course, the node with the most priming in its domain is the one that has just received priming from its superordinate node in the action hierarchy. For example, dit (send) in Figure 4a will simultaneously prime

(top-down) key (press) and key (release), so that each of these nodes should have greatest priming in their respective domains. Thus, when PRESS is activated, key (press) will reach threshold before any other node in the (press) domain. Once activated, a content node quickly quenches or inhibits its sequence node so that no other node in its domain can become activated.

**Serial order.** Classes of actions such as (press) and (release) are governed by serial order constraints: Pressing must precede releasing in the operation of a Morse key or any other device. Connections between sequence nodes represent these serial order constraints and ensure that the content nodes are activated in proper sequence. Specifically, an inhibitory connection between PRESS and RELEASE could ensure the precedence relation between these sequence nodes. Under this proposal, PRESS inhibits RELEASE and dominates in degree of priming when PRESS and RELEASE are simultaneously primed. However, once PRESS has been activated it returns quickly to resting level. RELEASE therefore becomes released from inhibition and dominates in degree of priming, thereby determining the sequence (press + release) for movements of this type.

#### The Timing of Actions: Timing Nodes

Timing and sequencing are closely related processes in the theory. Timing nodes both activate the sequence nodes and determine the rate of behavior. Specifically, timing nodes have a one-to-many connection to the sequence nodes within a system (discussed below) so that when the timing node becomes activated, it strongly primes its connected sequence nodes until it activates the most primed one. The most-primed-wins relationship between timing and sequence nodes can thus be seen to resemble that between sequence and content nodes. The difference is that sequence nodes do not determine what timing nodes become engaged or disengaged. To engage or disengage the timing nodes a high level decision within the pragmatic system (discussed below) is required.

This decision calls for a certain rate of speech or action (e.g. fast or slow). The possible rates are represented by an array of timing nodes each with different endogenous rhythm. When one of the timing nodes becomes engaged, its output is applied to the sequence nodes. The pulses from the timing node therefore determine when the sequence nodes become activated, which in turn determines the temporal organization of the output.

This view of timing leads to some interesting predictions. One is that timing and sequencing are closely related but independent processes. This means that the same sequence of actions can be produced with different timing characteristics or more interestingly, a sequence of actions can be altered while its timing remains intact. This latter phenomenon has been observed in recent studies of transposition errors in skilled typing, e.g. the mistyped as hte by a competent typist. Grudin (1983) found that the pattern of keystroke intervals in a word typed correctly is largely preserved when a transposition error is produced: the wrong letters are typed at the right times, indicating that the order and timing of the letters are independent.

Timing may also be independent of particular motor modalities since simultaneous activities using different effector systems often exhibit the same timing properties. The correspondences that have been observed in the timing of simultaneously generated speech and hand movements are one example. Another is Lashley's (1951) observation that salient rhythms tend to impose their timing characteristics on many different output systems which are active at the same time. Thus a salient musical rhythm can cause a listener to fall in step, speak, gesture with the hands,

and even breathe, all in time with the band. The simultaneous temporal coordination of our arms and legs in activities such as swimming is another example. All of these examples may arise from the coupling of different effector systems to the same timing node.

Timing nodes also play an important role in organizing the sequence and content nodes into systems, which are described in detail below. For example, the sequence and content nodes in the examples in Figure 4 are part of the action plan system, and the sequence nodes for this system are connected with a movement concept timing node. By way of contrast, sequence nodes within the muscle movement system are connected with a muscle timing node. These different timing nodes have different average rates of activation. For example, a movement concept timing node has a slower average rate of activation than a muscle timing node, since muscle flexions and extensions are produced faster than the larger behavioral chunks represented by movement concept nodes such as dit (send).

Timing nodes can, of course, only activate a sequence node that has been primed or readied for activation. If no sequence node has been primed, timing pulses can be repeatedly applied without activating any nodes whatsoever. This enables the timing nodes for different systems to begin emitting impulses at the same time. The goal-setting mechanism in the pragmatic systems simply calls for an action sequence at some overall rate and onset time without the need for an additional mechanism to start (and stop) the timing nodes for different systems in cascade, beginning with the timing node for higher level systems such as the movement concept system, and followed in succession by lower level systems, until the muscle timing system has been activated.

#### A Specific Example

How the timing and sequence nodes interact to determine whether, when, and in what order the content nodes controlling an action become activated is similar for every node within every system. We can therefore illustrate these processes by means of a single example from within the movement concept system: the activation of key (press) and key (release) in producing a novice dit on a Morse key. The reader is referred to MacKay (1982) for a more detailed account and hand simulation of a similar sequence of execution processes in speech production.

The content, sequence and timing nodes in question appear along with the connections between them in Figure 5. Unbroken connections are excitatory and the dotted connection between sequence nodes (in circles) is inhibitory. Some of these connections are built-in and others are formed by a process discussed in detail in MacKay (Note 1). Here we concentrate on the execution processes following the process of connection formation.

The decision to produce a dit simultaneously primes the movement concept dit (send) and starts the movement concept timing node. The first pulse from the timing node activates SEND because of its priming from dit (send). This causes activation of dit (send) which simultaneously transmits first-order priming to key down (press) and key up (release), and second-order priming to their sequence nodes PRESS and RELEASE. The inhibitory link between PRESS and RELEASE temporarily reduces the priming level for RELEASE so that PRESS becomes activated following the first pulse from the timing node. PRESS therefore primes every node in its (press) domain, but one of these, key down (press), having just been primed, has the most priming, reaches threshold soonest, and becomes activated under the most-primed-wins principle (see Figure 5).

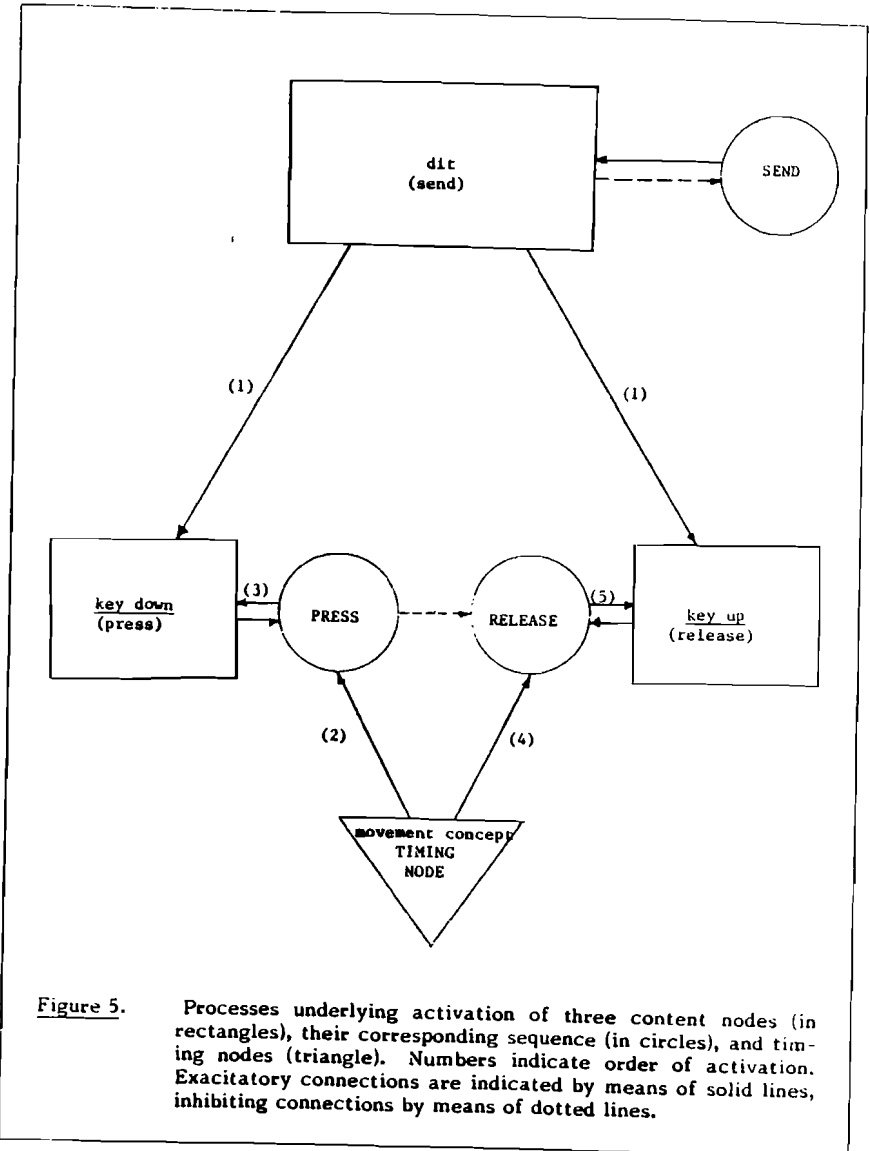


Figure 5. Processes underlying activation of three content nodes (in rectangles), their corresponding sequence (in circles), and timing nodes (triangle). Numbers indicate order of activation. Excitatory connections are indicated by means of solid lines, inhibiting connections by means of dotted lines.

Following activation, PRESS returns quickly (via self-inhibition) to its subthreshold resting level. This releases the inhibition on RELEASE which now dominates in degree of priming and becomes activated with the next pulse from the movement concept timing node. RELEASE therefore primes the entire domain of (release) nodes, but having just been primed, key up (release) has more priming than any other node in the domain, and becomes activated under the most-primed-wins principle.

### Generalizations of the Theory

So far we have developed a detailed theory for novice behavior with the following characteristics; a nonpermutable order of activation for the components (e.g. press must precede release), limited generality to the sequential rules such as (press + release), no nonsequential or simultaneous components, and no contextual dependencies in the coding of the components. In the present section we extend the theory to cover expert behavior with permutable behavior sequences, simultaneous components, contextually dependent coding and sequential rules having unlimited generality.

#### Expert behavior

Expert behavior differs in at least two respects from novice behavior under the theory. First, identical nodes with identical connections can be activated more quickly in expert behavior because of the increased linkage strength between the connections (see MacKay, 1982). Second, many more mental nodes are involved in the organization of expert behavior. For example, compare the novice vs. expert generation of the Morse sequence (dit dit dit dah) for the letter (v). The nodes subordinate to the individual dit and dah nodes (including the ones controlling muscle contractions) are identical for both novice and expert. However, the novice must send the sequence as four separate units, activating one after the other in turn, whereas the expert has additional mental nodes which organize the behavior into a single, automatically executed unit.

