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Abstract

Viapoint (VP) movements are movements to a desired point that are constrained to pass through an intermediate point. Studies have shown that VP movements possess properties, such as smooth curvature around the VP, that are not explicable by treating VP movements as strict concatenations of simpler point-to-point (PTP) movements. Such properties have led some theorists to propose whole-trajectory optimization models, which imply that the entire trajectory is pre-computed before movement initiation. This paper reports new experiments conducted to systematically compare VP with PTP trajectories. Analyses revealed a statistically significant early directional deviation in VP movements but no associated curvature change. An explanation of this effect is offered by extending the Vector-Integration-To-Endpoint (VITE) model (Bullock and Grossberg, 1988), which postulates that voluntary movement trajectories emerge as internal gating signals control the integration of continuously computed vector commands based on the evolving, perceptible difference between desired and actual position variables. The model explains the observed trajectories of VP and PTP movements as emergent properties of a dynamical system that does not precompute entire trajectories before movement initiation. The new model includes a working memory and a stage sensitive to time-to-contact information. These cooperate to control serial performance. The structural and functional relationships proposed in the model are consistent with available data on forebrain physiology and anatomy.

Key words: neural networks, viapoint movements, trajectory generation, vector integration to endpoint, gating, working memory, time to contact, perception-action cycle, dynamical systems.
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1. Introduction

Reaching plays an important role in the everyday functioning of people and other primates. In general, reaching movements involve the coordinated action of a large number of muscles spanning hip, shoulder, elbow, wrist and finger joints. In the course of a reach, these muscles are functionally constrained to form a synergy (Bernstein, 1967) or coordinative structure (Kugler, Kelso & Turvey, 1980; Turvey, 1990). How such synergies are controlled and organized by the central nervous system is a key question in the study of prehension.

Several classes of models have been proposed for the control and organization of (simple) PTP reaching movements, including motor programming models (Hoff & Arbib, 1993; Jeannerod, 1988), equilibrium point models (Bizzi, 1991; Hogan, 1984; Feldman, 1986), linear control models (Plamondon, 1992), nonlinear dynamical systems models (Schöner, 1990, 1994; Zaal, Bootsma & Van Wieringen, in press) and neural network models (Bullock & Grossberg, 1988; Kawato, Maeda, Suzuki & Uno, 1990). Whereas all of these models are consistent with certain aspects of the kinematics of reaching movements, they differ on several relevant dimensions, including: (i) the degree to which they can accommodate many motor psychophysical properties of reaching movements; (ii) the degree to which the proposed control structures are consistent with known neurobiological constraints, including volitional aspects of movement control; and (iii) the degree to which learning and performance depend continuously on currently available information, with no dependence on explicit foreknowledge of system geometry and minimal dependence on memory. Because the vector-integration-to-endpoint (VITE) model (Bullock & Grossberg, 1988) and its subsequent elaborations (e.g., Bullock, Grossberg & Guenther, 1993; Bullock, Cisek, & Grossberg, in press) stand out among existing models on these three bases, we use the VITE modeling strategy to study how the kinematics of a reaching synergy are controlled to generate via-point trajectories.

To date, most research on reaching has been conducted to characterize the kinematic properties of point-to-point (PTP) movements. In PTP movement, initial and final positions of the hand are given by instruction, but the intermediate trajectory is generated by the subject. In viapoint (VP) movements, the subject is instructed to make the hand pass over one intermediate position, the viapoint, during movement from the initial to the final position. Otherwise, no constraints are imposed on the trajectory. Generally observed features of PTP movements are nearly straight or slightly curved handpaths, and bell-shaped velocity profiles, whose symmetry varies as a function of movement duration (Atkeson & Hollerbach, 1985; Beggs & Howarth, 1972; Georgopoulos, et al., 1981; Guenther & Barreca, 1996; Morasso, 1981; Nagasaki, 1989; Soechting & Lacquaniti, 1981; Zelaznik, et al., 1986). For VP movements, the trajectory bends smoothly around the intermediate target position, and observed peaks in the handpath curvature coincide with local minima in the velocity profiles (Abend, et al, 1982; Flash & Hogan, 1985; Hogan & Flash, 1987; Uno et al., 1989). Furthermore, a tendency for movements of different lengths to be completed with approximately equal durations was observed to hold for both PTP movements and for segments of VP movements. This property is generally known as the 'isochrony principle' (Viviani & Terzuolo, 1983). Findings such as these suggest that the
submovements of VP movements are not performed independently. The question is how these dependencies arise from task-dependent operation of the underlying control structures.

In analyses of the kinematic properties of more complex movements, the notion of superposition often served as a guideline (Flash & Hogan, 1985; Hogan, 1984; Morasso & Mussa Ivaldi; 1982; Morasso, et al., 1983; Soechting & Terzuolo, 1987; Viviani & Cenzato, 1985; Viviani & Terzuolo, 1983). According to this notion, VP movements or script are assumed to result from a strict superposition of elemental movements. Marteniuk, et al. (1987), however, showed that task-specific constraints determine kinematic features of serial movements. By comparing two alternative sequential tasks (picking up a disk and either throwing it into a large box or fitting it into a tight well), this study revealed that the decelerative phase of the end effector's movement was prolonged in the latter, higher precision, task. A comparable task-specificity is expected in the handpaths of VP movements. From studies of handwriting, for instance, it is now known that the way strokes are performed depend on what strokes follow (Teulings, 1996), whereas a similar task-specificity has been found in aiming for a target with a hand-held stylus (Sidaway, Sekiya, & Fairweather, M., 1995). Also, data on the temporal patterns of rapid movement sequences in speech and typing (Sternberg, Monsell, Knoll & Wright, 1987) suggested that serial components are simultaneously active, and as a result, capable of mutual influence. This mutual influence expressed itself in the positive relationship between planned sequence length (measured in number of items) and both initial item reaction time and mean unit production time, for typing and speaking tasks. Here a key observation was that later elements of the planned sequence influenced the initiation time of the first element of the sequence.

Thus far, modellers of sequential hand and finger movements have mainly used internal scripts, or information arising within the neuro-muscular part of the perception-action system, to adjust onset and offset times or phase lags of their particular units of movement (cf. Bullock, Grossberg & Mannes, 1993). Some researchers (e.g., Flash & Hogan, 1985) have proposed that the interactions between submovements involve optimization-based pre-computation of entire trajectories. Not only would this impose large working memory loads, but the work of ecological psychologists has indicated that phenomena of motor equivalence and timing are features of the perception-action cycle (Beek & Bootsma, 1991; Gibson, 1979; Turvey, 1990), which argues against preformation of trajectories. Though some models have begun to incorporate perception to allow motor equivalence (e.g., Bullock, et al. 1993), the role of ecological timing variables has not yet been reflected in these models. Yet in many cases, it has been demonstrated that a change in activity, such as a movement onset or movement braking, is elicited when a threshold value of time to contact is reached during approach to a perceived object or boundary (Lee, 1976; Lee & Reddish, 1981; Lee and Young, 1986; Lee, et al., 1983; Riccio, 1993). Catching or grasping an object are examples from daily life in which it is likely that time to contact guides our behaviour.

In this paper, an extended version of the VITE model is proposed for the voluntary neural control of arm trajectory generation. This new model uses expropriospecific information, in the form of visually perceivable position vectors, difference vectors, and times-to-contact. The proposed neural circuit combines a neural stage sensitive to time-to-contact information (Lee, 1976) with elements of a synergy synchronizing, vector integration network (Bullock & Grossberg, 1988; Bullock et al., 1993), and elements of feedback sensitive, sequential gating
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networks (Boardman & Bullock, 1991; Bullock, Grossberg & Mannes, 1993). Without any optimization-based pre-computations, the resultant model system generates reaching trajectories that realize sequential plans while remaining sensitive to variations in the perception-action cycle. Hence, the model approaches the problems of trajectory generation from the viewpoint that information detection and performatory activity are co-organized in the achievement of a spatiotemporally constrained action (Beek & Bootsma, 1991). The model exploits the fact that action and perception are mutually dependent (cf. Gibson, 1979) and shows how this idea can be used to simplify the problems apparent in motor planning. It is demonstrated how task-specific features of PTP and VP movements emerge from interactions among multiple planning components, and how time to contact, as specified in the evolving relationship between the hand and the target object, temporally constrains trajectory formation. Because several of the main computational processes out of which the present model is constructed were introduced in the VITE model (Bullock & Grossberg, 1988; 1991), we will first summarize this neural circuit. During the exposition, we will support the proposed stages with neurophysiological evidence. Then an experiment is reported that was conducted to compare the kinematic properties of PTP and VP movements. On the basis of the obtained empirical data, the core VITE circuit is modified and extended to explain the observed characteristics of VP movements. The proposed control structures of the extended model are related to compatible data on forebrain physiology and anatomy. Simulations of the new model show several key properties of VP movements, notably, preparatory direction deviations, the isochrony principle (Viviani & Terzuolo, 1983), curved passage of viapoints, and the inverse relationship between curvature and velocity (Abend et al., 1982; Viviani & Terzuolo, 1980).

2. Synchronous trajectory generation by VITE

The VITE trajectory generator (Bullock & Grossberg, 1988 a,b; 1991) is a neural model that accommodates a large corpus of neurophysiological and behavioral data. Initial modeling studies showed how groups of effectors may be dynamically bound and unbound into synergies that perform synchronous reaching movements at a desired speed. They also offered an explanation for kinematic properties of reaching movements that included the bell shaped velocity profile, Woodworth's law, Fitts's law and variations in velocity profile symmetry as a function of movement duration. The model has been extended in the form of the DIRECT and DIVA models to incorporate inverse differential transformations between task space and motor coordinates for both reaching (Bullock, Grossberg & Guenther, 1993; Fiala, 1994, 1995) and speech production (Guenther, 1992; Guenther, 1994, 1995). These transformations were shown to enable motor equivalence and to be learnable with the help of perceptual information generated by action. Another variant called VITEWRITE incorporated voluntary amplitude scaling to extend the model to cursive handwriting (Bullock, Grossberg & Mannes, 1993). The most neurobiologically elaborated VITE model (Bullock et al. 1997) incorporated proprioception and gravity load compensation, while accommodating anatomical and physiological data on over a dozen distinct cell types that have been identified by prior single-cell recording studies.
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The simplest version of the VITE model, schematized in Figure 1, consists of the processing stages necessary for the priming and voluntary generation of variable-speed PTP movements. In the model, the movement vector needed to steer the hand from a current to a desired final position is computed continuously. In addition to incorporating stages that register current position and desired final position, as well as the movement, or difference, vector between these, the VITE model also incorporates a site for on-off gating of execution of the difference vector, allowing PTP movements to be enacted at variable speed. By making the required gating signal a variable scalar gain, or multiplier, the property of speed modulation is introduced simultaneously with the property of execution gating. When the gating signal is off, a movement vector can be primed without being immediately enacted. Such priming is necessary for deliberative activity and for minimizing the reaction time of movements whose adaptedness depends on quick execution in response to external signals.

