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Attentive Learning of Sequential Handwriting Movements: A Neural Network Model

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1. Introduction

Much sensory-motor behavior develops through imitation, as during the learning of handwriting by children (Burns, 1962; Freeman, 1914; Iacoboni et al., 1999). Such complex sequential acts are broken down into distinct motor control synergies, or muscle groups, whose activities overlap in time to generate continuous, curved movements that obey an inverse relation between curvature and speed. How are such complex movements learned through attentive imitation? Novel movements may be made as a series of distinct segments that may be quite irregular both in space and time, but a practiced movement can be made smoothly, with a continuous, often bell-shaped, velocity profile. How does learning of sequential movements transform reactive imitation into predictive, automatic performance?

A neural model is summarized here which suggests how parietal, frontal, and motor cortical mechanisms, such as difference vector encoding, interact with adaptively-timed, predictive cerebellar learning during movement imitation and predictive performance (Grossberg & Paine, 2000). To initiate movement, visual attention shifts along the shape to be imitated and generates vector movement using motor cortical cells. During such an imitative movement, cerebellar Purkinje cells with a spectrum of delayed response profiles sample and learn the changing directional information and, in turn, send that learned information back to the cortex and eventually to the muscle synergies involved. If the imitative movement deviates from an attentional focus around a shape to be imitated, the visual system shifts attention, and may make an eye movement back to the shape, thereby providing corrective directional information to the arm movement system.

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This imitative movement cycle repeats until the corticocerebellar system can accurately drive the movement based on memory alone. A cortical working memory buffer transiently stores the cerebellar output and releases it at a variable rate, allowing speed scaling of learned movements which is limited by the rate of cerebellar memory readout. Movements can be learned at variable speeds if the density of the spectrum of delayed cellular responses in the cerebellum varies with speed. Learning at slower speeds facilitates learning at faster speeds. Size can be varied after learning while keeping the movement duration constant (isochrony). Context-effects arise from the overlap of cerebellar memory outputs. The model is used to simulate key psychophysical and neural data about learning to make curved movements, including a decrease in writing time as learning progresses; generation of unimodal, bell-shaped velocity profiles for each movement synergy; size and speed scaling with preservation of the letter shape and the shapes of the velocity profiles; an inverse relation between curvature and tangential velocity; and a Two-Thirds Power Law relation between angular velocity and curvature.

2. Model Precursors

The new model, called Adaptive VITEWRITE (AVITEWRITE), builds on two previous movement models. The first is the Vector Integration to Endpoint (VITE) model (Bullock & Grossberg, 1988a, 1988b, 1991) (Figure 1). The VITE model successfully explained psychophysical and neurobiological data about how synchronous multi-joint reaching trajectories could be generated at variable speeds. VITE was later expanded (Bullock, Cisek, & Grossberg, 1998) to explain how arm movements are influenced by proprioceptive feedback and external forces, among other related factors. The firing patterns of six distinct cell types in cortical areas 4 and 5 were also simulated during various movement tasks (Kalaska et al., 1990). In order to allow a greater focus on issues related to the learning of curved movements, the AVITEWRITE model avoids explicit descriptions of muscle dynamics, and therefore uses components of the earlier VITE models of Bullock and Grossberg (1988a, 1988b, 1991).

A second basis for the AVITEWRITE model is the VITEWRITE model of Bullock, Grossberg, and Mannes (1993), (Figure 2). The curved trajectories of handwriting require more than simple point-to-point movements. Curved handwriting trajectories appear to be generated by sequences of movement synergies (Bernstein, 1967; Kelso, 1982), or groups of muscles working together to drive the limb in prescribed directions, whose activities overlap in time (Morasso et al., 1983; Soechting & Terzuolo, 1987; Stelmach et al., 1984). VITEWRITE uses such a synergy-overlap strategy to generate curved movements from individual, target-driven strokes. A key issue faced by all models which seek to generate curves by overlapping strokes is how to appropriately time the strokes to generate a particular curve. VITEWRITE avoids an explicit representation of time in the control of synergy activation by using features of the movement itself; namely, times of zero or of maximum velocity, to trigger activation of a subsequent synergy. However, movement in VITEWRITE is controlled by a predefined sequence of "planning vectors" which

cause unimodal velocity profiles for the synergies that control each directional component of a curve. VITEWRITE does not address how these planning vectors may be discovered, learned, and stored in a self-organizing process which can generate unimodal velocity profiles for each directional component of a curved movement. This challenge is met by the *Adaptive* VITEWRITE model.