These additional mental nodes for generating expert Morse code can be organized in several possible ways. The next two sections describe one of these ways, and the section on individual differences describes another. Here it is only necessary to note that in either of the ways, a single node represents each letter. Figure 6 represents the content and sequence nodes for the expert (Version 1) generating the letter V. The letter node represented I send the letter V (letter) or V (letter) for short is activated to initiate the entire sequence (dit dit dit dah) and is part of a domain consisting of the 26 alphabetic letters, an organization with consequences for the nature of the errors that experts make. As discussed below, actions substituted in error almost invariably belong to the same sequential domain so that experts sometimes substitute one letter for another, an error that is out of the question for the novice. Grudin (1983) noted several other differences in the errors of novice vs. expert typists and these differences can be explained in a similar way within the present theory.

**Context-dependent coding.** Another difference between the expert and novice is that expert coding is context-dependent. Thus a dit in expert Morse code represents an E if followed by a space, and I if followed by another dit, an S if followed by two other dits or a V if followed by a double dit and a dah.

Sequence is, of course, the essence of this context-dependent code. For example, three dits followed by dah represent V, but three dits preceded by dah represent B. In the description that follows, the components making up a letter have a control structure sensitive to the sequential pattern for the entire letter. We assume that runs are the primary components in this sequential pattern, i.e., single, double, triple or quadruple elements. Thus, V (dit dit dit dah) consists of a triple dit and a dah. Expert Version 1 also codes complex doubles containing intervening elements, represented here in brackets. Thus, dit ( ) dit represents a double dit enclosing a single, double, triple, or quadruple dah as in dit dah dit (R), dit dah dah dit (P), and dit dah dah dah dah dit (apostrophe).

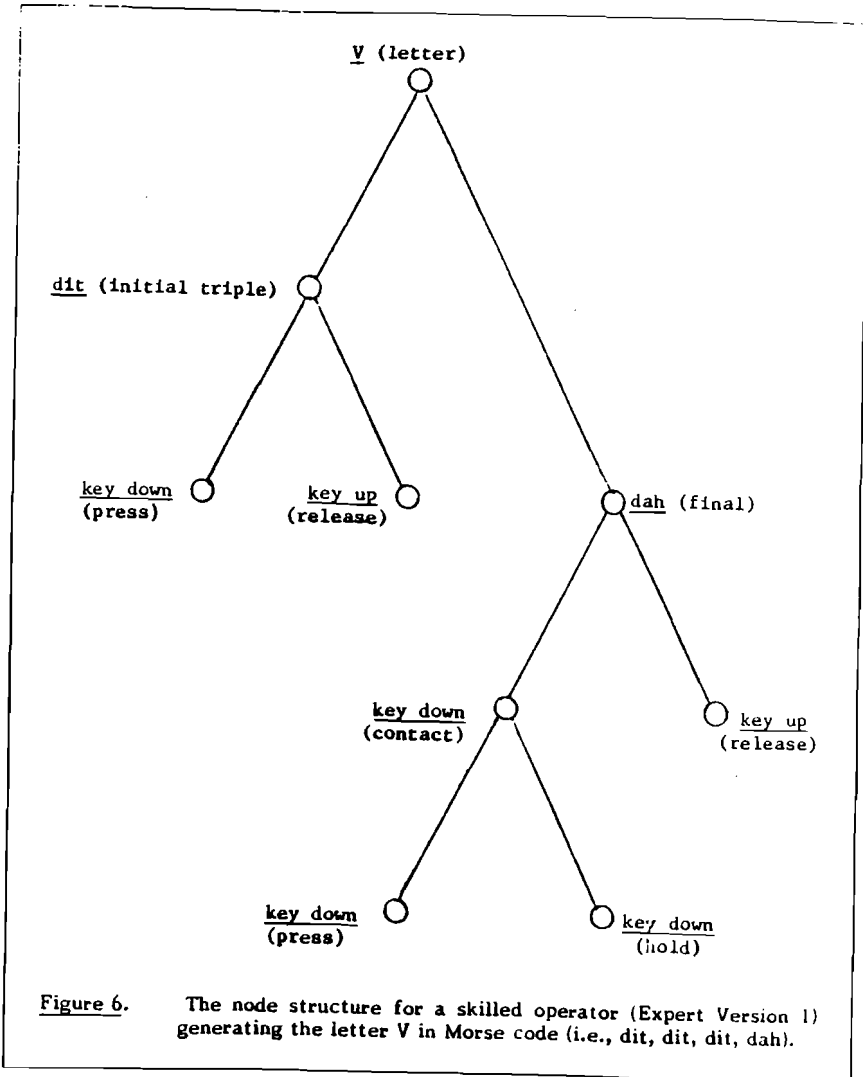


Figure 6. The node structure for a skilled operator (Expert Version 1) generating the letter V in Morse code (i.e., dit, dit, dit, dah).

Runs of this sort suffice to describe 21 of the 26 letters. The remaining 5 letters, and 4 of the punctuation marks involve alternations i.e., (dit) or (dit dah) dit. For example, dah dit dah dit (C) is a double (dah dit) and dit dah dit dah dit dah (period) is a triple (dit dah). These 'alternation' units can be considered secondary components, derived after the runs have been analyzed or extracted.

In Table 1 we list the complete set of superordinate content nodes (excluding the letter nodes themselves) that differentiate the expert from the novice under this

analysis. Using these nodes, Morse code can be generated automatically without paying attention to the sequence of operations below the level of the letter. If the letters are input in proper sequence, the preformed connections automatically determine the sequence of the lower level units in the sequence of action.

Other subtle details are required for a complete description of skilled Morse code and these subtleties predict further differences in the errors of experts vs. novices. Here, however, we wish to make a more general point. Although the expert makes use of additional content nodes, the sequence nodes and sequential rules (connections between sequence nodes) for controlling these additional nodes are simple and few in number. Given the content nodes described above, the only sequential rule required to generate all 26 letters is (initial + final + pause).

The present analysis of context-dependent coding can be contrasted with those of Wickelgren (1979) for behavior in general, and Norman and Rumelhart (1983) for skilled typing. Wickelgren (1979) was the first to emphasize that the nodes coding a complex action are sensitive to their sequential environment. In Wickelgren's proposal as many unique units are required for coding a given element of behavior as there are contexts in which the element can occur, where context refers specifically to the elements immediately preceding and immediately following a given element rather than to the sequential pattern of an entire letter as discussed above. Thus, under Wickelgren's proposal, skilled Morse code requires 9 dah nodes and 9 dit nodes. If #, . and \_ represent a pause, a dit and a dah in immediately adjacent contextual slots, then the 9 dits can be represented # dit #, # dit ., # dit \_, . dit #, . dit ., dit #, \_ dit #, \_ dit . and \_ dit . Altogether then, there are 18 context-sensitive nodes which become linked by means of unidirectional associations to give the sequence of components for a letter.

The present theory of context-dependent coding involves a much more abstract or conceptual representation of behavior than Wickelgren (1979). The units represent natural groups such as a triple dit that people seem to use in both sending and receiving Morse code. The present theory also predicts errors resembling the ones that actually occur, e.g., the doubling or tripling of the wrong element, whereas the Wickelgren theory has difficulty explaining errors of any sort in Morse code and predicts errors in other behaviors such as speech which simply never occur (see MacKay, Note 1).

The mechanism for sequencing behavior also differs in the two theories. As discussed below, the present theory uses general sequential devices such as DOUBLE and TRIPLE which can apply to any element whereas the Wickelgren theory requires a unique sequential connection for each and every pair of elements.

#### Hierarchical relations among sequence nodes

Expert generation of Morse code serves to illustrate a further extension of the theory: hierarchical relations among sequence nodes. In the representation of expert Morse code discussed above, a single node, V (letter), represents the sequence dit dit dit dah and is connected to two subordinate nodes; dit (initial, triple) and dah (final). Dit (initial, triple) is connected to two sequence nodes, INITIAL and INITIAL TRIPLE which are hierarchically related in the manner illustrated in Figure 7. Thus INITIAL TRIPLE is a superordinate sequence node which becomes activated at the same time as its subordinate sequence node INITIAL and further primes INITIAL following its first and second activation. However, INITIAL TRIPLE is connected to a counter which enables it to quench rather than further prime INITIAL, following the third activation, so that FINAL can become activated and the sequence completed.

Table 1

Content and sequence nodes for generating expert morse code

#### Expert Version 1

<u>Content Nodes</u>	<u>Example Letters</u>
1. dit (initial)	dit dah dit dit (L)
2. dit (final)	dit dit dah dit (F)
3. dit (initial, double)	dit dit dah (U)
4. dit (final, double)	dit dah dit dit (L)
5. dit (initial, triple)	dit dit dit dah (V)
6. dit (final, triple)	dah dit dit dit (B)
7. dit (quadruple)	dit dit dit dit (H)
8. dit (initial, alternate)	dit dah dit dit (L)
9. dit (final, alternate)	dit dah (A)
10. dah (initial)	dah dit dit dit (B)
11. dah (final)	dah (T)
12. dah (initial, double)	dah dah dit dah (Q)
13. dah (final, double)	dah dah (M)
14. dah (initial, alternate)	dah dit (N)
15. dah (final, alternate)	dah dit dah dit (C)

#### Expert Version 2

1. INITIAL
2. FINAL

<u>Content Node</u>	<u>Superordinate Sequence Nodes</u>
1. dit (initial)	1. INITIAL DOUBLE
2. dit (final)	2. INITIAL TRIPLE
3. dah (initial)	3. FINAL DOUBLE
4. dah (final)	4. FINAL TRIPLE
	5. FINAL QUADRUPLE

#### Individual differences

As a general rule, individual differences increase with the degree of skill: the greater the prior practice, the greater the individual differences. This general rule is well documented in the case of skilled typing (see Grudin, 1983 and Gentner, 1983 for example) and almost certainly applies to the generation of Morse code as well. What accounts for this relationship between skill and individual differences? The reason under the theory is that with practice, many different node structures, each

with their own special advantages and disadvantages can be formed to generate the