The target position vector (TPV) stage shown in Figure 1 represents desired positions, such as the positions of visible targets, in body-centered coordinates. These body-centered coordinates might be motor coordinates, such as muscle length coordinates, or spatial coordinates, such as polar or cartesian coordinates. In the present paper, which focuses on the trajectory of the hand in space, we will interpret VITE to be operating in body-centered spatial coordinates (Bullock, Grossberg & Guenther, 1993; Fiala, 1995). The present position vector (PPV) stage represents the actual position of the hand in the same coordinate system. The discrepancy between TPV and PPV is continuously computed at the difference vector (DV) stage, using excitatory signals from the TPV and inhibitory signals from the PPV. Difference vectors represent both magnitude and direction information, specifying the displacement needed to contact the target. At the DVxGO stage, the DV output signal is multiplied, or gated, by a GO signal. While the GO signal is zero-valued, any DV command is prevented from execution. Thus instating a TPV and computing a DV while GO is zero constitutes the operation of motor priming (Georgopoulos et al., 1986). When the GO signal becomes positive, the PPV stage starts integrating signals at a rate proportional to DV times GO. Voluntary changes in the amplitude of the GO signal can modulate movement rate without affecting the direction coded by the difference vector (DV).

Because of these relations, the DVxGO signal can be interpreted as a movement velocity command, and the PPV can be interpreted as a present position command. In fact, the global shape of the temporal evolution of the model’s DVxGO variable has been shown to match experimental velocity profiles for PTP movements of the hand quite well, and significantly better than alternative models (Bullock & Grossberg, 1988a, b; Nagasaki, 1989). In more complete versions of the VITE model, a distinction is made between a present position command and a perceived position vector (Bullock, et al., 1997), but for present purposes, these two functional roles may be attributed to a single PPV stage. In that case, PPV output defines that position of the end-effector that lower level, force generating, circuits attempt to instate. Among the models pertinent to lower level control is a sensory-spinal-muscular circuit known as the Factorization of LEngth and TEnsion (FLETE) model, which explain how positions can be maintained at variable
joint-stiffness levels (Bullock & Contreras-Vidal, 1993; Bullock & Grossberg, 1991). Thus the overall theory suggests that variable speed control and variable stiffness control are achieved at distinct levels within the motor hierarchy.

While performing a normal PTP movement, the TPV is constant during the entire movement. Initially, some discrepancy between the PPV and TPV is registered at the DV. When the GO signal is activated, the product DVxGO becomes positive. As a result, the PPV begins to change in the direction of the TPV. This causes the arm to move, and as it approaches the target the discrepancy between TPV and PPV, computed as the DV, declines toward zero. However, this does not immediately reduce the velocity, because whereas the DV is declining, the GO signal is growing. The product of these two signals first grows and then declines, giving rise to a bell-shaped velocity profile. Ultimately, the movement causes PPV to match TPV, at which time DV reaches zero, as does DVxGO. Therefore the PPV ceases to change, and the arm stops moving (assuming that the PPV command is well followed with help from lower order circuits, e.g., spinal circuits incorporated in the FLETE model). Note that the PPV command can stop changing even if the GO signal is large, provided that the DV is zero.

Because all outflow signals from the DV stage are multiplied by the same GO signal, whose value grows smoothly in the course of the movement, the components of a synergy tend to complete their motions synchronously, whatever the relative initial sizes of the components of the DV command. This temporal equifinality property even holds when the different DV components that are multiplied by a given GO signal have different onset times (Bullock & Grossberg, 1988b), provided that the range of onset times is not a large fraction of the movement time. This property promotes stable control of a temporal series of elemental movements. Consider, for example, the generation of via-point trajectories, in which the end effector must always reach in one direction before changing direction to move to the final target position. To effect the change in direction, many of the muscles that are contracting in the first part must lengthen in the second part, and vice-versa. Without synchronization of synergies, it would either be necessary to have a long pause at the via-point to allow lagging components to catch up, or it would be necessary to tolerate large positional and directional variances in the neighborhood of the via-point. In fact, the via-point is passed at a velocity well above zero, and trajectory variance is modest near the via-point (Flash & Hogan, 1985; Hogan & Flash, 1987; Uno et al., 1989).

3. The VITE model compared with neurobiological data

In the VITE model, the target position vector (TPV) stage and the gradual updating of the present position vector (PPV) movement commands are essential processes in generating a movement from a given position to a desired position. Evidence for gradual updating of a present position command toward a target value comes from experiments of Bizzi and his colleagues. Polit and Bizzi (1978) trained monkeys who were deprived of visual feedback to move their forearms from designated starting positions to different target lights. Before proprioceptive deafferentation, these monkeys were able to rotate their forearm to the target even when the accustomed initial position was changed, thus indicating a spatial position control system that could use proprioceptive information from the limb in place of visual feedback. After
deafferentation by dorsal rhizotomy (which severs all feedback from muscle and joint receptors),
the vision-deprived monkeys' forearm movements terminated at a position shifted away from the
target by an amount proportional to the upper arm's passive movement, whatever the initial angle
of the forearm. These findings stress the role of accurate target position and present position
specifications in setting up a movement trajectory (Bullock & Grossberg, 1988). Additional
experiments (Bizzi et al., 1982; 1984) suggested that the position setting for the arm is indeed
gradually updated instead of being controlled by abrupt changes in equivalent spring parameters
such as stiffness and resting length. In a similar setting, and after dorsal rhizotomy, the monkey's
forearm was surreptitiously changed from the initial starting position to the target position. After
the target light was activated and the arm released, the monkeys, deprived of all feedback, initially
moved their arm back towards the starting position, before reversing direction and moving toward
the target. The sooner the arm was released, the further it traveled back; and when no new target
was visually specified to the monkey, then after its release from the position to which it had been
displaced by the experimenter, the arm sprang back to its starting position. This full set of
phenomena have now been simulated in a version of VITE that was extended to include
proprioceptive feedback (Bullock et al., 1997; Cisek et al., 1997).

From the neurophysiological perspective, the VITE model makes claims about brain
mediated operations, and thus about cell types and pathways that should be observable in primate
brains. Because this issue has been extensively treated elsewhere, we will restate only the
essentials here. The most extensively developed version of the VITE model (see Bullock et al.,
1997) offers a computationally well-motivated explanation of a dozen or so distinct observable
cell types. The following remarks focus on four key interesting correspondences, involving the
most notable operations in the model: the difference vector computation, including pre-movement
priming; the "phasic" activity restricted to the movement time interval that would be observed at a
DVxGO stage; the "tonic" cell activities that would be observed at the TPV and PPV stages; and
the gating and velocity scaling operation performed by the GO pathway.

**Difference vector computation and motor priming.** If the VITE model is correct, then there must
be a cellular population that computes the direction from current position to desired position
continuously during movement, and this same cellular population must be primable in a task
where the monkey is given knowledge of the target before he is given "permission" to reach for
that target. Such a population is now known to exist. Vector encoding as a design principle for
the control of arm movement is supported by neurophysiological evidence on primate cells from
several precentral (e.g., areas 4 and 6) and postcentral (e.g., area 5) regions of the cerebral cortex
(Evarts & Tanji, 1974; Georgopoulos, 1986; Georgopoulos et al., 1982; 1986; Kettner et al.,
1988; Lacquaniti et al. 1995; Schwartz et al., 1988; Tanji & Evarts, 1976). These studies mea-
sured the activity levels and activity level changes of cell populations in arm controlling areas of
the cortex in monkeys trained to execute pointing movements in two or three-dimensional space.
It was found that the activity levels of many cells were direction dependent but not, as was
explicitly demonstrated by Kettner et al. (1988), dependent on the position of the target.
Moreover, the temporal behavior of VITE's difference vector stage is consistent with that of an
average potential of a population of neural cells as observed by Georgopoulos et al. (1982).
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later studies Georgopoulos and colleagues (Georgopoulos et al., 1986; 1993) studied how movement direction is encoded by a population of cells, in which each is broadly tuned to direction, and in which the distribution of preferred directions was nearly uniform. They found that the neural population vector, that is the resulting vector sum of all the individual cells' preferred directions weighted by their firing rates, encodes movement direction in a unique fashion. Below we show that if the DV stage is implemented in a similarly distributed way, one would observe the same property. Finally, vector cells in several regions of cortex have been shown to be pricable in the above studies.

Velocity and position commands. Among the cortical cells studied in the reports cited above, detailed research has shown that there are various subtypes (see Kalaska & Crammond, 1992, for review). Among these are phasic MT cells as well as tonic cells, which appear to correspond, respectively, to DVxGO and PPV cells (see Bullock, et al., 1997, for discussion). The observed tonic cells hold an activity level proportional to a position value -- as would be expected at a PPV stage. Schwartz (1993) performed a study in an area known to be dominated by phasic MT cells and was able to show that during a sinusoidal tracking task neuronal activities varied not just with movement direction but also with movement speed -- as would be expected at a DVxGO, or velocity command, stage. These results in a curve tracing task are complemented by a report by Hocherman & Wise (1993), who measured single cell activities in monkeys trained to perform PTP and VP movements. Together they indicate that movement direction is reliably foretold by direction and velocity sensitive cell populations in precentral cortex during PTP, VP, and curve tracing tasks. It can be concluded that a difference vector (DV) stage exists, and that it plays an essential and continuous role in determining movement direction.

Gating and velocity scaling by a GO pathway. The clearest evidence regarding movement gating by an internal GO pathway comes from work on the oculomotor system (e.g., Grossberg, Roberts, Aguilar & Bullock, 1997; Guitton, 1991; Hikosaka & Wurtz, 1983). In that system, it has been established that a planned eye movement vector command sent to the superior colliculus is normally expressed only when the gate through the superior colliculus is opened by termination of an inhibitory signal transmitted to superior colliculus by axons that originate in the substantia nigra pars reticulata (SNr). The SNr is one of the output nuclei of the deep forebrain aggregation of nuclei known as the basal ganglia. However, eye movements differ from skeletal movements in that their velocity is not subject to voluntary modulation. Thus when the nigral gate opens through the SC, it apparently opens in an all-or-none manner.