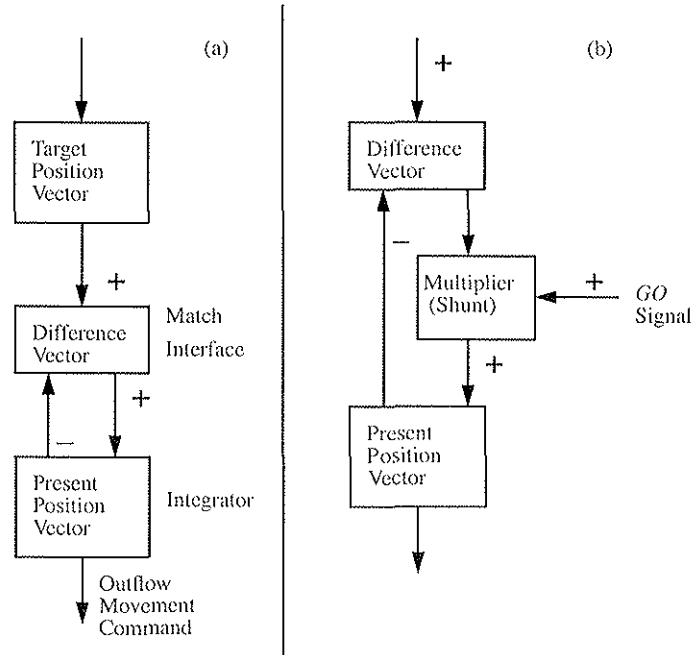


Fig. 1. (a) A match interface within the VITE model continuously computes a difference vector (DV) between the target position vector (TPV) and a present position vector (PPV), and adds the difference vector to the present position vector. (b) A GO signal gates execution of a primed movement vector and regulates the rate at which the movement vector updates the present position command. (Adapted with permission from Bullock and Grossberg, 1988a.)

AVITEWRITE describes how the complex sequences of movements involved in handwriting can be learned through the imitation of previously drawn curves. Although the system described herein could be modified to learn from the actual movements of a teacher, the present model learns by imitating the product of that teacher's movements, the static image of a written letter. AVITEWRITE shows how initially segmented movements with multimodal velocity profiles during the early stages of learning can become the smooth, continuous movements with the unimodal, bell-shaped velocity profiles observed in adult humans (Abend et al., 1982; Edelman & Flash, 1987; Morasso, 1981; Morasso et al., 1983) after multiple learning trials. Early, error-prone handwriting movements with many visually reactive, correctional components gradually improve over time and many learning trials, to become

automatic, error-free movements which can even be performed without visual feedback. A key factor in this transition is the use of synergy-based learning (see below), which retains some degree of stability across otherwise highly variable practice trials.

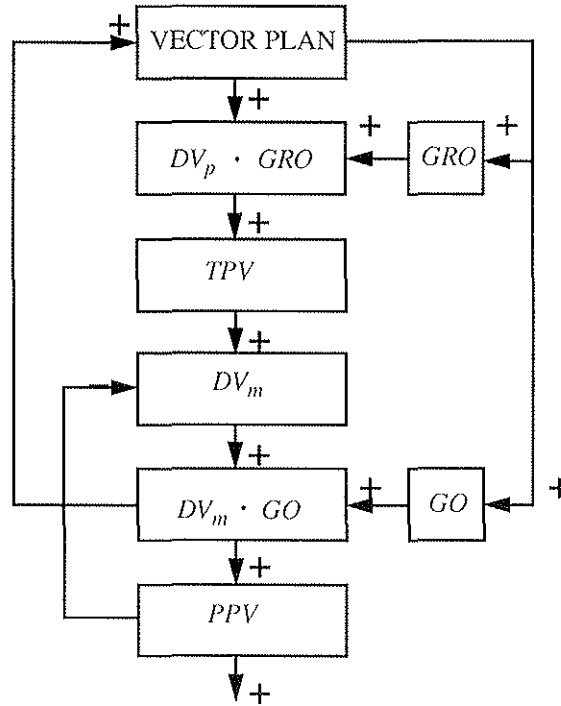


Fig. 2. The VITEWRITE model of Bullock et al. (1993). A Vector Plan functions as a motor program that stores discrete planning vectors DV_p in a working memory. A *GRO* signal determines the size of script and a *GO* signal its speed of execution. After the vector plan and these will-to-act signals are activated, the circuit generates script automatically. Size-scaled planning vectors $DV_p \cdot GRO$ are read into a target position vector (*TPV*). An outflow representation of present position, the present position vector (*PPV*), is subtracted from the *TPV* to define a movement difference vector (DV_m). The DV_m is multiplied by the *GO* signal. The net signal $DV_m \cdot GO$ is integrated by the *PPV* until it equals the *TPV*. The signal $DV_m \cdot GO$ is thus an outflow representation of movement speed. Maxima or zero values of its cell activations may automatically trigger read-out of the next planning vector DV_p . (Reproduced with permission from Bullock et al., 1993.)