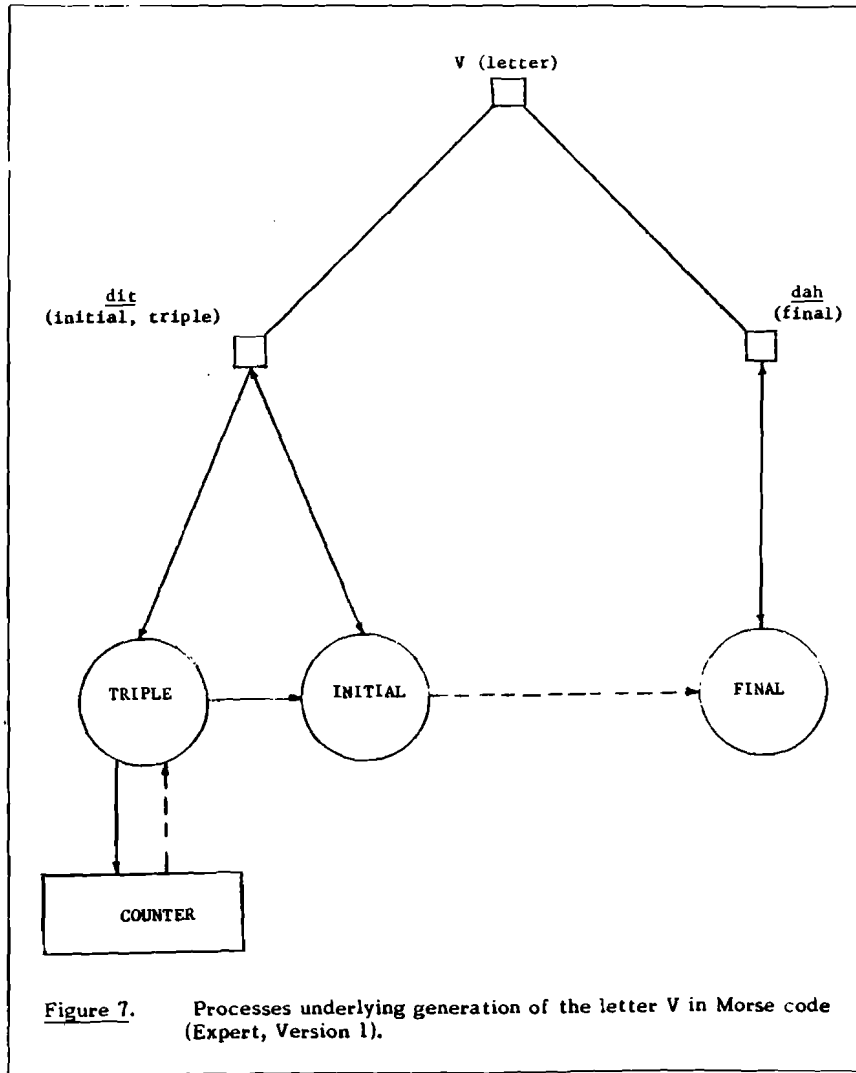


Figure 7. Processes underlying generation of the letter V in Morse code (Expert, Version 1).

same final output (e.g. sequence of key presses).

To illustrate this point, we describe an alternative and in some ways simpler node structure for generating an expert V. This representation (Expert, Version 2) shifts the burden of sequencing to superordinate sequence nodes and away from the content nodes. Not counting the muscle movement nodes or the letter nodes themselves, only 11 nodes are required to generate all 26 letters: 4 content nodes, 2 sequence nodes, and 5 superordinate sequence nodes (see Table 1.). The connections

in some ways more complex, however. Thus, V (letter) connects with dit (initial) with INITIAL TRIPLE, as well as dah (final) (See Figure 8.). INITIAL TRIPLE is superordinate sequence node which is connected with INITIAL and a counter node which enables INITIAL to become activated three times in the same way as for Expert Version 1.

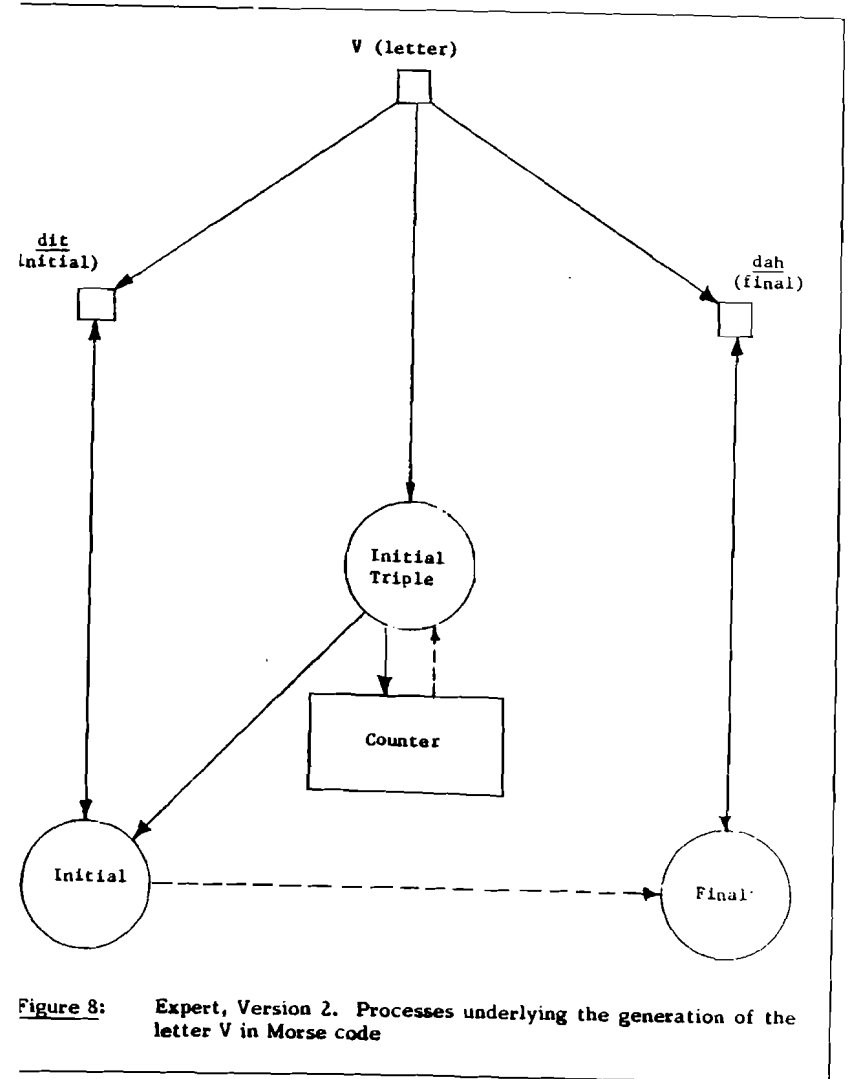


Figure 8: Expert, Version 2. Processes underlying the generation of the letter V in Morse code

### Simultaneous behaviors

As noted in the introduction, the components in Morse code are discrete and sequential at every level: one component ends before the next can begin. However, components for many other behaviors must be executed in parallel. Shifting gears in a standard-shift automobile is an example: the clutch is released at the same time as the accelerator is depressed. Unless these actions are in fact carried out simultaneously, the car may lurch forward and stall.

To illustrate what is involved, consider how the theory might represent the expert shifting of gears from second to third in such an automobile. The highest level node, shift second (third) represents the entire concept of shifting gears from second to third and is connected to a sequence node THIRD. As discussed below, THIRD is part of a general-purpose serial order rule (first + second + third + fourth ...) which can be used to sequence an indefinitely large number of behaviors.

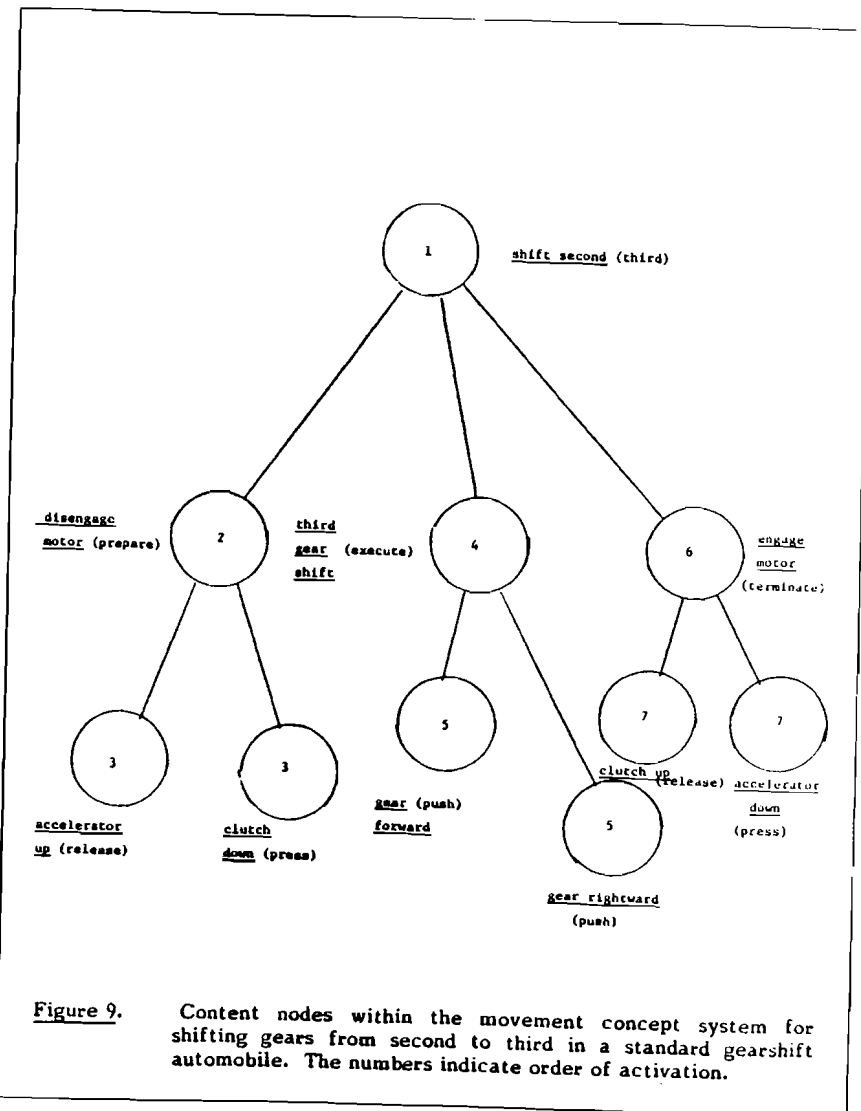
The remaining mental nodes and the connections between them for shifting from second to third are shown in Figure 9. When actually executing the gear shift, the order of events is as follows (see Figure 9.).

Activation of shift second (third) via sequence node THIRD introduces first-order priming to three content nodes, disengage motor (prepare), third gear shift (execute) and engage motor (terminate), and second-order priming to the sequence nodes coding the serial order rule (prepare + execute + terminate). The sequence node PREPARE is therefore activated first, which in turn activates disengage motor (prepare). This primes accelerator (up) and clutch (down) and their corresponding activating mechanisms UP and DOWN. Unlike other sequence nodes (coded verbally with the same names in everyday English), UP and DOWN do not interact with one another to represent a serial order rule: they must be activated at the same time in order to successfully carry out the behavior.