Similar, but more complicated, evidence suggests that both the SNr and the internal (also called medial) segment of the globus pallidus, the GPi, jointly perform a gating and velocity scaling operation for planned movement commands sent to the motor thalamus and precentral cortex. Horak and Anderson (1984a, 1984b) studied the influence of changing globus pallidus activity on rapid arm-reaching movements, and discovered that electrical stimulation reduced movement time, whereas kainic acid lesions of these sites increased movement time. Whereas movement speed obviously was influenced, the accuracy of movement and the sequential activation of muscles involved in the task were not. Furthermore, in conditions in which no targets
were specified, stimulation did not lead to motion. These observations are in agreement with the notion that the GO signal acts multiplicatively on all channels of the synergy specified at the DV stage. More generally (see reviews in Jankovic and Talosa, 1993), it is well established that Parkinson's disease results from loss of dopamine producing cells in the basal ganglia (in the substantia nigra pars compacta). Artificially induced Parkinson's disease in monkeys shows that a primary symptom is bradykinesia, or slowing of movement. In advanced stages of the disease, bradykinesia advances to akinesia: inability to execute a planned voluntary movement. Both early and advanced stages are consistent with reduced opening of the gate controlled by the GO pathway.

Gating of both thalamo-cortical loops and the superior colliculus by the basal ganglia is now very generally accepted, but its precise role within a more inclusive motor system design remains to be clarified. Prior to looking for the perhaps subtle variations across neural population activities that can choose between alternative mechanisms, it is necessary to have precise hypotheses to test. The following sections take two steps toward formulation of such hypotheses. The first details an experiment conducted to compare the kinematics of PTP and VP movements. The aim of this comparison was to further the process of identifying statistically reliable behavioral indices that may prove to be "signatures" of the mechanisms that make VP trajectories different from mere concatenations of PTP trajectories. The second section proposes a mechanism consistent with the measured signatures. The extended arm-control model introduced below incorporates aspects of the known cortico-basal ganglionic system for eye-movement control, in particular dual excitatory and inhibitory projections from planning sites to executive sites, and execution gating realized partly by release from inhibition. This hypothetical mechanism is much different than the optimization mechanisms proposed heretofore to explain VP movements, although experimental evidence linking the basal ganglia with reinforcement learning (Schultz, Apicella & Ljungberg, 1993) suggests a way to incorporate a biology-based optimizing process.

4. Experimental Method

Subjects. Four right-handed subjects, 19-24 years in age, participated. Two subjects were aware of the purpose of the experiment.

Apparatus. The subjects were comfortably seated in a chair positioned in front of a table with a square pattern of 13 visible light emitting diodes (LEDs), as depicted in Figure 2. The center-to-center distance between the 1.0x1.0 cm LEDs was 30.0 cm. A computer program was designed to light up the LEDs that specified the movement targets. A single IRED was mounted on a small box in which the subjects had to insert their index, middle and ring finger so as to slide it across the tabletop surface. The movements of this sliding endeffector were recorded with a 2-D Selspot system connected to a microcomputer. The sampling frequency was 156 Hz.
Design. Four distinct types of movement were performed: PTP, 1-VP, 2-VP and target switch movements. At the start of a trial, a single LED was turned on, indicating the position from which the subjects had to start their movement. After 1000 ms, the other LEDs specifying the targets of the point-to-point or the viapoint trajectories were lit for a duration of 4000 ms. When, after 3000 ms, the LED corresponding to the starting position turned off, the subjects had to initiate and execute the movement as quickly as possible. In the preparation of the experiment, VP conditions were explained as a PTP movement via an intermediate point. From this clarification the correct order of later target traversal became immediately clear to the subjects. In the target switch trials, the LED indicating the starting position was lit for 3000 ms. After 1000 ms the target LED was lit; 2175 or 2225 ms thereafter, this target LED switched off and another light switched on indicating the new target. PTP movements were specified by two LEDs, 1-VP movements by three LEDs, and 2-VP movements by four LEDs.

The subjects were told to move as fast as possible and not to be too concerned about the accuracy of their performance. They were discouraged from making corrections after the initial movement was terminated. No restraints were set on the overall body posture and the participation of other degrees of freedom. That is, the subjects were free to move other body parts such as the shoulder and the thorax.

To constitute the movement conditions, the paths were evenly distributed over the LED-table. In Table 1, the performed paths are specified in terms of the LED numbering scheme used in Figure 2. The four levels of the table, separated by double lines, correspond to the four movement types. Conditions in the upper three levels (PTP, 1-VP and 2-VP movements) were also performed in reverse directions. The trajectory performed in the specified LED sequence was designated 'A', whereas the opposite completion was designated 'B'. For target switch conditions, a distinction was made between early (175 ms) and late (225 ms) repositioning of the target. In the following, the numbers of conditions always refer to those in Table 1.

Every experimental session started with 20 practice trials in which the subjects familiarized themselves with the task. The 420 randomly ordered trials consisted of 42 conditions which were presented 10 times each. These trials were recorded in a single session which lasted two and a half hours. Two fifteen minute breaks were allowed during this session.

Data reduction. Velocity profiles in the x and y dimensions were obtained by taking the time-derivative of the raw position data followed by smoothing with a recursive second-order low-pass Butterworth filter (cut-off frequency 25 Hz). From these velocity profiles, the tangential velocity was calculated. The tangential acceleration profile was computed by differentiating the tangential velocity profile after which the series were filtered with a recursive second-order low-pass Butterworth filter (cut-off frequency 15 Hz).

A peak-detection algorithm was applied to the tangential velocity profile. A point value was accepted as an extremum ($V_{\text{peak}}$ or $V_{\text{min}}$) when the surrounding eight sample values were all smaller (for $V_{\text{peak}}$) or all larger (for $V_{\text{min}}$) than the point value in question. Movement onset and
movement offset were determined by searching for a velocity threshold of 4 cm/s on the outer sides of the extrema in the time series of the tangential velocity. The time between these threshold crossings will from now on be referred to as the MT (movement time) and the time series of kinematic values (position, velocity) between these crossings will be referred to as the trajectory. The velocity had to remain lower than the 4 cm/s threshold for at least 60 ms for a particular point to qualify as the onset or offset of movement.

For the PTP and VP movements the trajectory curvature (TC) was computed at five temporally equidistant points. The TC points were proportions of the total MT associated with the segment; the TC was measured at points corresponding to .17, .33, .50, .67, .83 of the MT of the segment. To compare the TC of movements between the same LEDs embedded in different conditions and tasks (PTP or VP movements), the 1-VP movements were divided in two segments. The first segment was determined from the start until the time of \( V_{\text{min}} \), the second segment from thereon until the end. At each of those instants the TC was computed according to

\[
TC = \left( \frac{d^2y}{dx^2} \right) \left( 1 + \left( \frac{dy}{dx} \right)^2 \right)^{3/2}
\]

and then an average TC per MT proportion per condition per subject was computed. Thus 5 TC computations were made for each PTP trajectory, 10 TC computations were made for each 1-VP trajectory, etc.

In order to compute the difference in directionality between shared segments of PTP (AB) and VP (ABC) movements, the maximal distance from the movement trajectory to the line segment AB defined by the LED positions was calculated for each trial in the two conditions. For each datapoint along the measured trajectory, the distance from the point to the line segment was calculated. Subsequently, the peak distance value in the resulting time series was determined with the help of a peak-detection algorithm. A final estimate of the true maximal distance of the trajectory from the line segment AB was computed by averaging over five temporally successive distance values (spanning 32 ms), with the middle value being the previously detected peak. The resultant estimates for the peak distances were averaged per condition and per subject and analyzed statistically. The same was done for the times at which the maximal distances to the line segment AB were detected, as well as for the mean distance from the movement trajectory to the line segment AB during the first and the second half of the movement trajectory between A and B.

### 5. Results and discussion

*Spatial performance.* Typical examples of the observed trajectories in the four movement conditions are depicted in Figure 3. As can be seen, point-to-point performances were roughly straight (panels A-D). However, on close inspection, minor deviations from the shortest line connecting the initial and final targets are apparent in some trials (e.g., panel C).
Undershoots of the intermediate point(s) were observed in some VP movements and overshoots in others (panels E-H). A smooth curve around the intermediate point(s) was clearly visible. Table 2 presents the average total distance covered along the paths of motion for each condition. These means show that the average distance covered was always longer than the minimum, or straight line, distance.

The movements from the target switch trials bent smoothly towards the relocated target in most cases (panels I-J). The initial parts of the target switch trajectories roughly resembled those of the PTP movements. In some trials, subjects initially failed to register that the target had switched. Late realization that it had switched led these subjects to perform two PTP movements. The 2-viapoints and the target switch trajectories were characterized by high variability, especially in the tangential velocity profile.

**Velocity profiles.** Figure 4 shows the velocity profiles of the trajectories depicted in Figure 3. The unimodal velocity profiles of the PTP movements and the bimodality in the velocity profiles of the 1-VP and the target switch movement are readily observed. Of all PTP movements, 99% contained one velocity peak in the tangential velocity profile. For 1-VP movements, 95% of all the trials contained two velocity peaks. For 2-VP and target switch movements the consistency in performance was markedly lower: 39% contained three peaks and 67% possessed two peaks in the velocity profile, respectively. Comparing the velocity profiles of 1-VP and 2-VP movements in Figure 4 indicates that the valleys of the latter were less pronounced than the former, which was a common finding.

To assess isochrony of the two segments of the 1-VP movements, the ratio of time till the mid-trajectory $V_{\text{min}}$ to the total MT was computed. This isochrony measure for 1-VP movements had a mean of 0.47 and a SD of 0.07 (range from 0.31 to 0.81). The value of .47 is near the perfect isochrony value of 0.5.

**Straightness and curvature.** From the general kinematics described above, it is clear that PTP and 1-VP movements were performed most consistently. Therefore, those two movement types were best suited for examining how VP movements differ from mere concatenation of two (or more) PTP movements. Any systematic difference between the kinematics of a submovement in a VP movement and the kinematics of the corresponding PTP movement is evidence against a pure serial concatenation of submovements. However, the absolute biomechanical requirements associated with changing directions at the viapoint makes it likely that sufficiently refined measurements will detect some departure from pure concatenation near the viapoint, unless the two segments are separated by a zero velocity phase, which was not true in this experiment where subjects were instructed to complete the movement quickly. Of most interest from the neural
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control perspective, therefore, was whether forthcoming movements have effects that are detectable in the initial portion of prior movements, far from the viapoint and long before some interaction is physically unavoidable.