The AVITEWRITE model architecture is briefly outlined below (Figure 3) and described later in detail in the Model Description (Figure 9). At the start of movement, visual attention (1) focuses on the current hand position and moves to select a target position (2) on the curve being traced. A Difference Vector

representation (3) of the distance and direction to the target is formed between the current hand position (*PPV*) and the new target position (*TPV*). This Difference Vector activates the appropriate muscle synergy (4) to drive a reactive movement to that target. At the same time, a cerebellar adaptive timing system (5) (Fiala et al., 1996) learns the activation pattern of the muscle synergy involved in the movement and begins to cooperate or compete (6) with reactive visual attention for control of the motor cortical trajectory generator (7). A working memory (8) transiently stores learned motor commands to allow them to be executed at decreased speeds as the speed and size of trajectory generation are volitionally controlled through the basal ganglia (9). Reactive visual control takes over when memory causes mistakes. Both the movement trajectory and the memory are then corrected, allowing memory to take over control again. As successive, visually reactive movements are made to a series of attentionally chosen targets on the curve, a memory is formed of the muscle synergy activations needed to draw that curve. After tracing the curve multiple times, memory alone can yield error-free movements.

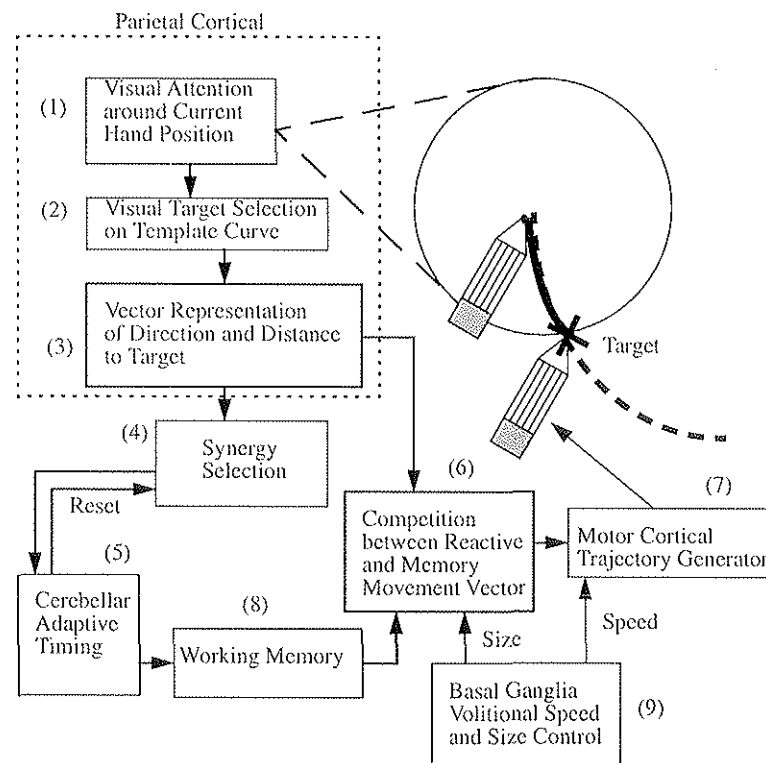


Fig. 3. Conceptual diagram of the AVITEWRITE architecture. Numbers in parentheses indicate the order of discussion in the text.