Once accelerator (up) and clutch (down) have been coactivated (simultaneously activated), the most primed sequence node is EXECUTE, which therefore becomes activated and leads in turn to the activation of third gear shift (execute). This in turn primes and leads to the coactivation of gear forward (push) and gear rightward (push), bringing about the smooth flow of movement seen in expert shifting. By way of contrast, beginners usually shift from second to third in three movements (to neutral, to the right, and finally, forward), which accounts in part for their more jerky performance (see Schmidt, 1982).

The remaining primed but as yet unactivated sequence node is TERMINATE, which now becomes activated under the most-primed-wins principle, thereby activating engage motor (terminate). This primes clutch (up) and accelerator (down) which likewise become coactivated in the manner discussed above.

This view of the nodes controlling coordinated behavior not only accounts for the successful execution of everyday actions such as driving a car but allowing reasonable assumptions, makes interesting predictions concerning the nature of the errors that will occur. One frequently occurring error among beginners, predicted under the theory, is omission of the rightward component in the sequence (forward + right + forward) when shifting from second to third. The resulting shift to first rather than third is especially likely under the most-primed-wins principle since the rightward component is relatively unpracticed: forward and backward shifts from neutral are more common (occurring for shifts 1-2, 2-3 and 3-4 as well as reverse) than rightward shifts (occurring only for shift 2-3). Since degree of priming depends on linkage strength, which in turn depends on practice, producing the forward rather than rightward shift is more likely than vice versa under the most-primed-wins principle.



Another error which is especially common when learning to drive is to sequence rather than coactivate accelerator (up) and clutch (down). The resulting stalls are explained as follows: Verbal instructions usually refer to clutch and accelerator positions as up or down, terms which the learner is likely to assume refer not to cotemporaneous but sequential actions governed by the everyday serial rule (up + down), seen for example in going up and down stairs or in tapping the foot or finger. However, releasing the clutch before depressing the accelerator will stall the car, especially on an incline (see Schmidt, 1982).

A third class of errors predicted under the theory can occur from any gear position and results from the substitution of accelerator (down) and clutch (up) for accelerator (up) and clutch (down) while attempting to disengage the engine. The error is natural enough (the accelerator component has for whatever reason acquired greater priming in the (down) domain) but has a startling consequence: the car will suddenly accelerate rather than decelerate as expected.

### Sequence rules with unlimited generality

The rule discussed above for shifting gears (first + second + third + fourth....) illustrates a general purpose rule that can be used to sequence the activation of any set of mental nodes. All that is required is the formation of a connection between the mental nodes and the appropriate sequence node. For example, a sequence of 10 nonsense syllables could be learned by forming connections between the highest level nodes representing each nonsense syllable and the corresponding sequence nodes (first + second + third ...). However, with sequences greater than 9 or 10 items, humans find such associations difficult to form (many repetitions or practice trials are required for correct performance), perhaps because each sequence node has a large number of prior associations with other content nodes and must simultaneously interact with the 8 or 9 other sequence nodes that are involved.

### Permutable sequences and the determining tendency

The final extension of the theory begins with the observation that content nodes provide the basic associations underlying action and cognition, while sequence and timing nodes provide the determining tendency for specifying what domain of association is appropriate and when. Psychologists have long recognized that the basic associations cannot function by themselves: a control process or determining tendency is needed for determining what domain of association is appropriate at any given point in time (see Seltz, 1927). Our ability to either add or multiply any pair of integers (from 1 to 10) nicely illustrates the nature of this more general problem and its solution within the present framework. Consider for example the numbers 6 and 3, their associated product (18), dividend (2), difference (3) and sum (9). How do we retrieve the appropriate association (say the sum) without retrieving and rejecting the other (inappropriate) associations (product, dividend or difference)? In short, what is the determining tendency that facilitates the appropriate association?

Priming from the node representing the operator (+, -, x, /) is the determining tendency under the theory. Consider Figure 10 which illustrates the node structures for representing the propositions  $6 + 3 = 9$  and  $6 \times 3 = 18$ . Note that the integer nodes 6 and 3 are identical in each proposition. This means that the input  $6 + 3$  will prime the node represented  $6 \times 3$  (components), although not as much as the input  $6 \times 3$ . However, this weak priming explains why subjects in a speeded recognition task find it difficult to reject incorrect propositions such as  $6 + 3 = 18$  and  $6 \times 3 = 9$ , where the content nodes have an underlying association but require a different operator.

Finally, note that the same network of nodes can serve to solve equations containing the permuted sequences  $9 = 3 + ?$ ,  $9 = 6 + ?$ ,  $18 = 3 \times ?$ , and  $18 = 6 \times ?$ . In these sequences the result and one of the component integers are given so that the remaining integer can be determined by the permutable rule (integer + operator + integer) which enables the integer nodes to become activated in either order.

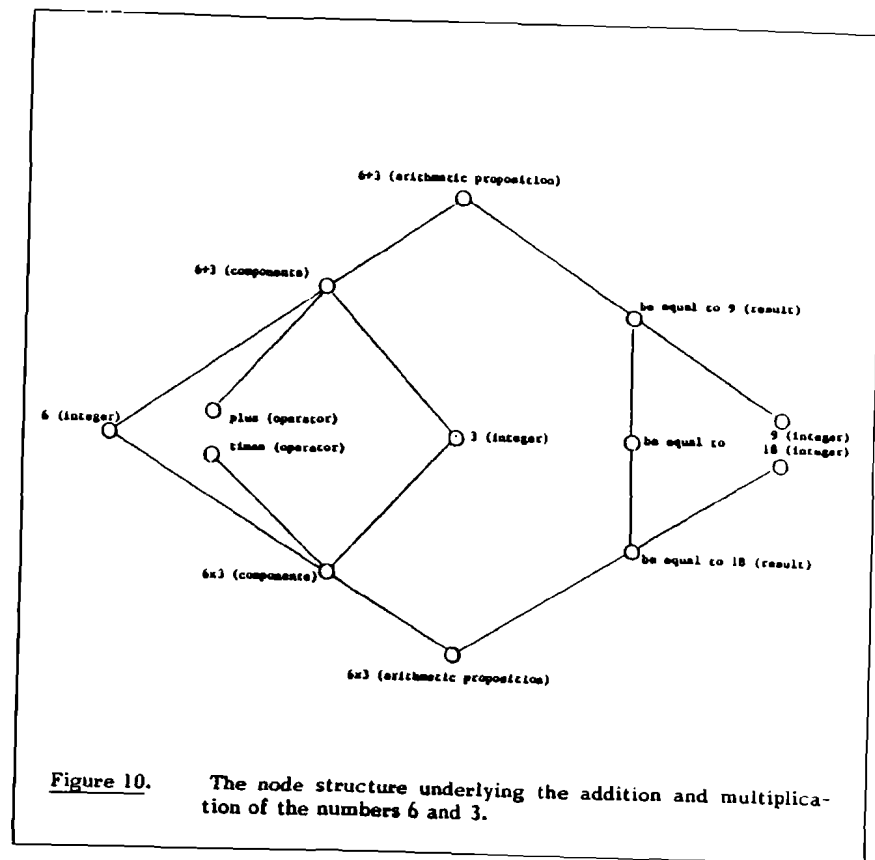


Figure 10. The node structure underlying the addition and multiplication of the numbers 6 and 3.

### Systems Controlling Action

The discussion so far has focused on detailed examples of the control of behavior via content, sequence and timing nodes. However, considering behavior more generally, we find that these nodes are organized into systems, each following the same organizational principles, but each having unique capabilities of its own. As we will see, one of the reasons for this organization into systems is to enable specific types of thought to take place without the occurrence of muscle movement or action *per se*.

Each system is controlled by two sources, one internal to the system itself, the other external. Timing nodes are the internal source of control. Each system has a set of timing nodes which must be engaged if content nodes within the system are to become activated. Each system also has a set of sequence nodes which represent the serial order rules for the components of action the system is responsible for.

Up until now we have been discussing content, sequence and timing nodes within the system known as the movement concept system. Below we discuss this system

more systematically, along with its relationship to three other systems that normally play a role in controlling everyday actions; the muscle movement system, the action plan system, and the pragmatic system. Figure 11 illustrates a general schema of the relationship between these systems. Also included for the purpose of comparison are three additional systems needed for the control of speech. In addition to comparison are three additional systems needed for the control of speech.

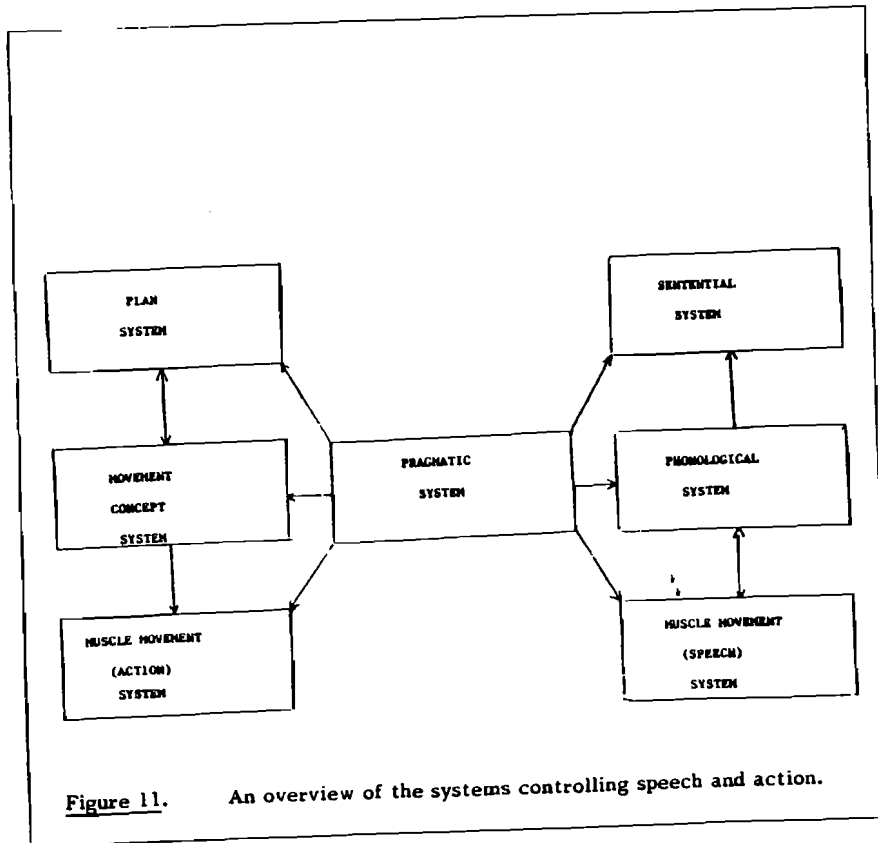


Figure 11 must not be taken to represent stages such as those postulated in information processing frameworks. In stage theories, a given type or stage of processing is carried out and then and only then is control passed on to the next stage. Systems, on the other hand, are capable of operating in parallel: it is neither necessary nor usually the case that an action is completely processed within one system before the next system begins processing. Also unlike stages, systems can operate independently: one system can process an action without receiving output (first order priming) from its immediately higher level system and without causing activation within its immediately lower level system.