To the extent that the planning of a subsequent submovement affects the performance of the initial submovement in the execution of a 1-viapoint task because of a whole-movement optimization process, this effect might be reflected in the trajectory curvature (TC) of the initial submovement. It is possible that the neural controller redistributes the required directional change along the whole trajectory in such a way as to avoid the high curvature that would be seen at the viapoint in a simple concatenation. Similarly, as proposed in the minimum-jerk model, the whole trajectory may be reformed so as to minimize the rate of change of acceleration. To locate differences of curvature, and in particular to test for a systematic early change in curvature, the TC in VP trajectory segments was compared to the TC in corresponding PTP movements. Two two-way repeated measures ANOVAs with movement type (PTP vs. 1-VP) and time-of-sample (five instants of TC measurement) as within-subject factors were performed because the VP movements were divided into two segments. The ANOVA comparing the first segment of the 1-VP movements with the PTP movements that corresponded to the same targets yielded no significant effects (conditions 3A, 4B, 5A, 9A & B and 10B). In the ANOVA with the second segment of the 1-VP movement (conditions 3B, 4A, 5B, 9A & B and 10A), there was a significant main effect of time-of-sample (F(4,12) = 18.24, p < 0.005). The latter effect was mainly due to significant differences for the first and the last sample of the second segment's curvature, viz. directly following the viapoint and during the final homing phase of the trajectory. Taken together, these results imply that there were no detectable preparations in the curvature of the first submovement of 1-VP movements. They also indicate that the visually apparent curvature at the two ends of the second segment are statistically reliable.

Movement direction. The absence of an early curvature change does not imply the absence of any early interactions between planned movement components. Visual inspection of viapoint trajectories in the present and in other studies revealed that 1-VP movements (ABC) often begin with a deviation in the direction opposite to that of the second target (C) before bending toward this target when approaching the viapoint (B) (see Figure 5). In contrast, PTP movements (AB) from the same starting point (A) toward a target identical to the viapoint in the corresponding 1-VP movements (B) are characterized by straight trajectories.

To assess the difference in directionality between PTP and 1-VP movements, the maximal distance from the movement trajectory to the line segment AB was estimated for each trial in the two conditions (see method section). A repeated measures ANOVA was performed on the intra-individual means of this measure with movement type (PTP vs. 1-VP) and workspace (conditions 4B-10B vs. 3A-9A) as within-subject factors. This ANOVA yielded a significant main effect of movement type, F(1,3) = 76.5, p < .02, in the absence of any other significant effects. 1-VP movements reached larger maximal distances from the line segment AB than (corresponding) PTP movements (10.8 cm vs. 6.5 cm). The observed deviations of the trajectories of the 1-VP movements were in the predicted direction, that is, in the direction opposite to that of the second target (C). No statistical effects were found in the ANOVA performed on the times at which the
maximal distances from the line segment AB were reached (240 ms for the 1-VP vs. 230 ms for the PTP movements). To determine during which part of the trajectories the difference between 1-VP and PTP movements was most pronounced, the average distances between these trajectories and the line segment AB during the first and during the second half of the movements from A to B were compared in a repeated measures ANOVA. In this analysis, a significant interaction effect was found between the factors movement type (1-VP vs. PTP) and movement part (first vs. second half): The average distance to the line segment AB was significantly larger during the second half of the AB segment of 1-VP movements (6.8 cm) than in the other three movement type-movement part combinations.

Insert Figure 5 about here

Conditions 5A and 9B (between LED 8 and 10) were not used in the preceding analyses because the movements produced in condition 9B, the 1-VP condition, showed an inflection toward instead of a bowing away from the second target (C) during the initial part of the movement (i.e., from A to B). Because a similar (even larger) inflection was observed in condition 5A, the corresponding PTP condition, it is reasonable to assume that this inflection occurred because of the specific biomechanical constraints operative in the region of the workspace in which conditions 5A and 9B were defined (flexion around the elbow joint while moving the hand from right to left and towards the body).

Experimental conclusions. From the results of the preceding analyses it can be concluded that in a 1-VP movement, the trajectory toward the viapoint is affected by the task requirement to move on toward a second target. Because this effect would be absent if VP movements simply consisted of a concatenation of PTP movements, a model is required in which the requirement to move to a second target after having reached the first interacts with the trajectory formation toward the first target. Because, in the VP movements, a deviation from a straight PTP movement occurred in a direction opposite to that of the second target, the interaction in question is likely to take place at the planning level, that is, at the level of the neural controller, and not solely at the biomechanical level. As shown below, the observed difference in directionality between VP and PTP movements, as well as the inferred interaction in the planning of VP trajectories, can be modeled with VITE, because in this model movement direction is specified in terms of a difference between vectors. Using a present position and multiple target positions, multiple DV's can in principle be instantiated in case of VP movements. These multiple DV’s interact on-line and result in a net executed movement direction. Such an interacting vector model has many precedents in physical science, and the multi-vector idea has been used in VITEWRITE as well as in a navigating version of VITE called NAVITE (Aguilar-Pelaez, 1995). In the latter, an obstacle avoiding trajectory toward a target was continuously computed as a weighted combination of an attractor DV (computed vis-a-vis the target) and repeller DV’s (computed vis-a-vis obstacles).

In the model presented in the next section, a planning stage mediating an interaction between multiple DV’s is introduced. The design incorporates the hypothesis that in a VP movement the DV associated with the final target begins as a net repeller, but becomes an
attractor once the time to contact the viapoint reaches a critical value. That it begins as a net repeller rather than as a zero vector is related to a hypothesis that deliberative choice requires an ability to actively inhibit attractive but temporarily unrewarding courses of action.

6. Heuristic description of the extended model

The proposed circuit is schematized in Figure 6. Before specifying the model mathematically, it will help to give a heuristic description of what we believe to be happening during a typical subject's performance of the viapoint task. We imagine that to begin, a subject simultaneously activates two distinct target representations, T₁ and T₂, in a working memory. For each of these the subject also computes distinct planning difference vectors, pDV₁ and pDV₂, between his current PPV and the represented targets. These pDVs project by separate excitatory and inhibitory pathways to the executive difference vector, or eDV, stage. The inhibitory pathways exist to prevent premature performance of planned DVs. However, to guarantee prevention of premature performance, the strength of the inhibitory projections must be stronger than the corresponding excitatory projections -- a result that can be achieved by self organization through a local learning rule (e.g., Gaudiano & Grossberg, 1991). Thus, despite the excitatory inputs, there is initially no output from the eDV stage. A competitive choice field with distinct sites CF₁ and CF₂, respectively excited by T₁ and T₂, then chooses/schedules T₁ as the initial target. As a result, CF₁ gates off the inhibitory pathway from the pDV₁ stage to the eDV stage. This unmasks the excitatory inputs from pDV₁ to eDV, and an output is generated from eDV that reflects the evolving mix of the excitatory input from pDV₁ and both the excitatory and inhibitory inputs from pDV₂. This mix evolves because upon activation of the GO signal, the PPV is updated by eDVxGO, and PPV updating leads to new pDV₁ and pDV₂ values.

During the movement, another, perceptual, network site is computing the time to contact (TTC) of the hand with the viapoint, i.e., the perceivable point corresponding to T₁. When the TTC falls below a critical threshold, which indicates that contact is imminent (CI), a pulse is generated that causes rapid suppression of activities T₁ and CF₁. As CF₁ declines, CF₂ grows and quickly wins the competition, i.e., is chosen. Then CF₂ output suppresses the inhibitory projection from pDV₂ to eDV, and thereby unmasks the excitatory input from pDV₂ to eDV. Consequently, eDV output is now dominated by a mix including excitatory input from pDV₂ and any residual excitatory and inhibitory input from pDV₁. However, because T₁ has been suppressed, there is soon no activity at pDV₁. Thereafter, the eDV is wholly determined by excitatory input from pDV₂. As the hand approaches the target corresponding to T₂, TTC once again falls below threshold, and generates a pulse. This time, the pulse suppresses both T₂ and CF₂. In fact, the circuit's structure is such that the pulse generated by perception of imminent contact will always suppress the most recently activated Tj and associated CFj, j = 1 or 2. Thus the TTC related pulse's action is non-specific, and has the correct effect without need for any target-specific learning.

The above description becomes complete when supplemented by a description of the dynamics of GO signal generation. We assume that the GO signal is the output of a two cell, excitatory cascade, G₁ followed by G₂. This cascade is excited when the first winner is chosen in the choice field, and is re-excited by any subsequent winners. As a result, excitatory output from
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G₂ gates on the executive channel from eDV to PPV. When TTC reaches threshold as the hand nears the viapoint, the resultant inhibitory pulse, which suppresses T₁ and CF₁, also inhibits G₁ and G₂. This causes a partial reset of the GO signal pathway. However, its output begins to grow again as soon as the inhibitory pulse has ended. Thus activation and deactivation of the GO pathway is linked to activity in the choice field. At the end of movement, the TTC pulse again inhibits the GO pathway, which then remains inactive because it is no longer excited after all targets have been deleted from the choice field.

7. Key hypotheses for extending the VITE model to encompass VP movements

Separation of planning and execution stages. One key hypothesis of the extended model is that interaction can occur between at least two planned components dimensionally consistent with the (unitary) difference vector stage within the original VITE model. In the new model, the DV stage of Figure 1 is therefore replaced by two stages, namely the planning difference vector stage (pDV) and the executive difference vector (eDV) stages. The pDVs are continuously computed by comparing the representations of desired target positions (Tᵢ) of a movement, with the present constellation of the effector system (PPV). Both of these latter stages, the Tᵢ and the PPV, can in principle be continuously updated by sensory inputs, i.e., they can be treated as registering perceptual variables. Thus the basic design allows the process of trajectory generation to remain sensitive to perturbations of the perception-action cycle. However, in this study the spatial loci -- and consequently the vector representations Tᵢ -- of the targets, are assumed to remain constant throughout the movement time, as is the case in viapoint experiments. The pDV outflow signals converge at the eDV stage, the gated output of which is used to update the present position vector, or PPV, stage.

Vector summation in a population of executive cells with broad directional tuning. The eDV stage is imagined to be a stage in which a resultant movement vector emerges from interactions among two or more inputs from the pDV stage and possibly other stages, e.g., stages that register the locations of obstacles. Because this stage is an executive stage, i.e., a stage that directly determines the form of movement, it must be structured in a way that allows it to participate in the kinds of motor learning that are needed to ensure accurate performance. Grossberg and Kuperstein (1986) argued that whenever accurate performance of a movement vector is required, each distinct movement vector (whether a difference vector or a position vector) should either be represented by, or address (i.e., project to and maximally activate) a distinct subset of a cellular population, which could provide a distinct context for learning the motor production parameters that are necessary for accurate response production given that context. This design principle seems to be used ubiquitously in the brain. Thus vector signals emerging from the semicircular canals are used to address sites within a neural map in the vestibulo-motor system (Robinson, 1992); retinal and eye position signals are used to address sites within maps in the oculo-motor system (Anderson, 1995); and vector inputs to motor cortex appear to address motor cortical cells in a direction-dependent way. Because we treat the eDV stage as a model of motor cortex, we therefore mapped the pDV outputs into an entire population of model cells that constituted
the eDV stage. In accordance with theoretical results on self-organized learning in sensory-motor pathways that mediate motor equivalent reaching (Bullock, Grossberg & Guenther, 1994), and in accord with the empirical observations of Georgopoulos and colleagues (Georgopoulos, Schwartz & Kettner, 1986; Georgopoulos, Taira & Lukashin, 1993) on movements made in a restricted region of space, we assumed that each eDV stage cell was tuned to the cosine of the angle between the cell's preferred direction and the pDV direction. It follows that an eDV cell's activity is maximal when the cell's preferred direction coincides with the pDV. We also assumed, again in accord with the data, that the cells' preferred directions were distributed uniformly across the 2-D space in which the task was performed. From this it follows that the response of the cell population varies smoothly with the input direction.