Several properties of human handwriting movements emerge when AVITEWRITE learns to write a letter. Size and speed can be volitionally varied (Figure 3, (9)) after learning while preserving letter shape and the shapes of the velocity profiles (Plamondon & Alimi, 1997; Schillings et al., 1996; van Galen & Weber, 1998; Wann & Nimmo-Smith, 1990; Wright, 1993). Isochrony, the tendency for humans to write letters of different sizes in the same amount of time, is also demonstrated (Thomassen & Teulings, 1985; Wright, 1993). Speed can be varied during learning, and learning at slower speeds facilitates future learning at faster speeds (Alston & Taylor, 1987, p. 115; Burns, 1962, pp. 4 45-46; Freeman, 1914, pp. 83-84). Unimodal, bell-shaped velocity profiles for each movement synergy emerge as a letter is learned, and they closely resemble the velocity profiles of adult humans writing those letters (Abend et al., 1982; Edelman & Flash, 1987; Morasso, 1981; Morasso et al., 1983). An inverse relation between curvature and tangential velocity is observed in the model's performance (Lacquaniti et al., 1983). It also yields a Two-Thirds Power Law relation between angular velocity and curvature, as seen in human writing under certain conditions (Lacquaniti et al., 1983; Thomassen & Teulings, 1985; Wann et al., 1988). Finally, context effects become apparent when AVITEWRITE generates multiple connected letters, reminiscent of carryover coarticulation in speech (Hertrich & Ackermann, 1995; Ostry et al., 1996), and similar to handwriting context effects reported by Greer and Green (1983), and Thomassen and Schomaker (1986).

3. Movement Synergies

Movement synergies are groups of muscles that work together in a common task. The brain seems to control complex movement tasks, such as walking or handwriting, by issuing commands to a few muscle synergies, as opposed to specifying the movement parameters for scores of individual muscles separately (Bizzi et al., 1998; Buchanan et al., 1986; Kelso, 1982; Turvey, 1990). Using muscle synergies greatly simplifies the control and planning of movement by lessening the number of degrees of freedom requiring executive control (Bernstein, 1967; Turvey, 1990). Only at lower levels of the central nervous system, such as in the brainstem and spinal cord, would the motor synergy commands branch out to individual muscles. A key question is how these movement synergies are controlled.

Human movements can be broken down into individual movement segments, or strokes. Each stroke corresponds to the activities of particular muscle synergies. When the muscle synergies controlling a limb are activated synchronously (Figure 4b), there is a tendency to make simple, straight movements (Hollerbach & Flash, 1982; Morasso, 1986) with bell-shaped velocity profiles (Abend et al., 1982; Morasso, 1981; Morasso et al., 1983), (Figure 4b). Curved movements may be generated by a linear superposition of straight strokes due to asynchronous synergies (Figure 4a and 4c) (Morasso et al., 1983; Soechting & Terzuolo, 1987; Stelmach et al., 1984). Thus, a key issue is how the timing of strokes is determined. In curved movements, each synergy generates its own bell-shaped velocity profile. A simple example is a "U" curve (Figure 5), drawn as a combination of three strokes: one for a synergy in the

negative, vertical direction; a second in the positive, horizontal direction; and a final stroke in the positive, vertical direction (Figures 5b and 5c). The observation that the curved movements of handwriting obey an inverse relation between curvature and velocity (Lacquaniti et al., 1983) can be attributed to the direction reversal and synergy switching which occurs at points of high curvature, as at the bottom of a "U" curve (Figure 5d and 5e).

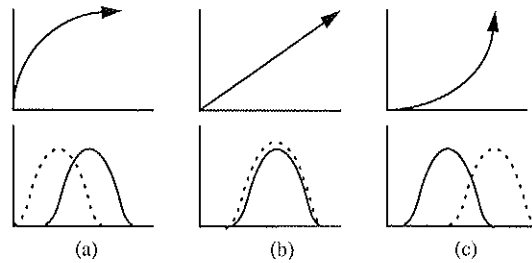


Fig. 4. Varying the relative timing of synergy activation can yield different curved movements. Synchronous synergy activation yields straight movements (b) while asynchronous synergy activation can yields curved movements in (a) and (c). The dotted and solid curves represent synergies that control movements in the positive y and x directions, respectively.

4. The VITE Model of Reaching

How is movement direction represented in the brain? Much research (e.g., Andersen et al., 1995; Georgopoulos et al., 1982, 1989, 1993; Mussa-Ivaldi, 1988) suggests that motor and parietal cortex compute a vectorial representation of movement direction in motor and/or spatial coordinates. The VITE model (Bullock & Grossberg, 1988a, 1988b, 1991) showed how a vectorial representation of movement direction and length could generate straight reaching movements with bell-shaped velocity profiles (Figure 1). Such a Difference Vector (DV) is computed as the difference from an outflow representation of the current hand position, or Present Position Vector (PPV), to a target, or Target Position Vector (TPV) (Figure 6). The DV is multiplied by a gradually increasing GO signal, that is under volitional control, whose growth rate can be changed to alter movement speed while preserving movement direction and length (Figure 1). The "GO" signal seems to be generated with in the basal ganglia (Hallett & Khoshbin, 1980; Georgopoulos et al., 1983; Horak & Anderson, 1984a, 1984b; Berardelli et al., 1996; Turner & Anderson, 1997; Turner et al., 1998). The DV times the GO signal is an outflow representation of movement velocity that is integrated at the PPV until the present position of the hand reaches the target.