### Muscle movement systems

Muscle movement systems control the organization of muscle movements for the trunk, limbs and fingers as well as internal organs such as the larynx and velum. Full-fledged movement occurs when the lowest level alpha motor-neurons representing specific sets of muscle fibers become activated by their triggering mechanism — a muscle sequence node. Activated nodes within higher level (mental) systems prime their connected muscle movement nodes but unless a muscle sequence node is activated, only imagined actions occur. These internally generated actions are the basis for mental rehearsal of a movement sequence (see MacKay, 1981).

Nodes within muscle movement systems govern the activation in sequence of particular muscles and sets of muscles. This means that the connections between nodes within these systems are strengthened by practising or repeatedly activating these particular muscle movements. Predictions concerning an individual's relative skill at different muscle movement activities therefore do not depend on nonspecific processes that might be called general motor skill, and existing data support this view. Skill within muscle movement systems is specific not just to a particular limb, but to the strength, speed, and direction of movement of the limb. As Smith (1961, p.219) points out, "Individual differences in limb action abilities (considering reaction latency, strength, and speed as the components of such action) tend to be highly specific to the component, to the limb involved in the action (arm or leg), the direction it is moved (forward or backward), the dynamic or static nature of the action (speed vs. measured strength), and the phase of the action (reaction latency vs. speed of movement). For some of these findings, cross-validation using other published data is available and lends additional support to the hypothesis".

This same general principle applies to different uses of the same muscles. Henry and Whitely (1960) found no significant correlation between static or isometric strength and dynamic or movement strength for a 90-degree horizontal arm swing from the shoulder pivot. They concluded that "neuromuscular control patterns are apparently specific and different when the (same) muscle is moving a limb as compared with causing simple static tension" (p.24).

It should be kept in mind, however, that although we can produce and practice particular muscle movements by themselves, we normally do not do this. Mental nodes (which are not specific to particular muscles) normally control the muscle movements that we practice in everyday life. As a result, practice or repeated activation of these mental nodes can generalize to many different muscle movements and effector systems. Take Morse code as a simple but typical example. Since mental nodes govern this skill, practice in generating Morse code with the right forefinger can be generalized to use of the middle and ring fingers, to the left hand or to the foot. The same basic principle is true of all other complex skills (see MacKay, 1982).

### The movement concept system

Nodes within the movement concept system frequently involve body parts for which the sequence of actions is highly automated. We have already discussed two examples in some detail: shifting gears in a car and generation of the letters in Morse code. Movement concept nodes represent not particular muscles but general categories of movement without reference to muscles. For example, a node representing a movement concept such as 'press key' specifies no particular muscle or muscle movement since the key could be pressed with either the left or the right hand, with either one or more than one finger on the key, with either a wrist or finger movement or most likely, both. Sequence nodes within the movement concept

system represent serial order rules such as (press + release) for generating a Morse code 'dit', and these sequence nodes are likewise independent of particular muscle or movements.

There are of course many connections between the lowest level movement concept nodes and particular muscle movement nodes, and some of these connections have become very strong as a result of practice, e.g. the connection between say the 'press key' node and the nodes for the muscles controlling the right index finger (the right hand). It is nevertheless possible for a higher level decision (within the pragmatic system discussed below) to override this habit, enabling key press performance with another finger, another hand or the foot. As indicated in Figure 1, this decision may be transmitted directly to the muscle movement system, priming and causing activation of the appropriate limb system.

### The action plan system

Content nodes within the action plan system, unlike the movement concept system, are not directly connected to muscle movement nodes and do not represent even broad classes of movements. By way of concrete example, an action plan node can represent an intention such as 'get bread from the bakery', which can be achieved in many different ways such as say walking, bicycling, taking a bus or driving in one's car. Such actions involve many different effector systems and virtually unlimited number of different movements. In contrast, a movement concept such as shifting a gear from second to third involves a relatively limited number of movements and muscle movement systems associated with the right arm. In addition, the action plan system deals with relatively novel rather than automated actions and requires the use of feedback and involves the entire body rather than a body part such as the arm.

To illustrate the action plan system in greater detail, consider the execution of a preplanned shopping trip such as the one illustrated in Figure 12. The plan is to drive to hardware store A, bakery B, clothing store C and furniture store D before returning to home H, where the cognitive representation of A, B, C, D and H has spatial characteristics resembling Figure 12a. Figure 12b represents the nodes and their connections for executing this shopping trip. How these particular nodes become connected differs in important respects from the process of node activation discussed here. Node formation can occur at any time and proceed in any order unlike node activation which must occur at certain times and in proper serial order.

The execution sequence is as follows (see Figure 12b). The goal node, HBDCAF (goal), representing the entire shopping trip is activated first. This primes both stops (head out) and stops (head back) and the corresponding sequence nodes representing the serial order rule (head out + head back). These sequence nodes (operating under the most-primed-wins principle) activate stops (head out) first, which primes its subordinate nodes, store B (near) and store D (far), and the corresponding sequence nodes representing the serial order rule (near + far). The sequence node NEAR now becomes activated under the most-primed-wins principle, which in turn activates store B (near), thereby triggering the action concepts for driving route hb (from point h to point :hpo.b):ehpo.. The most-primed-wins principle now reapplies to activate the sequence node FAR which in turn activates store D (far), thereby triggering the action concepts for driving route bd. The most-primed-wins principle applies to the sequence nodes again to activate stops CAH (head back), which primes home H (final stop) and stores CA (head back) along with their corresponding sequence nodes representing the serial order rule (head back + final stop). The most-primed-wins principle now activates stores CA (head back), which primes store C (near) and store A (far) along with their corresponding sequence nodes represent-

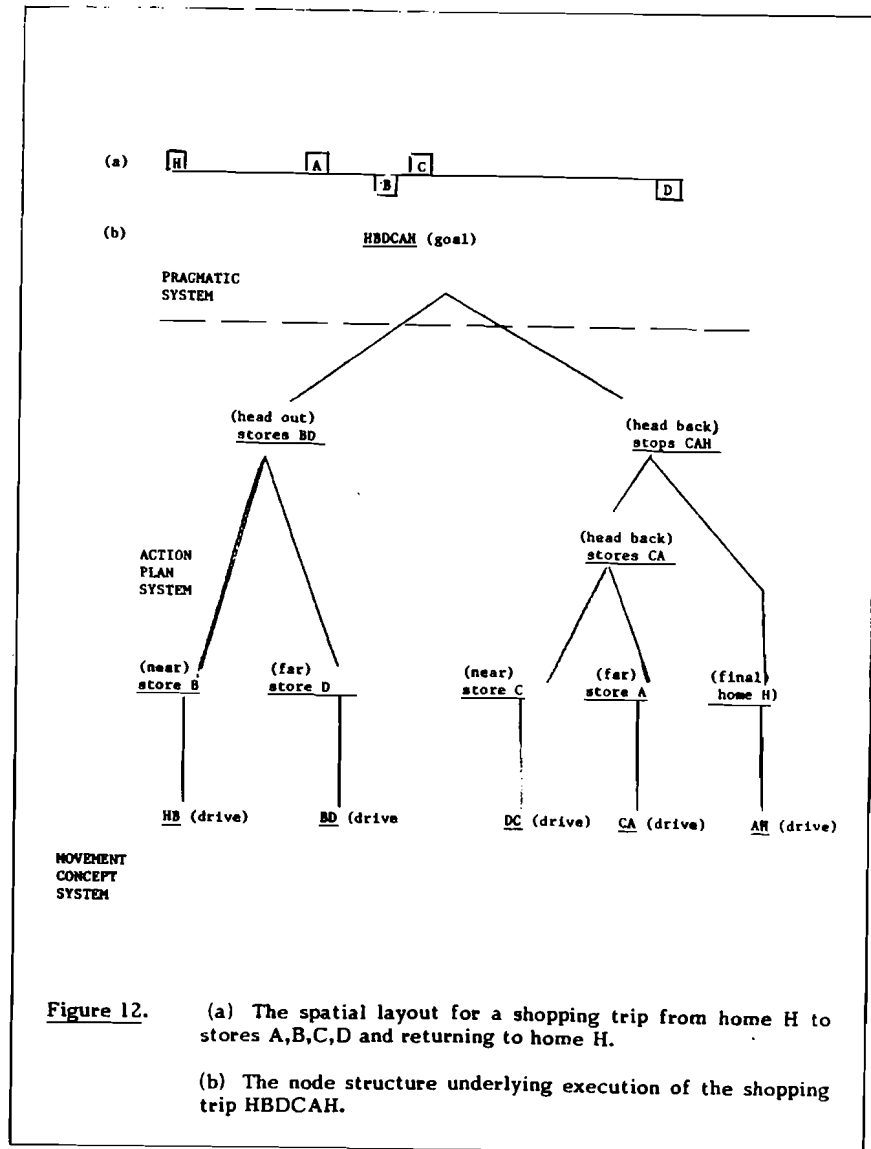


Figure 12. (a) The spatial layout for a shopping trip from home H to stores A, B, C, D and returning to home H. (b) The node structure underlying execution of the shopping trip HBDCAF.

ing the serial order rule (near + far). The most-primed-wins principle now activates store C (near), which triggers the action concepts for driving route ca. When the most-primed-wins principle reapplies again it activates the home H (final) node and the associated action concepts for driving route ah.

This view of action plans accounts for how broad classes of preplanned behavior are sequenced in everyday life, and with the addition of reasonable assumptions, makes interesting predictions as well. Assume, for example, that the cognitive representation for the location of stores B and D is inaccurate, such that B is represented as the far store and D the near store. Under these circumstances, the most likely error under the theory is to bypass store B during the search for D, since store B will fail to match the memory representation for D.

Vagueness is also easily represented in the model. Suppose, for example, the planner knows that B and D are "head out" stores, but can't remember which comes first. Under these circumstances, the model predicts that the planner will search for store D, B (near), stopping at the first store matching the memory representation of either D or B, and store (far) where = D if near store = B, and = B otherwise.

### The pragmatic system

The pragmatic system carries out five major processes or functions discussed below; the integration of perception, speech and action, goal setting, rate setting, evaluative functions, and the determination of output mode.