One major caveat should be mentioned here, although its resolution is not expected to affect the essentials of the present theory. Although Georgopoulos and colleagues have repeatedly interpreted motor cortical cell activities to specify Cartesian vectors, there are abundant empirical (e.g., Caminiti et al., 1991; Scott & Kalaska, 1995) and theoretical reasons (e.g., Bullock & Grossberg, 1988; Bullock, Grossberg & Guenther 1993; Mussa-Ivaldi, 1988; Sanger, 1993) for believing that motor cortical vector cell activities measured during the movement time specify vectors in a motor space and only appear to specify Cartesian vectors within small regions of the arm's space of possible configurations. Our simplified implementation of a population model is an approximation that omits the sensory motor transformation needed in a more accurate model, and should not be taken as an endorsement of the idea that motor cortical cells are invariantly tuned to Cartesian directions of the end-effector across the entire work space.

**Scheduling and completion-triggered deletion of planned movements.** Correctly ordered performance of a series of movements can be produced by a two-layer working memory constituted by a serial ordering field (SOF) and a choice field (CF) linked by excitatory pathways from cells in the SOF to corresponding cells in the CF. If both layers are on-center, off-surround feedback networks (e.g., Grossberg, 1978), then with appropriate settings of parameters, the SOF can combine competition with self-excitation to allow storage of a normalized gradient of activity distributed over item (target) representations; and the CF can, by using stronger competitive interactions, make a choice of the cell corresponding to, and excited by, the most active item representation in the SOF (Boardman, 1994; Boardman & Bullock, 1991; Bullock, Grossberg & Mannes, 1993; Grossberg, 1978; Grossberg & Kuperstein, 1986). In the SOF, the gradient of activations serves as a specification of serial order, because the choice field will choose the stored targets for execution in descending order of activation. Thus the specification of serial order is an emergent property of the dynamical system. Boardman & Bullock (1991; Boardman, 1995) have shown that such a sequencing working memory, or SWM, can explain reaction time and other rate-related data patterns -- in particular the effect of later planned items on performance of earlier planned items -- that have been observed in the serial movement production tasks studied by Sternberg et al. (1987). We hypothesize that the same SWM that can explain the Sternberg et al. data is part of the system that schedules performance of VP movements. Thus, we are treating VP movements as another example of serial performance of a primed movement sequence.
A property of the SWM proposed by Boardman & Bullock (Boardman, 1995) is that execution of the next item in a sequence awaits receipt of information indicating completion, or expected completion, of the currently executing item. Receipt of such information allows feedback inhibition to flow from the current winner in the CF back to itself and to its associated target representation in the SOF of the SWM. This feedback inhibition deletes the currently winning target's representation from the SOF of the SWM, which removes that target's excitatory input to the CF. In consequence, the inherent choice field competitive dynamics pick a new winner from among the remaining targets in the SOF of the SWM network. To work properly, there must be a set of feedback inhibition cells that correspond one-to-one with the SOF and CF cells. This field of feedback inhibition cells may be called a deletion field, or DF.

To summarize, the SWM comprises three fields: the SOF (serial order field), the CF (choice field), and the DF (deletion field). Because of the one-to-one correspondence between cells in these three fields, the SWM can also be thought of as comprising a set of cellular triads that participate in broad competitive interactions. In the original SWM network of Grossberg (1978) and in the variant proposed by Boardman & Bullock to explain the Sternberg et al. data, pathways between the SOF and the CF can be gated by an arousal signal, onset of which allows activation of the CF. Sometimes known as winner-take-all networks, choice fields have been used in many prior neural network theories. Such choice fields serve as one of the essential components of competitive learning networks (Grossberg, 1978) and therefore of all adaptive resonance networks (e.g., Carpenter and Grossberg, 1987).

Regulation of serial execution by time to contact (TTC) perception. The informative signal used by the SWM to indicate completion of execution, and thus to initiate a target deletion, can take various forms. In the present case, we propose that the effective signal is provided by a neural network capable of detecting when the hand is about to contact a target. Thus SWM dynamics in combination with a TTC stage determine the timing properties of sequence execution. Whenever available, visual information is probably used to specify TTC. Visual feedback is thus proposed to serve two purposes: it informs the system about the locations of target and end-effector, and it provides temporal information present in the ongoing movement. How a neural network can use binocular visual and oculomotor information to specify target position vectors in a body-centered spatial coordinate system is described in detail elsewhere (Bullock et al., 1993; Greve et al., 1992; Guenther et al. 1994). In the present paper, we emphasize the role of temporal information specified by activity of neural populations that detect time to contact, or TTC. Our hypothesis is that TTC information is used to initiate deletion of a chosen target and to thereby terminate an executing DV and cause the SWM output to release execution of a subsequent DV, provided that any targets remain in the gradient field of the SWM.

During movement, information about the time until arrival at a desired position is encoded at the TTC population. Time to contact information is contained in a ratio of variables that already exist in the model or in its assumed visual inputs. In particular, TTC can be defined as the ratio of the residual distance to target (i.e., the amplitude of the spatial DV between the end effector's position and the chosen target's position) to the rate of change of this distance. The latter rate of change can be directly specified visually as the velocity of the end-effector, or
estimated internally as eDVxGO. The value of the TTC ratio begins large and then generally declines toward zero during the movement. When activity in the TTC population falls below a positive but small threshold level, then it no longer inhibits output from the field of feedback inhibition, or deletion, cells, which are associated one-to-one with the excitation-linked pairs of cells in the two layers of the SWM. Within the field of deletion cells, only that cell associated with the current winner will be active, because CF output is the only source of excitatory input to a deletion-field, or DF, cell. When its inhibitory output is released from TTC inhibition, the active DF cell suppresses the associated activity in both layers of the SWM. In effect, this deletes the previously winning target from the SWM and allows the most active remaining target to be chosen. This in turn leads to inhibition of the inhibitory pathway from the associated pDV population to the eDV stage, which unmasks the excitatory projection from the same pDV population to eDV.

**Activation and reset of the GO pathway by the sequencing working memory (SWM).** We also hypothesize that the GO pathway can be activated by cells in the SWM's choice field and reset by cells in the SWM's deletion field. Thus the same deletion cell activity that inhibits the representations of the most recently chosen target token within the CF of the SWM also inhibits the activity of the GO pathway, in effect resetting it. Resetting of the VITE model's GO signal prior to initiation of a new movement has always been necessary in tasks modeled to date. The need for resetting becomes clear in the present case if we note that without such resetting, an abnormally large movement command would occur shortly after choice of the new target, because both terms in the product, eDVxGO, would be simultaneously large. This would cause excessive accelerations and destroy the circuit's tendency to generate a velocity profile whose symmetrical form is nearly invariant (after normalizing to remove time and amplitude scaling factors). An important advantage of invariance was noted by Atkeson & Hollerbach (1985), who used a Newtonian analysis to demonstrate that motor learning can be simplified if the velocity profile has a form that remains invariant, up to such rescaling factors. Resetting of the GO signal was critical to the success of the VITEWRITE model, and is part of what allows the close match, shown below, between model-generated trajectories and observed via-point trajectories. The trajectories of VP movements reported in the experimental study show that the transition from one target-directed movement to another is associated with a significant inflection (trough) in the velocity profile. The observed peak velocity relations of the two parts and the observed isochrony of movement duration are also assured by GO signal reset during the transition.

**Analog and symbolic roles of target representations.** Another hypothesis embodied by the model is that target representations serve a dual role during performance. In particular, they serve an analog role, as in the original VITE, when they are compared with the PPV to compute the pDV. But they also serve a symbolic role when they lead to non-analog activation of sites in the SOF, within which analog variations of activity levels are instead used to implicitly represent serial order. Thus the model highlights a possible evolutionary linkage between the emergence of internal serial planning and the emergence of symbolic representations formed by ignoring analog information. In particular, it suggests that by ignoring analog information as a specifier of the
value of a spatial coordinate, it became possible to "recycle" analog information as a specifier of serial order.

8. Model extensions compared with behavioral and neurobiological data

*Time to contact and perceptual control of motor switching.* To succeed with a discrete movement -- for example to catch or hit a ball, to duck under a beam while locomoting, to pounce on unsuspecting prey, or to brace oneself in anticipation of collision with a looming object -- an actor typically needs predictive information about when to initiate the movement. To time initiations of such interactive movements, information specifying time to contact between two perceivables, a variable often denoted by the Greek letter tau (τ, after Lee, 1976), is of particular relevance. Film analysis by Lee & Reddish (1981) showed that an aquatic bird, the gannet -- which plummets, with wings outstretched, toward the ocean surface (and its prey, fish) -- initiated wing folding not at a fixed distance from the surface but rather when tau reached a critical value. Thus, the offset of active wing extension and the onset of synchronous wing folding was shown to be based on information about time to contact (TTC) in this species.

The proposed existence of a TTC detecting stage is also consistent with neurophysiological data presented by Wang & Frost (1992). Pigeons were seated in front of a computer screen, on which an approaching 'soccer ball' was projected. Whenever the ball appeared to come close to the pigeon's eye along a collision course, cells in the dorsal posterior part of the nucleus rotundus abruptly increased their firing activity. The abrupt increment in cell activity was found to be independent of speed or distance of the approaching object, and occurred at a constant time before predicted collision. Moreover, a tight relation between the activity of the rotundal looming-sensitive cells and the electromyographically measured activity of the large pectoralis flight muscle was observed (Wang & Frost, 1992). These result suggest that information specifying time-to-contact is detected by the nervous system and used to initiate movements.