The VITE model explains behavioral and neural data about how a motor synergy can be commanded to generate a synchronous, multi-joint reaching trajectory at variable speeds. VITE describes how synchronous movements may be generated across synergistic muscles with automatic compensation for the different total contractions undergone by each muscle group. Many properties of human reaching

movements emerge from VITE's performance, including the equifinality of movement synergies, a rate-dependence of velocity profile asymmetries, and variations in the ratio of maximum to average movement velocities (Bullock & Grossberg, 1988a, 1988b, 1991).

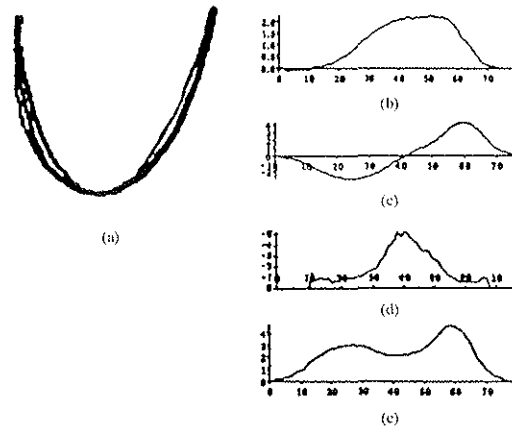


Fig. 5. (a) A "U" curve written by a human; (b) and (c): x and y direction velocity profiles, respectively; (d) movement curvature; (e) tangential velocity. (Reproduced with permission from Edelman and Flash, 1987.)

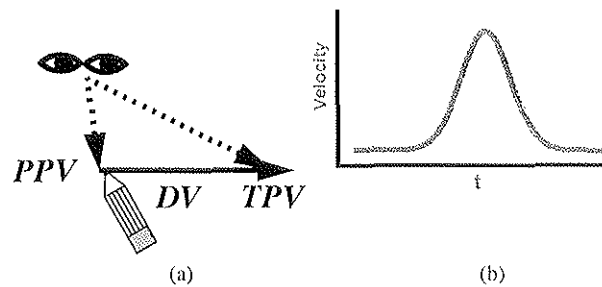


Fig. 6. (a) Illustration of a Difference Vector (DV) formed from the current hand location, given by a Present Position Vector (PPV), to a Target Position Vector (TPV). The DV is integrated in a VITE circuit to generate a straight movement with a bell-shaped velocity profile (b).

The expanded VITE model of Bullock, Cisek, and Grossberg (1998) assigned functional roles to six cell types in movement-related, primate cortical areas 4 and 5, and integrated them into a system which is capable of "continuous trajectory formation; priming, gating, and scaling of movement commands; static and inertial load compensation; and proprioception" (Bullock et al., 1998, p. 48). In this more detailed model, Difference Vector cells resemble the activity of posterior parietal area 5 phasic cells, while Present Position Vector cells behave like anterior area 5 tonic cells.

5. The VITEWRITE Model of Handwriting

The VITEWRITE model of Bullock, Grossberg, and Mannes (1993) (Figure 2) extended the VITE reaching model to explain handwriting data. In VITEWRITE, curved movements are generated using a velocity-dependent stroke-launching rule that allows *asynchronous* superposition of sequential muscle synergy activations with unimodal, bell-shaped velocity profiles for each synergy. Scaling the size of *DVs* by multiplication with a volitional *GRO* signal allows size scaling without significantly altering the trajectory shape or the shape of the velocity profile. Similarly, altering the size of the volitional *GO* signal alters trajectory speed without changing trajectory shape. The movements generated by VITEWRITE yield the inverse relation between curvature and tangential velocity observed in human performance, as well as the Two-Thirds Power law relation between angular velocity and curvature observed in humans under some writing conditions (Lacquaniti et al., 1983; Thomassen & Teulings, 1985; Wann et al., 1988). VITEWRITE also shows how size scaling of individual synergies via separate *GRO* signals can change the style of writing without altering velocity profile shape. Such independent scaling of muscle synergy commands is supported by the study of Wann and Nimmo-Smith (1990), which yielded data that "do not support common scaling for x and y dimensions" (p. 111).