The integration of perception, speech and action. All forms of behavior and perception become integrated within the pragmatic system. For example, both speech and action originate and receive a common representation within the pragmatic system: A single component or set of components within the pragmatic system can represent an action such as getting up and opening a door and a sentence such as "Could you please open the door?"

The actions of either describing or showing someone the layout of one's home or apartment further illustrate the nature of the rules and representations coded within the pragmatic system. Linde and Labov (1975) had subjects describe their apartment layout and found that most (over 95%) adopted a "tour strategy": they began by describing the room nearest the front door and then described each succeeding room as if it were part of a guided tour, e.g. "A closet is to the left of the front door as you come in and the kitchen is to the right".

This tour strategy provides a means of sequencing large numbers of sentences coded within the sentential system (the analogue of the action plan system shown in Figure 11). Note, however, that the tour strategy is neutral with respect to speech vs. action. The same strategy could be used for guiding the action of showing someone around one's home rather than just describing it.

Like sequence rules, the tour strategy can apply to more than one particular content. One could just as readily use the tour strategy for describing one's place of work or the home of a relative or friend. Extending this observation, MacKay (in preparation) argued that a set of pragmatic sequence rules underlies the tour strategy. Under this proposal, pragmatic sequence nodes code serial order rules such as (left + right) and these rules can be used for sequencing either action (e.g. look first to the left and then to right in giving the guided tour), or speech (e.g. a description such as "The fridge and stove are to the left as you enter the kitchen and the sink is to the right"). Note that such rules are applicable to many other types of behavior, e.g. "step first with the left foot and then with the right" in marching.

The pragmatic system also contains sequence rules for integrating speech and action. Numerous illustrations are found in Schank and Abelson's (1977) descriptions of routine behaviors. For example, consider the stereotypical sequence of events

involved in going to a restaurant for dinner. The expected sequence is (1) enter (and get shown to a table), (2) order, (3) eat, and (4) exit (including leaving a tip and paying the bill). Under the theory, pragmatic content nodes represent these expected events along with sequence rules such as (enter + order) and (eat + exit) for determining their order of occurrence.

It is of considerable interest that pragmatic sequence rules such as (enter + order) or (left + right) are no more complex than either action plan rules such as (head out + head back) for a return-to-destination trip, or movement concept rules such as (press + release) for a Morse code dit. If the sequence rules for higher and lower level nodes are found to be equally complex in a wide range of behaviors, it might be argued that a fundamentally similar solution to the problem of serial order has been adopted at all levels of the nervous system.

Evaluative processes. The pragmatic system contains evaluative propositions representing attitudes and feelings concerning our social, psychological and physical representations of the world. In addition to many other functions (see Bower, 1981), this evaluative representation can sometimes be used to sequence behavior. For example, sequential rules such as (important + less important) tie into the evaluative representations and enable one to order a series of say, household chores, beginning with the most important and ending with the least important one.

General goals. The pragmatic system represents the most general purpose of an action sequence, i.e. what the action is intended to accomplish in the outside world. This representation normally includes one's current environmental situation and many other real-world social and psychological constraints on behavior. For example, consider the goal of asking someone to shut the door. The pragmatic system must take politeness constraints into account in determining whether to express this goal as a command, (Shut the door), a question (Could you please shut the door?) or a statement (It's cold in here with the door open). Which of these three means of expression gets chosen under the most-primed-wins principle depends on the degree of priming from other pragmatic nodes coding politeness propositions for the given situation.

The rate of action. The pragmatic system sets the rate or tempo of action by determining how fast the timing nodes for all other systems become activated. How the pragmatic system does this depends on whether or not the action is critically dependent on feedback. Expert Morse code generation is an example of an action which is not critically dependent on feedback. Here the pragmatic system directly determines the rate of output by adjusting the rate setting or activation rate of the (coupled) timing nodes for the movement concept and muscle movement systems.

The situation is rather different for action sequences which are critically dependent on feedback. An example is hammering a nail until flush: since the nail could have changed angle on the previous stroke, the pragmatic system must evaluate the feedback from one stroke before the next stroke can begin.

The shopping trip discussed above is another example of a feedback-timed action sequence. Besides representing the spatial parameters of the trip (illustrated in Figure 12a) and the memory representation for recognizing the stores to be visited, the pragmatic system contains a node representing a concept such as "It is time for shopping." This node primes both HABCDH (goal) and action plan time (shopping trip), the action plan timing node which is engaged for shopping trips. This results in the activation of stores BD (head out) and store B (near), which triggers the behavior of driving route hb. However, subsequent pulses from action plan time (shopping trip) depend on environmental feedback represented in the pragmatic system. This

feedback signals that one phase of the shopping trip has been completed so that the next can begin.

**Cognition vs. action.** The pragmatic system determines the mode of output; thought or imagined action vs. fully articulated action. For fully articulated action, the pragmatic system engages all three timing nodes for the action plan, movement concept and muscle movement systems, but for imagined action, it engages only the higher level timing nodes for the action plan and movement concept systems, so that no muscle movement nodes become activated and no overt behavior takes place. In this way, thought can proceed without the negative consequences that sometimes accompany action.

This is not to say that cognition invariably precedes action or that all higher level systems invariably take part in the execution of an action. Two examples serve to illustrate how actions can be executed without the help of higher level nodes. One is Roy's (1982) observation that people sometimes forget the original goal of an action while continuing to carry out its component parts. The other is a hypothetical example dealing with the use of Ameslan (American sign language). For producing Ameslan, a movement concept system for gestures of the arms and hands replaces the phonological system of English for gestures of the respiratory, laryngeal and articulatory organs. However, the higher level sentential nodes representing words and phrases are virtually identical for Ameslan and English. Now consider the case of a person with no knowledge of Ameslan who inadvertently happens to produce the gesture with the arms that means 'tree' in Ameslan. The gesture has been produced as a nonsense action without the help of the higher level nodes that routinely contribute to its production by someone who knows Ameslan.

But although the action is clearly feasible, it is deficient in control, memorability and appropriateness. The person without the movement concepts for Ameslan will not be able to precisely reproduce or even remember the action at a later time. Nor will that person be able to produce the action in appropriate contexts i.e. in a conversation about trees with someone who knows Ameslan. The situation of the apraxic who can produce the components of an action but cannot produce the action as a unit in its appropriate context is in many ways analogous: Due to cortical damage, higher level nodes are no longer contributing to the action, and although the lower level nodes are able to execute the components of the action, there is obvious impairment. The absence of higher level cognitive control can also lead to more subtle deficits: MacKay (1982) experimentally simulated the production of nonsense actions resembling the Ameslan example discussed above and showed that the flexibility and fluency of an action suffers in the absence of higher level nodes.

#### Errors in Action and Their Relation to Attention and Intention

Errors in everyday behavior provide a challenge for theories of action since theories which cannot account for the errors that occur are incomplete or inadequate as accounts of the mechanisms underlying behavior. To determine whether the present theoretical framework can handle errors in action, we examine three broad categories of error from the everyday behavior of normal individuals. We then explore the relation between intention and errors and develop a way of describing intentions within the present theoretical framework. Finally, we discuss the relation between attention and errors and describe a way of representing attention in the present theory that overcomes some of the problems with earlier theories.

#### Errors in action

**Data driven errors.** Irrelevant but simultaneously ongoing perceptual processing sometimes causes errors in action. Meringer and Mayer (1895) and Norman (1981) compiled several naturally occurring speech errors of this type, but the Stroop effect represents a well known experimental demonstration of the same phenomenon (see Norman, 1981). Subjects in Stroop experiments are presented with color names printed in several different colors of ink and the task is to ignore the word and name the color of the ink as quickly as possible. Errors are especially frequent when the color name differs from the name for the ink (e.g. the word green printed in red ink) and the most common error is data driven: the printed name (green) substitutes the required name describing the color of the ink (red).

Data driven errors are readily explained in the present theory as effects of bottom-up priming. The same mental nodes become involved in perception (bottom-up) and behavior (top-down) and the most primed node in a domain becomes activated under the most-primed-wins principle, regardless of whether its source of priming is from above or below. As a consequence, a node receiving bottom-up priming can become activated in error simply because it has acquired more priming than the intended-to-be-activated node in the same domain, i.e., the node receiving priming from a superordinate node in the action hierarchy.

**Decay of priming errors.** Errors due to decay of priming resemble absent-mindedness: The person forgets what they are doing in the process of carrying out an action, and must somehow begin again. Norman (1981) provides a dramatic but otherwise characteristic example where a man went to his bedroom but could not recall what he wanted there until he returned to his work (writing), discovered that his glasses were dirty and returned to the bedroom to fetch the handkerchief he had wanted for cleaning them.

Such absent-mindedness reflects decay of priming in the theory. When activated, an action plan node primes its subordinate nodes which then become activated in proper sequence. However, priming decays over time and with sufficient delay between priming and activation, the subordinate nodes in the action hierarchy can lose so much priming that no action can take place.

Thus, in the above example, an action plan node primed nodes for going to the bedroom, retrieving the handkerchief and cleaning the glasses. However, while actually going to the bedroom, priming of the nodes for retrieving the handkerchief and cleaning the glasses decayed to resting level so that no action could occur. These nodes became reprimed only later during the subsequent attempt to use the dirty glasses for reading.

**Capture errors.** Capture errors (see Norman, 1981) seem to reflect a combination of decay of priming and bottom-up effects: An action commonly associated with a given environment replaces the intended action (because of decay of priming). The following example from William James (1890) is typical: A man went to his bedroom to change clothes for dinner but forgot what he was doing, put his pyjamas on instead of his dinner clothes, and found himself getting into bed, much to his surprise. Apparently, the bedroom environment had a bottom-up effect on the selection of the higher level plan (going to bed vs. going to dinner) and as Norman (1981) points out, theories of action must make provisions for such bottom-up effects.

Such errors have two possible explanations within the present framework. One involves decay of priming as in the errors discussed above. The bedroom environ-

ment primes at least two nodes; one for changing clothes, the other for going to bed. The node for changing clothes is primed from above via the plan to go to dinner, and being the most primed, becomes activated under the most-primed-wins principle. This causes subordinate nodes for removing clothes and for putting on new ones to become primed. Assume, however, that this priming has decayed for reasons similar to those discussed above: The most-primed-wins principle must be applied again to reestablish the superordinate goal. Having accumulated priming from stimuli arising from undressing, from sight of the pyjamas and perhaps other sources as well (e.g. feelings of fatigue), the node for going to bed may have most priming at this point in time and therefore becomes activated, with the ensuing errors, putting on pyjamas and going to bed.