The nucleus rotundus is a thalamic nucleus that receives a strong visual projection from the optic tectum (OT). In birds, it is part of a pathway called the tecto-rotundal-ecostriatal pathway, which parallels the colliculo-pulvinar-extrastriate pathway in mammals (Frost, Wylie & Wang, 1990; Pettigrew & Konishi, 1976). In each group, a relatively direct complete circuit is formed by a return projection from visual cortex to the optic tectum or superior colliculus (SC), which is the mammalian homologue. This descending projection is complemented by disinhibitory frontal projections to OT/SC mediated by the basal ganglia (including the striatum and the substantia nigra). In amphibians that lack significant cerebro-cortical visual centers, there is a tecto-thalamo-striatal pathway which returns to modulate tectal activity. Moreover, the striato-tectal component of this circuit is present in less or more elaborated forms in amphibians and all land vertebrates (Butler & Hodos, 1996). The fact that this pathway traverses the basal ganglia (including striatum and substantia nigra in primates), which is the proposed anatomical site of GO signal generation (Bullock & Grossberg, 1988b; 1991) provides grounds for our hypothesis that GO and TTC can cooperate in the temporal control of reaching behavior. Equally interesting in the context of the present model, it has been shown in the frog that if the thalamic stage is
surgically destroyed, then the frog's optic tectum is disinhibited and the frog thereafter readily attacks large, looming stimuli as if they were prey. Also consistent, there is now a strong empirical association between selective pulvinar activation and the switching of attention between alternative spatial loci (review in Butler & Hodos, 1996).

The looming-sensitive mechanism studied in birds serves as only one illustration of how time to contact information can be used at the level of neural control. Other movement execution control mechanisms based on time to contact, including continuous control schemes (e.g., Lee, et al., 1993; Schöner, 1994) have been proposed. In contrast to cases of diving or looming toward the eyes, trajectories in reaching often do not lead to optical expansion cues. Bootsma & Oudejans (1993) demonstrated that in many situations information about future time of contact is contained in the relative rate of constriction of the optical gap that separates the moving object from a designated position, or in the ratio of the distance between two objects to the rate of change of this distance. In the terms of our model, we assume that subjects use the ratio of the residual distance between desired position \( (T_i) \) and present position \( (PPV) \) to the hand's perceived velocity towards the target.

Working memory and basal ganglia mediated control of motor cortex. Besides the introduction of control by TTC perception, the primary addition to the model comes in the form of the SWM. A detailed treatment of the relationship between the model's SWM circuit and corresponding brain structures is beyond the scope of this paper. However, several general remarks are in order. The model suggests that there is a working memory whose output field makes a choice, and that such choices both activate the GO pathway and disinhibit the eDV stage. These postulates agree with several properties of forebrain regulation of behavior. First, it has been shown that striatal lesions cause a precipitous drop in the probability of successfully completing execution of a movement sequence (Berridge & Whishaw, 1992; Cromwell & Berridge, 1996). It is also well established (e.g., Goldman-Rakic, 1990) that a working memory sensitive to information about spatial targets exists in prefrontal cortex, and that this working memory is critical for tasks requiring an animal to wait through a delay interval before initiating a response. It is also known that this zone of prefrontal cortex projects to the striatum, the input zone for the basal ganglia, and that lesion of the prefronto-striatal projection causes a loss of working memory functions, including delayed responding. We also note that the basal ganglia output affects motor cortex most strongly by a projection from the globus pallidus through the motor thalamus to the supplementary motor area (SMA), which has also been strongly implicated in the performance of primed movement sequences (review in Passingham, 1993). Finally, it is interesting to note that there are recurrent, or feedback, connections from motor thalamus to the striatum. These observations indicate that the kind of connectivity assumed in the model can be found among brain areas that have been linked to the functionality afforded by the model circuit. However, a comprehensive and detailed treatment is a topic for future research.

9. Mathematical specification of the model
Our description of the model has characterized a dynamical system, whose behavior can be studied if it is fully specified as a system of differential equations. In this section, we detail the system of equations for the case of a 1-VP movement simulation, and clarify the simplifying assumptions that we made in order to reduce the complexity of the simulations in those areas where relevant results have already been reported, e.g., for the SWM component of the model. Where instructive, we also derive expressions for equilibrium values of key variables as they would exist at particular junctures during the evolution of a VP movement were the inputs to the cells with those activities to stabilize. Though the inputs may or may not stabilize during priming or movement in the cases examined, and though the cell activities therefore may not quite reach the computed values, such analyses reveal why the system exhibits the behavior shown in the subsequent section, which graphically presents the simulation results. To avoid a needless multiplication of variable names, we refer to a neural network site by the name of the activity level variable assigned to that site. Thus, for example, both a site i in the target position field and the activity level variable associated with that site will be referred to as $T_i$.

**Target position vectors ($T$).** To initialize the system prior to movement, it is necessary to make the internal target position vectors $T_i$ correspond to the perceivable target positions, $PT_i$, $i=1,2$. Later, it is necessary to suppress each $T_i$ activity once the corresponding target has been reached. This suppression is done by signal $DF_i$ from the deletion field, gated by output CI (for "contact imminent") from the TTC field. Thus we have:

$$\frac{dT_i}{dt} = a(PT_i - T_i) - CI \cdot DF_i$$  \hspace{1cm} (1)$$

where term $a$ controls the rate at which the $T_i$ can be updated to reflect the value $PT_i$. In this study, it is assumed that variables $T_1$ and $T_2$ have both reached equilibrium, i.e., values $PT_1$ and $PT_2$ respectively, prior to the beginning of movement. In effect, variable $a$ is assumed to have been positive long enough to allow the $T_i$ to become equal to the $PT_i$, and zero thereafter. CI is zero until contact with one of the targets is imminent, and then becomes positive. Each $T_i$ sends output to corresponding cells in two neural fields: to pDV; and to SOF $i$.

**Serial order field (SOF).** We also assume that all targets $i$ activate a corresponding representation $SOF_i$ in the serial order field prior to movement. However, analog information in the $T_i$ activity level is not propagated to $SOF_i$. Therefore all significantly positive activities $T_i$ send the same signal toward their corresponding site $i$ in the SOF. In order to create the unequal SOF activations needed to implicitly code serial order, it suffices that the signal $F(T_i)$ sent to site $i$ of the SOF be weighted by its value as a target. We assume that a larger weighting $W_i$ for target $T_i$ leads to an inequality in SOF activities such that $SOF_1$ is initially larger than $SOF_2$. For simplicity, we omit some details needed for more general treatments of SWMs and formalize this as:

$$\frac{d(SOF_i)}{dt} = F(T_i) \cdot W_i \cdot B(SOF_i) \cdot [F(T_i) - CI \cdot DF_i]$$  \hspace{1cm} (2)$$
where \( F(T_i) = 1 \) if \( t < 0 \) and \( F(T_i) = 0 \) otherwise. Then each \( \text{SOF}_i \) will equilibrate at value \( W_i B \) prior to \( t=0 \), when the movement is initiated. Furthermore, each site \( \text{SOF}_i \) will hold its activity \( W_i B \) after \( F(T_i) \) shuts off until the CI gated deletion signal \( \text{DF}_i \) suppresses it. We set \( B=2 \), \( W_1 = 1 \) and \( W_2 = 0.5 \) for the simulations.

**Planning difference vector (pDV).** The pDV stage cells continuously compute the difference between the vectors \( T_i \) and the present position vector, \( P \). Thus we have:

\[
\frac{d(pDV_i)}{dt} = a(- pDV_i + T_i - P)
\]

where term \( a \) is a rate constant, set to value 30 in the simulations. Prior to movement, \( T_i \) and \( P \) are both active. Therefore pDV \( i \) will have equilibrated to value \((T_i - P)\) prior to movement initiation. For a two dimensional movement, each pDV stage site \( i \) must have two spatial components. For these simulations, it was convenient to use polar coordinates, so each pDV stage site \( i \) had one component that registered the angle, \( q_i \), from \( P \) to \( T_i \), and one that registered the distance \( R_i \) between \( P \) and \( T_i \).

**Executive difference vector (eDV).** To show that the computations postulated by the theory can be implemented by a neural population, the eDV stage was realized by a population of size 72. Each eDV cell \( j \) received inputs from all pDV cells \( i \) via target-gated excitatory channels, and via inhibitory channels that can be selectively gated off by the choice field. Moreover, inputs from the pDV stage reflect both the distance component \( R_i \) of the source pDV and the cosine of the angle, \( q_i - q_{j'} \), between eDV cell \( j \)'s preferred direction and the angular component, \( q_{j'} \), of the source pDV. Thus:

\[
\frac{d(eDV_j)}{dt} = a [-eDV_j + f(T_{i'}) [R_{i'} \cos(q_{j'} - q_j) - h(CF_{i'}) \cos(q_j - q_{j'})] \] (4)

where \( k > 0 \) indicates a stronger inhibitory than excitatory projection from the pDV to the eDV stage. For the simulations reported below, \( k = 2 \). To assure that pathways from the pDV stage to the eDV are enabled only if the associated target representation is active, we let \( f(T_{i'}) = 1 \) if \( T_{i'} > 0 \) and \( f(T_{i'}) = 0 \) otherwise.

**Selectively gated inhibitory projections from pDV to eDV.** By setting equation 4's term \( h(CF_{i'}) = \max(1 - IN_i, 0) \), we can represent the assumption that the inhibitory pathway from the pDV stage to the eDV stage is normally gated on, such that \( h(CF_{i'}) = 1 \), but may be turned off by signal \( IN_i \). Signal \( IN_i \) comes from an inhibitory interneuron that has zero activity unless excited by CF site \( i \). It is excited by CF site \( i \) only if the latter becomes sufficiently active to win the competition, which is assured by the structure of the CF if CF \( i \) reaches a level equal to half of its maximal value \( B \). CF activation of inhibitory interneuron \( i \) was formalized by

\[
\frac{d(IN_i)}{dt} = a (\max(CF_i - B/2, 0) - IN_i)
\]

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and $B = 2$ as in equation 2.

**Competitive choice.** Each choice field cell $i$ receives an arousal-gated excitatory input from site $i$ in the SOF as well as two inhibitory inputs. One is a TTC-gated recurrent inhibitory input from site $i$ in the deletion field. The other is a competitive feedback inhibitory input from sites $j$, not equal to $i$, in the IN field. This was formalized as

$$\frac{dCF_i}{dt} = (B - CF_i) \times AR \times SOF_i - (D + CF_i) \times (IN_j + CI \times DF_i)$$  \hspace{1cm} (6)$$

where $AR$ is a tonic arousal signal that initiates and sustains performance of the serial plan by allowing each active cell in SOF to attempt to push its corresponding cell in CF above the threshold, $B/2$, for generating an output. (Though set to zero in our simulations, parameter $D$ is included for completeness. Larger positive values enable more rapid suppression of CF activity.)