The second explanation resembles the first but requires neither loss of priming nor reapplication of the most-primed-wins principle to superordinate domains. Under this explanation, the error reflects the general principle of subordinate autonomy discussed in MacKay (1982). Specifically, the particular clothes to be worn for a given occasion are unlikely to be specified within a higher level plan: We often delay choosing specific clothes until we have determined what clothes are available in the closet. As a consequence, the pyjamas node may acquire greatest priming (for reasons such as those discussed above) when the activation mechanism is applied to the domain of clothes nodes, so that pyjamas are donned. This primes from below the goal of going to bed, which results in the error of going to bed.

Under this explanation, capture errors closely resemble the "associative errors" in speech recorded by Meringer and Mayer (1895) and Norman (1981). A typical example is the substitution of "Lick Observatory" for the intended "Palomar Observatory," made by a speaker who was highly familiar with Lick Observatory near Stanford. The explanation is as follows: In forming a sentence plan, the noun node for observatory becomes activated. This primes a set of noun phrase nodes from below, including the one for "Lick Observatory" (noun phrase). This node acquires more priming for whatever reason and automatically becomes activated under the most-primed-wins principle, causing the error.

#### Intention and errors

Errors are closely related to the issue of intention since an intention is by definition violated in producing an error. What are intentions and how are they expressed in action (when they are)?

We are here concerned with intentions during the course of action rather than the knowledge one may have about one's own intentions prior to initiating an action. These 'intentions in action' represent an answer to the question "What are you trying to do" and any theory of action must capture three basic characteristics of such intentions: their indirect relation to action; their multifaceted nature; and their close connection with the units of performance (see MacKay, 1983). We argue below that the present theory captures all three of these characteristics.

Indirect relation between intention and action. Intentions may or may not become expressed in action. Errors represent one example where actions and intentions fail to correspond and context-dependent intentions represent another. For example, one can have a context-dependent intention to light a candle when in need of light but if that need never arises, the intention never becomes expressed in action.

The present theory readily explains this indirect relationship between intention and action. Under the theory, intentions correspond to the priming of sequence and

content nodes in preparation for action. These intentions then become expressed in action when the timing nodes for the lowest level muscle movement system become activated. Activating these timing nodes often depends on a specific cue such as darkness in the candle example discussed above. And even when the timing nodes are activated, the intended action does not always occur. Incongruities between intention and action are to be expected in a theory where a node must not only be strongly primed, it must be more primed than any other node in its domain in order to become activated under the most-primed-wins principle.

The multifaceted nature of intentions. One not only intends to execute the components of an action but to execute them in the proper sequence and at an appropriate rate. To illustrate this multifaceted nature of intentions, consider the intention of lighting a candle. Components such as striking a match, applying it to the wick of the candle until it ignites, and blowing out the match are an integral part of the intention. But so is the proper sequence: the sequence "Strike match, blow out match and hold match to candle" clearly violates one's intention to light a candle.

The present theory readily captures this multifaceted nature of intentions. The components of an intended action correspond to the top-down priming of content nodes in an action hierarchy and the intended sequence corresponds to the priming of sequence nodes. All that is required for action is the 'go signal' or activation pulse from the appropriate timing node.

The relation between intentions and the units of performance. Intentions are closely related to the units for carrying out a task. Consider for example the units underlying the operation of a lathe (from Welford, 1968, p.193): "At any given instant we should find a detailed muscular action in progress--say, a twisting of the wrist to turn a handwheel on the tool carriage. The action would, however, be only one of a series required to move the tool over the surface of the work. This again would be only one part of the cycle of operations required to machine the article concerned, and the article might be only one of several needed for the job of construction on which the man was engaged". As Welford (1968) points out, the performance units underlying these actions must be hierarchically organized, such that the larger units at each level encompass the smaller, "organizing, coordinating, steering and motivating those that lie below".

Consider now the intentions underlying these actions as reflected in answers to the question "What are you trying to do?" The man is simultaneously intending the action (e.g. gauging), the series of actions (moving the gauge systematically over the wood), the cycle of operations (making a table leg) and the job of construction (making a table). Like the performance units, then, the intentions are hierarchically organized, and vary with the level under consideration.

The present theory readily explains this close relationship between intentions and the units of performance. Since intentions correspond to the priming required to activate the sequence and content nodes, intentions constitute an essential ingredient in the control of action, and the components of intention and action are coreferential in the theory.



### Attention and Errors

Current theories sometimes attribute errors to lack of attention, but attention often goes undefined and acquires animistic properties in these theories. In what follows we attempt to develop an alternate view of attention that overcomes some of these flaws.

Under the present theory, attention is the perceptual analogue of intention: it corresponds to the priming of nodes representing an anticipated perception. By way of illustration, consider an example from visual perception (Kaufman, 1974): A subject is instructed to expect a duck when presented with Jastrow's ambiguous rabbit-duck. The subject will see the duck rather than the rabbit because the instructions activate a proposition node representing the concept "A duck will be presented". This proposition node primes the nodes in a visual concept system which represent ducks and their characteristic attributes. These nodes therefore become activated under the most-primed-wins principle and determine perception of the ambiguous figure.

Consider now an example involving attention in action (from Norman, 1981). A man has decided to stop at the fish store on the way home from work but is paying attention to something else at the intersection where he must detour to the fish store. As a result he fails to go to the fish store as intended but goes straight home, his usual pattern of behavior.

Such failures of attention can be explained in the same way as the decay of priming errors discussed above. When we plan an action such as detouring to a fish store on the way home, connections are formed between action plan nodes and nodes within the visual concept system, here the nodes representing the perceptual cues for the turn-off. These visual concept nodes, therefore, become primed during the course of the action, so that when the cues themselves appear, the visual concept nodes become activated under the most-primed-wins principle and strongly prime the plan nodes for making the detour. The outcome is error-free behavior as planned.

What happens when one fails to pay attention and is thinking about some other plan when the cues for making the detour appear? Thinking about some other plan implies that the fish store plan is no longer activated, so that both the plan for making the detour and the visual concept nodes representing the intersection are suffering from decay of priming. As a consequence, bottom-up priming from the visually experienced intersection may fail to reach the action plan node for making the detour in sufficient strength. As a result, the more frequently activated plan of driving straight home may predominate at this critical choice point and become activated under the most-primed-wins principle.

The concepts of critical choice points and competing mental activities are of course not new (see Reason, 1979; Freud, 1914). However, viewing attention as the priming of high level perceptual nodes is new and obviates an appeal to animism seen in earlier theories. For example, Reason (1979) maintained that attention must be devoted at critical choice points in an action sequence to prevent the intrusion of a parallel mental activity as in Freudian and data driven errors. However, attention played the role of a homunculus which must be on the lookout for these choice points when two competing action patterns share common elements or are both associated with same environmental situation. If the homunculus is asleep i.e., insufficient attention is being paid, then the most frequent or most recently activated of the two competing actions will occur, whether correct or not. If the homunculus is awake, it inhibits the stronger habit, allowing the appropriate behav-

ior to occur. As in Freud's theory, civilized behavior requires a homunculus to inhibit stronger or more primitive impulses. In contrast, however, the present theory views appropriate behavior as the result of maintaining the priming of nodes controlling the intended sequence of action.

### Movement Disorders

One way of "testing" any theory of skilled action is to determine whether it can account for the errors that occur in the performance of brain-damaged patients. In what follows we test the node structure theory against current clinical data on the movement disorder known as apraxia. As Heilman (1979) points out, complex learned behaviors become disorganized in apraxia but not because of paralysis, weakness, deafferentation, abnormality of tone or posture, abnormal movements such as tremors and chorea, intellectual deterioration, poor comprehension or uncooperativeness. We begin by examining two general phenomena (environmental susceptibility and hemispheric asymmetry) which are characteristic of virtually all apraxias. We then apply the theory to three main forms of apraxia (callosal, ideational and ideomotor) which play a prominent role in the recent literature.

### Environmental susceptibility

Environmental susceptibility is a general phenomenon associated with cortical damage: The patient requires the appropriate context or situational props in order to commence and direct an action and becomes easily distracted by irrelevant contextual cues. For example, an apraxic may begin the task of collecting and sorting out the dirty laundry but ends up cleaning the bathroom instead since the environment (a dirty bathroom) primed another course of action (Roy, 1982). Such an error is, of course, less likely to occur when the apraxic maintains a situational prop (the clothesbasket) in hand. Similarly, apraxics are often unable to demonstrate the use of a tool except in its appropriate environmental context. If asked to mimic the action of hammering a nail in the absence of both hammer and nail, they have difficulty carrying out the action.

Why does perceptual input play such a dominant role in the behavior of apraxics and other patients with cortical damage? Environmental susceptibility introduces serious problems for current theories of motor control (see Roy, 1982), but follows straight forwardly from the present framework. Under the theory, cortical damage impairs the effectiveness of higher level nodes, thereby reducing the degree of top-down priming in an action hierarchy. However, bottom-up priming is by definition unimpaired in apraxia and, therefore, acquires an exaggerated influence on which node receives most priming and becomes activated. No problem arises when these environmental cues are congruent with the required action: The bottom-up priming from the tool or the environmental context will facilitate the appropriate action. However, inappropriate actions become likely in the presence of irrelevant cues, such as the dirty bathroom. These irrelevant cues provide strong bottom-up priming which predominates over the weaker top-down priming for the intended action, so that inappropriate nodes become activated under the most-primed-wins principle and data driven errors become the norm.

By weakening top-down priming, cortical damage will also increase the likelihood of decay of priming errors: Under the theory, apraxics are likely to omit as well as substitute components within a sequence of actions.

### Hemispheric asymmetry

A steady stream of findings over the past 20 years indicates that the left hemisphere plays a special role in the sequencing and timing of behavior (whether verbal or nonverbal). For example, left hemisphere lesions in right-handed people selectively impair the sequencing of movements such as pushing a button, pulling a handle and pressing a bar in the Kimura-bar test (Kimura, 1977). However, right hemisphere lesions selectively disrupt spatial abilities: These patients experience difficulty perceiving the spatial relations between objects (as in copying an abstract design or drawing a diagram or map) and positioning objects spatially (as in assembling the pieces of a jigsaw puzzle or building a structure out of blocks).

Current theories are in agreement that deficits arising from right hemisphere lesions reflect an inability to code spatial patterns or relations between objects. The reasons for the left hemisphere effects are more controversial. Almost all cases of apraxia in right-handed people originate from left hemisphere lesions. Since the left hemisphere is usually dominant for language in these patients, it has been suggested that a verbal control system located within the left hemisphere is responsible for directing and sequencing skilled behavior. Thus, left hemisphere lesions cause apraxia by disrupting the control of action via internal speech or other linguistic means.