**Deletion cells.** As soon as a choice is made in the choice field, the chosen site excites a corresponding site in the deletion field. This was formalized by

$$\frac{d(DF_i)}{dt} = b \times (\text{max}([CF_i - B/2], 0) - DF_i)$$  \hspace{1cm} (7)$$

This indicates that the DF site corresponding to the chosen target charges up as soon as the choice emerges in the CF. However, as indicated in equations 1, 2, and 6, DF activation has no effect on the network until the contact imminent signal, $CI$, is generated by the TTC network. After that occurs, then by equation 6, $CF_i$ is reset to a value of zero or below, after which equation 7 implies that $DF_i$ will decline back to zero activity.

**GO signal generation.** The GO signal is generated by a two cell cascade that is excited by the CF and inhibited by any $CI$-gated DF output signal. This was formalized by

$$\frac{dG_1}{dt} = (b - G_1) \times F(CF) - G_1 \times (1 + \sum CI \times DF_i)$$  \hspace{1cm} (8)$$

$$\frac{dG_2}{dt} = (b - G_2 - G_1) \times G_1 - G_2 \times (1 + \sum CI \times DF_i)$$  \hspace{1cm} (9)$$

where $b = 30$, $F(CF) = k_2 \times CF_i$, and $k_2 = 0.135$.

**The present position vector ($PPV$).** We assume that the output of the eDV stage is multiplied by the scaled GO signal, $k_3G_2$, and then transformed into a muscle coordinate command that can be used to drive the muscles that control the arm. Learning and use of such a transformation during a perception action cycle has been formalized and simulated in recent reports on the DIRECT model (Bullock et al. 1993; Fiala, 1994, 1995; Guenther & Barreca, 1996), so we chose not to implement this part of the system. Though we did not model the arm muscle control, it was necessary to update the present position vector during the movement. As the hand moves, it provides velocity feedback through vision that can be used to update the present position vector.
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stage. To derive the net velocity vector that would exist for the hand, we assume that the GO-gated eDV output commands are correctly followed by the arm. Then, the eDV output signals may be used to compute the hand's motion direction, as an activity weighted average, of the preferred angles of the active eDV cells. The Cartesian hand position vector CP was initialized with the hand's initial Cartesian coordinate position, and its components were updated by

\[
\frac{d(CP_x)}{dt} = A \times \cos(q_i) \times G_2 \times k_3
\]

\[
\frac{d(CP_y)}{dt} = A \times \sin(q_i) \times G_2 \times k_3
\]

where \(k_3 = 1.85\), and \(A\) was the activity level, or amplitude, of the most active cell in the eDV population. Variable \(A\) is equivalent to the network's representation of the residual distance to target. The polar coordinate equivalent, \(P\), of the Cartesian position \(CP\) was used to compute the pDVs, as in equation 3. The time derivative of \(P\) served as a measure of the hand's tangential velocity.

**Time to contact and the contact imminent signal.** To reference time to contact, we use the standard symbol, \(\tau\). Though \(\tau\) is assumed to be visually specified, we did not model visual processing. Instead we approximated the results of such processing by computing \(\tau\) with

\[
\tau = A/((.02 + \text{abs}(dA/dt)))
\]

where again \(A\) is the residual distance to target represented by the maximal activity in the eDV population. We assume that the contact imminent cell is excited by the neural center that computes \(\tau\) whenever the value of \(\tau\) falls below a threshold, but inhibited by the \(\tau\) center whenever \(\tau\) is at or above that same threshold. This was formalized by

\[
\frac{d(CI)}{dt} = (b - CI) \times H(\tau) \times (1 + \text{max}(0, 1 - H(\tau))) \times CI
\]

where \(b = 30\) and \(H(\tau) = 10\) if \((\tau < \Gamma \& dA/dt < 0.0)\), else \(H(\tau) = 0.0\). Threshold \(\Gamma\) was set equal to 1300. Note that \(dA/dt\) begins positive, as the eDV population is initially excited, but that it then turns negative as movement begins to reduce the residual distance to target.

10. Simulation results

One of our goals was to show that both PTP and VP movements could be simulated with a single set of parameters, and the parameters given in the prior section fulfill that requirement. For these simulations, we composed the eDV stage from 72 nodes, in order to cover 360 degrees of preferred directions in 5 degree increments. Target and end effector positions, represented with polar coordinates \(R\) and \(q_i\), were relative to the initial starting position. A fourth order Runge-Kutta method was used to numerically integrate the model equations with a time step of 0.01. In order to approximate the observations of Georgopoulos et al. (1986; 1989; 1993) that
movement direction is uniquely specified by the neuronal population vector, which is an activity-weighted average of the preferred directions of active cells, we also formed an activity-weighted average of the preferred directions of active cells. However, to speed computations, we computed the activity weighted average of the preferred directions of only the three most active eDV cells. Because the 5 degree quantization of the eDV space occasionally caused this average to change by several degrees over one time step, we also smoothed the time series of preferred directions. To show that this simplification was justified because of the shape of the distribution of eDV activities during the formation of a via-point trajectory, we have depicted in Figure 7 the positive or negative activities of all eDV stage cells at each of three different times.

Insert Figure 7 about here

In Figure 8 the path and the velocity profiles of a simulated PTP movement from position a to b are shown. The general characteristics, notably a straight handpath and a bell shaped velocity profile, can be readily observed. Simulations, not addressed in this paper, showed that slow velocities (small $G_0$ in equation 5) led to a pronounced right-tail asymmetry in the velocity profile $dP/dt$, as compared to the roughly symmetric velocity profiles observed in simulations with higher velocities. These features are consistent with psychophysical findings showing that the deviation from a symmetric velocity profile, as exhibited by human actors, is duration dependent (Bullock & Grossberg, 1988a,b; 1991; Nagasaki, 1989).

Insert Figure 8 about here

The path of a VP movement from position a to c via b and the associated velocity profiles are depicted in Figure 9. The trajectory curves smoothly around the intermediate target point, as can also be seen in the experimental data (see also Abend et al., 1981; Uno et al., 1989). Moreover, comparison of the paths between a and b of a PTP and a VP movement showed a considerable direction deviation of the latter in the first segment of the movement, which is in agreement with the results reported in the experiment.

Insert Figure 9 about here

The tangential velocity profile and the velocity profile in the x-dimension associated with the via-point trajectory are bimodal, while the velocity profile of the y-dimension decelerates in a continuous way and when the intermediate target is reached changes sign in accordance with the reversal of direction along the y-dimension. In general, the characteristics are in good agreement with our and prior experimental findings (Abend et al., 1981; Flash and Hogan, 1987; Uno et al., 1989). Other key properties present are the tendency of duration equality for components of different size, more generally known as the 'isochrony principle', and the proportional relation between amplitudes and peak velocities.
To exemplify the important role of the TTC stage in the temporal performance of the model, Figure 10A shows plots of the temporal evolution of the tangential velocity, that is \(\frac{dP}{dt}\), and the executive difference vector \(eDV_j\). Figure 10B shows the GO-signal and the CI (contact imminent) signal, which appears as a spike of activation between times 370 and 560 ms. Note that the onset time of the CI signal leads, and therefore predicts, the time of occurrence of local minima in the eDV amplitude and in the tangential velocity profile. As expected because of the causal link between the two, the CI spike coincides with a trough in the GO signal. Note also that the decline toward the trough in the tangential velocity profile begins long before the CI spike and long before the beginning of the trough in the GO signal. This shows clearly that the beginning of the trough of the tangential velocity profile is due solely to the decline of the initial eDV associated with movement to the intermediate target (the viapoint), and is not due to the (future) partial suppression of the GO signal by the CI spike. However, the rise out of the trough of the tangential velocity profile is much slower than it would be if the CI signal did not "reset" the GO signal, so reset of the GO signal has a significant role in preventing large accelerations, and high velocities, near viapoints. Because of the predictive nature of the CI signal, the mid-course partial suppression of the GO signal is significantly underway before the time of the minimum of the eDV amplitude. Therefore the partial suppression of the GO signal by the CI signal initially sharpens deceleration into the viapoint and causes the minimum of the tangential velocity profile to reach a lower value than it would without GO signal reset.

Also affecting the minimum value of the tangential velocity profile is the minimum value reached by the eDV amplitude. As can be seen in Figures 7 and 10, the eDV amplitude in the middle of the VP movement never reaches zero. How close it comes to zero depends on two factors: the TTC threshold for release of the CI signal and the angle between the planning DVs associated with the first and second segments of the VP movement. Thus, if the TTC threshold is set too low, then switching is no longer predictive and there is a pause at the viapoint, because the eDV and tangential velocity reach zero. And by equation 4, as the angle between the pDV associated with the first and second segments of the VP movement approaches 180 degrees, a larger proportion of those eDV cells active just before the switch are inhibited by the new pDV, and a larger proportion of formerly inactive cells must be brought to a higher state of activation. This fact creates a fundamental, inverse, relationship in the model between curvature of the trajectory and tangential velocity: as the angle between \(pDV_1\) and \(pDV_2\) approaches 180 degrees, the curvature of the trajectory near the viapoint increases, the near-viapoint eDV amplitude decreases, and so does the product eDVxGO, which determines the tangential velocity. Figure 11 shows that within a viapoint trajectory, the model also exhibits an inverse relationship between local tangential velocity and local curvature.

An inverse relationship between curvature and tangential velocity has been repeatedly observed in experimental studies (Morasso, 1981; Abend et al., 1982; Wann, Nimmo-Smith &
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Wing, 1988). This empirical relation was formulated as a power law relating angular velocity to curvature by Lacquaniti, Terzuolo & Viviani (1983). Rewritten as a relationship between tangential velocity, $V(t)$, and curvature $C(t)$, the law has form $V(t) = kC(t)^{1/3}$. In the paper of Bullock et al. (1993) on the VITEWRITE model, a close correspondence was observed between model and the power law. (A perfect correspondence is not to be expected, because the power law itself is not a perfect descriptor of human performance (Wann, et al., 1988).) No similar analysis was undertaken here, because the present model is similar to the VITEWRITE model in those aspects that affect the curvature-velocity relationship.

11. Conclusions

Analyses of the data from the viapoint experiment demonstrated that whereas there was no evidence for a change in curvature in the initial segment of a VP movement, there was evidence for a change in the direction of the initial segment. The fact that this change of direction was away from the final target in a 1-VP movement suggested the applicability of a model that precomputes movement vectors without also precomputing curvature of the entire trajectory prior to movement. The VITE model satisfied these requirements, but required extensions to explain how movement vectors computed with respect to several forthcoming targets could interact from the very beginning of movement execution, how correct serial choices could be made in real time, and how perceptual variables could control switching time in conformity with the task requirement that the subject moves quickly from the initial to the final position while passing over the viapoint(s). The task represents a very commonly encountered class of serial control problems, in which too early a switch would cause undershoot of the initial goal, whereas too late a switch would lead to a pause before the second action. The solution was to use a value of time-to-contact that allowed the earliest switching consistent with avoidance of an undershoot error. In summary, the VITE model extensions involved incorporation of three additional stages: a planning vector stage, a sequencing working memory and choice system, and a time-to-contact detecting stage. Task specific features emerge from the co-operation of these system components during a perception-action cycle.

In the planning vector stage, the dimensions of forthcoming movements in several distinct directions, to several simultaneously visible targets, can be continuously computed in parallel. Such simultaneous computations would be of great adaptive value. For example, a predator capable of performing such computations could thereby make an informed choice to move toward the nearest of several visible prey. The object of predation could likewise choose to move toward the nearest of several refuges, or to evade the nearer of two predators. However, computation of the dimensions of several forthcoming movements places an animal at risk of premature or even confused performance, because all plans active at the planning vector stage must be capable of exciting the executive vector stage. One way to prevent premature performance is to inhibit the executive vector stage in a way that is sure to cancel each excitatory input to the executive stage until a choice to go ahead with one of the prospective movements has been made. To guarantee cancellation, the inhibitory projections from the pDV to the eDV must be somewhat stronger than the excitatory projections. One consequence is that in the context of a serial plan, the inhibitory
input from the second planned movement can cause a perturbation in the trajectory of the first planned movement. This is how we explain the empirically observed deviation in the initial segment of VP movements: it is a consequence of an inhibitory "force" required to block premature execution and thus to allow deliberative action by animals.

For the internal aspects of managing serial performance scheduling and choice, it is necessary to have a neural field within which two or more plans can be prioritized in some way, and a related field that can advance for immediate performance only the highest priority plan. For the present simulations, we adapted the model of Boardman & Bullock (1991; Boardman, 1995), who in turn adapted the serial rehearsal models of Grossberg (1978) and Grossberg & Kuperstein (1989). All of these SWM models incorporate the natural assumption that the most active competitor is chosen for initial performance. A key property of these models (see Boardman, 1995) is that they can accommodate the full range of latency data reported by Sternberg et al. (1987), including those aspects that imply interaction among elements of a planned speech sequence. Ward (1995) recently used the same competitive ordering principle as a basic assumption in a connectionist model of language generation. The present application thus helps bridge between the literature on serial production of language and the literature on serial reaching movements.

The present paper illustrates one way that ecological analyses of perception and action and computational analyses of neural networks can cooperate to understand control principles that may be embodied by the central nervous system for trajectory formation, and more generally for composing streams of behavior that are and remain adapted to the perceptible environment. The management of serial performances requires coordination of active internal processes with events arising within a perception action cycle. In this study, we have suggested that time-to-contact plays an important role in the control of switching between one element of a planned sequence and a subsequent element. Here we follow a long series of precedents in the ecological analysis of perceptual control of action, though in many prior applications the serial nature of the task, and hence the need to use TTC in concert with internal processes to control a transition between actions, was not highlighted. Our treatment shows that the TTC detection network can control transitions by sending a non-specific signal to the deletion field of a sequencing working memory. In this case, its role in initiation is indirect: it initiates the next action by removing the current action from the competition for control of the output channel.

It is of interest to see how far this principle can be generalized, that is, if the same kind of analysis can be applied to other cases in which TTC can in principle play a role in movement termination and initiation. Two examples will suffice to indicate some of the issues. First, it is well known in speech production that targets are better treated as regions than as points, and Guenther (1995) recently incorporated ideas from the VITE and DIRECT models in his DIVA (Directions Into Velocities of Articulators) model, which incorporates such regions as a basic postulate. It may be that the emergence of such regions can be attributed to the use of learned TTC thresholds to terminate approaches to points near the center of such regions. Second, in the VITEWRITE model of cursive handwriting -- a task that may be assumed to involve circuitry that overlaps considerably with that used to generate via-point reaches -- internal detection of the maxima and zero-crossings of velocity command signals were used to launch successive strokes, and each
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stroke generator had its own GO channel because of the need for parallel execution of strokes that overlapped by one half-cycle of a VITE generator. The current model could work equally well on the assumption of independent GO channels, and the VITEWRITE model might be successfully modified to use learned time-to-contact thresholds to control launching and deletion of planned movements. The current model may better reflect performance of novel serial orderings using largely forebrain circuitry and non-specific switching signals, whereas cursive handwriting and speech performed by well-practiced subjects reflects significant additional skill components, perhaps from anticipatory cerebellar processing based on perceptuo-motor learning in highly specific pathways.

This consideration raises the problem of the evolution of adaptive timing and the variety of its mechanistic substrates. If an animal can learn to use different threshold values of TTC to control its behavior, then by definition it has an adaptive timing competence. However, it is not strictly necessary for an animal to possess special circuitry that computes an actual ratio to effectively use information specifying TTC, because a given value of the ratio is equally well specified by temporal coincidence of any of the values of distance and velocity that in combination imply a given value of the ratio. Learning a TTC threshold for action might therefore be based on noticing signal combinations. This is of interest because the cerebellum, which has long been viewed as a signal-combination detector (e.g., Albus, 1971), has recently been implicated experimentally as (also) a site of adaptive timing (Keele & Ivry, 1990; Thompson, 1986; Perrett et al., 1993; Steinmetz, 1990). Work by Bullock, Fiala & Grossberg (1994; Fiala, Grossberg & Bullock, 1996) has produced a biochemistry-based model of how phase-advanced action components can be learned by Purkinje cell populations in any predictive task context to which the cerebellum is sensitive. Interestingly, the cerebellar model is based on data from eye-blink conditioning studies, in which the animal must learn how to use specific ambient information to time its response so as to avoid contact of a forthcoming air-puff with its eye. The role of alternative adaptive timing mechanisms should be clarified by future empirical and modeling research aimed at elucidating the changes that occur between early and later stages of practice of sequentially structured actions performed in rich perceptual contexts.
References


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Zaal, F.T.J.M., Bootsma, R.J., and P.C.W. Van Wieringen, in press. Dynamics of reaching for stationary and moving objects: Data and model. (submitted for publication)

Figure 1. The VITE circuit.

Figure 2. Top view of the experimental setup. Numbered squares designate locations of the LEDs available for selection as targets.
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Figure 3. Representative examples of spatial trajectories, performed by subject four in the space depicted in Figure 2. The dots represent the location of the specified targets. The left column contains panels of movements directed from the left to right. In the right column the movement direction is from the bottom to the top. The unit on the axis is centimeters. Panels A, B, C, D, E, F, G, H, I and J show, respectively, condition 2A, 1B, 6A, 7B, 9A, 8B, 14A, 13B, 21 and 22.
Figure 4. Tangential velocity profiles corresponding to the trajectories depicted in Figure 3. The horizontal axis shows the elapsed time in ms; the vertical axis shows the tangential velocity in cm/s.
Figure 5. A PTP (AB) and a VP (ABC) movement with a corresponding initial segment (conditions 3A and 9A, respectively). The gray line is the point-to-point condition. Clearly visible is the diverging direction of the initial segment of the VP movement.
Figure 6. Schematic overview of the model: $T_1$ and $T_2$ are desired target positions apparent in a viapoint paradigm, specified in egocentric coordinates. These signals together with a specification of the current position of the endeffector, the PPV, enable the system to compute planning vectors at the planning vector stage (pDV). The planning vectors converge at the executive vector stage, denoted eDV. The eDV outflow signals are multiplied by a GO signal to form the DV*GO velocity command to the arm, movement of which causes visual updating of the PPV. Visually perceived temporal information is registered at the time to contact (TTC) stage. The TTC stage output via the contact imminent (CI) node to several sites coordinates a smooth transition between movement toward the viapoint, $T_1$, and movement to the final target, $T_2$. Excitatory pathways are denoted by arrowheads and inhibitory pathways by filled circles.
Figure 7. The full 360° range of DV_j activity levels at the eDV at time of first V_{peak} (A), time of V_{min} (B) and time of second V_{peak} (C) of a VP movement from position a via b to c (see Figure 5). In each case, the central of the three DV_j averaged in the simulations is marked by an *. X-axis: the 72 five-degree bins representing the centers of the eDV nodes' receptive fields. Y-axis: activity of the eDV nodes.
Figure 8. (A) Simulated 'endeffector' path of the neural network for a 500 ms PTP movement from position A to B. (B) The associated tangential velocity profiles and the velocity profiles in the x and y dimension of the simulated PTP movement. On the x-axis time in 10 ms and the y-axis: velocity in cm/s.
Figure 9. (A) Simulated 'endeffector' path of the neural network of a 800 ms VP movement from position A to C via B. The dashed line is the 'endeffector' path of the PTP movement from Figure 8. (B) The associated tangential velocity profiles (dP/dt) and the velocity profiles in the x and y dimension of the simulated VP movement. On the x-axis time in 10 ms and the y-axis: velocity in cm/s. Parameter values as in the Figure 8 caption and the text.
Figure 10. Simulated time course of the neural network activities. (A) $\frac{dP}{dt}$ and $DV(t)$ for a 800 ms. VP movement (See Figure 5). (B) The GO signal ($G$) and the CI signal during an 800 ms. VP movement. Parameter values as in the Figure 8 caption and the text.
Figure 11. Relationship between tangential velocity $V(t)$ and curvature $C(t)$ of a simulated 800 ms viapoint trajectory. Velocity was computed as $V(t) = (V_x^2 + V_y^2)^{0.5}$ and curvature was computed as $C(t) = (V_x A_y - V_y A_x) / V(t)^3$. 
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Table 1. Conditions, corresponding straight-line path lengths, LED designations, number of usable samples, reaction times, and movement times. The RTs and MTs are means with the associated standard deviations given in the subscript. N is the number of trials that remained after the initial data analyses. For the first 15 conditions, movements were made according to the sequence of the LEDs specified in the third column (version A), as well as in the reverse sequence, and the means shown collapse data across versions A and B. Conditions 16 and 17 were only performed in the depicted LED sequence. In the target switch conditions (18-22), movements were only completed in the sequence shown. The upper RT and MT for the target switch conditions correspond to an early target switch, the lower values to the late target switch.
### Table 2

The mean path lengths of the recorded movements of the four subjects for various conditions. The standard deviations are given in the subscripts.

<table>
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<tr>
<th>Covered distance</th>
<th>Point-to-point (90 cm)</th>
<th>Point-to-point (30 cm)</th>
<th>1-Viapoint (109 cm)</th>
<th>2-Viapoint (102 or 112 cm)</th>
<th>Early target switch (120 cm)</th>
<th>Late target switch (120 cm)</th>
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<td>111_{14}</td>
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