This view of left hemisphere apraxias has been discredited by both clinical and experimental data. On the one hand, clinical tests of aphasia and apraxia are poorly correlated and surgically induced left hemisphere lesions outside the speech area often result in apraxias with no demonstrable aphasic symptoms whatsoever (Kolb and Whishaw, 1980). On the other hand, whole classes of aphasia without apraxia and of apraxia without aphasia are everywhere apparent. For example, animals are capable of generating complexly sequenced actions but are, of course, incapable of speech. Likewise, animals with frontal lesions exhibit apraxic symptoms without even the possibility of a causal language deficit.

The present view of left-hemisphere apraxias is immune to these criticisms. Under the node structure theory, content nodes for speech and action are partly overlapping and partly independent: they become integrated within the pragmatic system but are separate and independent within lower level systems (see Figure 11). Damage to the pragmatic system can, therefore, disrupt both speech and action whereas damage limited to a lower level system can disrupt speech without disrupting action or vice versa. For example, damaging only the phonological system will disrupt speech but not action.

Localized and selective damage to content nodes only cause limited incapacities in specific behaviors and these behaviors are easily relearned. However, apraxia (and aphasia) can arise in another and much more serious way, namely through disconnection or disruption of the sequence and timing nodes for a class of behaviors. Such lesions would not only disrupt the sequencing and timing of many actions but in all likelihood would cause inability to activate many of these behaviors as well. Moreover, because of the role of sequencing and timing nodes in activating, strengthening and forming new connections, relearning these behaviors would be difficult.

Consider now the issue of hemispheric asymmetry. An accumulating body of evidence (Tzeng, Hung & Wang, Note 2) suggests that the sequence and timing nodes are located in the left hemisphere for both speech and action. This being the case, it makes sense that left hemisphere lesions are likely to disrupt the activation, sequencing and timing of speech or action or both, as noted above.

One of the predictions of this view is that left hemisphere lesions should also disrupt the perception of sequence and timing since the same nodes govern both perception and production within higher level systems. Congruent with this prediction lesions within the left but not the right hemisphere interfere with the perception of temporal order (Efron, 1963) and of rhythm (Robinson and Solomon, 1974) for both visual and auditory stimuli. Such findings suggest that sequencing and timing may represent a general function of the left hemisphere, so that the present theory can be viewed as specifying the principles underlying functioning of the left hemisphere. Whether similar principles govern functioning of the right hemisphere remains an open question.

### Forms of apraxia

**Callosal apraxias.** Callosal apraxias result when the corpus callosum becomes severed, thereby disconnecting the left and right cerebral hemispheres. In right-handed patients, the symptoms are as follows: The patient retains virtually normal use of the right hand but has difficulty imitating or performing these same actions on command using the left hand. The ability to use the left hand to demonstrate the characteristic use of a well-known object, e.g. a comb, is also impaired but not as severely (see the above discussion of environmental susceptibility).

These symptoms are readily explained under the node structure theory. In a right-handed person, the control mechanisms for activating, sequencing and timing the higher level aspects of action are localized in the left hemisphere. As a result, callosal lesions disconnect these left hemisphere control mechanisms from content nodes located in the right hemisphere. Since right hemisphere content nodes control the organization of action in the left hand, these patients become unable to use their left hand for generating complex actions.

We emphasize again that the above discussion applies only to right-handed persons. For persons who are ambidextrous or left-handed, there is evidence to suggest that the sequencing and timing mechanisms for both speech and action may be represented bilaterally or in the right hemisphere.

**Ideational apraxia.** Ideational apraxia frequently occurs with lesions to the dominant (usually left) parietal lobe in the region of the angular gyrus and associated subcortical structures (Heilman, 1979). Ideational apraxias can imitate actions and demonstrate how to use an object without making errors but have difficulty initiating the same movements on the basis of verbal instructions. The problem is not comprehension of the instructions since these patients can indicate understanding by correctly pointing to a picture of the action.

Performing a series of acts leading to a goal is also difficult for ideational apraxics: Even when they can perform the individual acts making up the sequence, they often get the order wrong. For example, when called upon to light a candle, the patient may light the match and then blow it out before applying it to the wick.

Ideational apraxias have several possible bases within the present theory. One is a disconnection syndrome: The lesion has disconnected the systems for action (e.g. the action plan system) from systems for speech (e.g. the sentential system). Since the problem here is not so much with movement *per se* as with integration of verbal instructions and motor responses, these patients can imitate actions and manipulate objects appropriately, but cannot initiate actions on command (cf., Geschwind, 1975).

The theory suggests a different basis for ideational apraxics experiencing difficulties sequencing an action. The sequence nodes are the problem here. If a lesion weakens or distorts the inhibitory interactions between sequence nodes, whole classes of actions will tend to become misordered. Such a lesion may also impair the quenching and self-inhibitory mechanism that enables sequence nodes to return to resting level following activation. This would increase the likelihood of perseveration errors; i.e. repetition of a given behavior or behavior component.

**Ideomotor apraxia.** Ideomotor apraxia frequently occurs with lesions to the dominant (usually left) parietal lobe and subcortical white matter in the region of the supramarginal gyrus (Heilman, 1979). The plan of action seems intact for these patients but the individual components of a gesture are jerky, clumsy and uncoordinated, whether in performance to command, imitation or use of actual objects. The subgroup with solely cortical damage seems generally incapable of recognizing their own actions as being clumsy. When shown films of smooth vs. clumsy movements, these patients often pick the clumsy act as the correct one (Valenstein and Heilman, cited in Heilman, 1979). When miming an action such as using a hammer, these apraxics are also known to use a body part instead of the imagined object (e.g. the fist is used to represent the head of the hammer rather than to hold the handle).

The clumsiness or arhythmia of ideomotor apraxics is readily explained under the node structure theory. The rhythmicity or smoothness of an action is a function of the timing nodes, which also determine the tempo or rate of action. However, the problem here is not that the overall rate is too fast or too slow but that it is inconsistent: Fast pulses are intermixed with slow ones, so that the sequence of movements appears jerky, clumsy and unpredictable. The fact that some of these apraxics cannot distinguish between clumsy and graceful movements is to be expected under the theory, since the higher level nodes for perceiving and producing actions are identical. It is also possible that the higher level systems for analyzing visual concepts have undergone damage in these patients, contributing further to their inability to distinguish clumsy from fluent actions.

The use of a body part as substitute for an imagined object (e.g. a finger for a spoon or a fist for a hammer head) is somewhat more complex under the theory. Here the patients seem to be substituting a similar but inappropriate action (hitting an object with the fist or getting food into the mouth with the finger(s) in these examples). Moreover, the substituted action involving the body part may be generally more frequent, a major contributor to errors of this sort under the theory. The fact that body parts are present in experience whereas an imagined object is not could also contribute to these substitutions (see the above discussion of environmental susceptibility): As expected under the theory, the performance of these patients typically improves dramatically when using an actual rather than imagined object (Heilman, 1979).

#### The Physiological Plausibility of Node Structure Theory

All theories are intended to go beyond existing data and to stimulate either direct or indirect tests. For theories in human neuropsychology, however, direct tests are often impossible and indirect tests are difficult and time-consuming. Before testing the neural implications of a theory based originally on behavioral data, a preliminary evaluation of its physiological plausibility is desirable: What neural mechanisms are required or suggested by the theory and how plausible are these mechanisms given the current state of our physiological knowledge?

Each node in the theory consists of one or more interconnected neurons and increases in linkage strength for the connections between nodes may reflect the increased efficiency of neural transmission across synapses that results from repeated post-synaptic activation (Eccles, 1972). At least in higher level systems, however, priming cannot be equated with short-term potentiation across a synapse, and activation cannot be equated with the firing of a neuron, since neural potentiation and firing obey very different time characteristics from those required for the priming and activation of higher level nodes. Rather, activation of a node may correspond to rates of firing of a neuron that can be sustained without decrement by means of an excitatory collateral. Priming would then correspond to the range of firing rates which are below the threshold of the excitatory collateral and which cannot therefore sustain activity of the parent neuron. An inhibitory collateral with an even higher threshold may then introduce the self-inhibition that follows activation of the parent neuron.

Given a physiological instantiation such as this, the node structure theory requires a nervous system with five general characteristics, the plausibility of which we examine below. One general characteristic is a large number of components with a multiplicity of connections between them. Since each node consists of one or more neurons, the theory requires billions of neurons with hundreds of connections to and from each one. In line with this requirement, the human nervous system contains over 140 billion neurons (Kolb and Whishaw, 1980) and each of these can synapse with and receive synapses from over 1000 other neurons (Eccles, 1972).

Functionally specific morphological subdivisions within the nervous system are a second requirement of the theory: neurons must be organized into systems and domains or functionally distinct pools. In line with this requirement, the nervous system seems to be organized into many subcomponents with specific although not always completely understood functions. As Brodal (1973, p.687) points out, "It is the rule, rather than the exception that even a small nucleus (or pool of neural cell bodies) can be divided into parts or territories which differ with regard to cytoarchitecture, glial architecture, vasoarchitecture, fiber connections, synaptic arrangements and by its chemistry." Neural compartmentalization characterizes even the lowest level spinal systems controlling muscle movement. Consider the alpha motoneurons for example, the lowest level nodes within muscle movement systems. The cell bodies of alpha-motoneurons are clustered into pools at every level in the spinal cord and like a domain, each pool is functionally distinct, innervating motor units within a single muscle or group of anatomically related muscles (see Schmidt, 1982).

The third general requirement is that the nervous system be organized into motor, sensory and association systems each with a hierarchy of levels of function. Evidence supporting this general organizational structure has been accumulating since the time of Hughlings-Jackson and is well documented in recent literature (see for example Kolb & Whishaw, 1980).

A fourth general requirement is a set of semi-specific activating systems which function like sequence nodes. Recent evidence indicating that the reticular formation contains many individual nuclear groups with semi-specific rather than completely nonspecific activating functions (see Kolb & Whishaw, 1980) renders this requirement physiologically plausible even though the actual function of these nuclear groups remains to be determined.

The fifth general requirement is that voluntary actions be accompanied by a rhythmic activity corresponding to the periodic pulses from the time nodes. This requirement seems physiologically plausible in view of recently observed correla-

tions between the onset of some voluntary activities and rhythmic bursts from mid-brain and forebrain structures in the rat (Bland & Vanderwolf, 1972). The 4 - 7 cps 'theta' pulses from the hippocampus to the forebrain specifically suggested to Kolb & Whishaw (1980, p.241) that the forebrain "is controlling voluntary movements to ensure that they are appropriate in sequence, time and place." Whether pulses from hippocampal timing nodes to sequence nodes in the forebrain are the basis for the theta rhythm is currently unknown but this and other hypotheses concerning the neural substratum for the present theory seem sufficiently plausible to warrant further test.

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