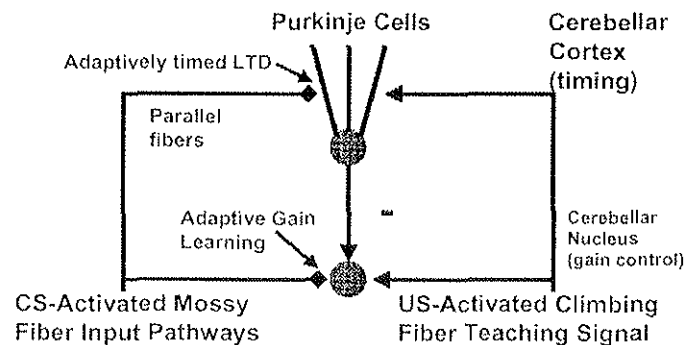


Fig. 7. Cerebellar spectral timing circuit: Long Term Depression (LTD) occurs over at the parallel fiber-Purkinje cell synapse when an unconditioned stimulus (US) is paired with a conditioned stimulus (CS) over multiple presentations. (Adapted with permission from Grossberg and Merrill, 1996). See text for details.

The Adaptive VITEWRITE model yields performance which is equally consistent with available handwriting data. In addition, AVITEWRITE addresses the main limitation of VITEWRITE, which is its inability to learn and remember the motor plan that, once learned, yields such good performance. The original VITEWRITE model does not address "the self-organizing process that discovers, learns, and stores representations of movement commands" (Bullock et al., 1993, p. 22). The pattern of "planning vectors" which formed VITEWRITE's motor program, or plan, needed to be predefined in order for the system to generate a movement or write a particular letter. In contrast, AVITEWRITE learns how to generate letters by

itself, and then remembers how to write them. The cost in so doing is a considerably larger learned memory. It remains to be seen whether and how the very parsimonious synergy-launching rule that was used in VITEWRITE can be assimilated into this learning scheme.

6. Adaptive Timing in the Cerebellum

Given that curved movements may be generated by asynchronous activation of multiple muscle synergies, we need to understand how the time-varying activation of asynchronous muscle synergies, or strokes, is learned. Several mechanisms have been proposed to learn how to adaptively time responses to stimuli. Possible timing mechanisms include delay lines (Moore et al., 1989; Zipser, 1986), a spectrum of slow responses with different reaction rates in a population of neurons (Bartha et al., 1991; Bullock et al., 1994; Grossberg & Merrill, 1992, 1996; Grossberg & Schmajuk, 1989; Jaffe, 1992), and temporal evolution of the network activity pattern (Buonomano & Mauk, 1994; Chapeau-Blondeau & Chauvet, 1991). Given the need to learn time delays of up to four seconds in eye blink conditioning, delay lines of sufficient length do not appear to be present in the cerebellar cortex (Fiala et al., 1996; Freeman, 1969). Network noise over a four second interval seems to preclude temporal network evolution mechanisms (Buonomano & Mauk, 1994; Fiala et al., 1996).

Accumulating evidence suggests that adaptively timed learning of strokes may be achieved by *spectral timing* in the cerebellum. Fiala et al. (1996) and others (Ito, 1984; Perrett et al., 1993) have suggested that the cerebellum may be involved in the opening of a timed gate to express a learned motor gain, as when a rabbit learns to blink after hearing a tone previously associated with an air puff. In this conception (Figure 7), a signal associated with a Conditioned Stimulus (CS) arrives via the cerebellar (mossy fiber)-to-(parallel fiber) pathway at a population of Purkinje cells and triggers a series of phase-delayed activation profiles, or depolarizations, of the Purkinje cells, called a Purkinje cell "spectrum" (Figure 8b). When a signal associated with a subsequent Unconditioned Stimulus (US) arrives via climbing fibers at some fixed Interstimulus Interval (ISI) after the CS, then Long Term Depression (LTD) of active Purkinje cells may occur at that time (Figure 8a), leading to disinhibition of the cerebellar nuclei at that time (Figure 7); hence the term "adaptive timing" (Fiala et al., 1996; Grossberg & Merrill, 1992, 1996; Grossberg & Schmajuk, 1989). The staggered temporal pattern of Purkinje cell depolarizations following the initial CS ensures that some Purkinje cells will be active, and subject to Long Term Depression, at the time that the US arrives via the climbing fibers (Figure 8a).

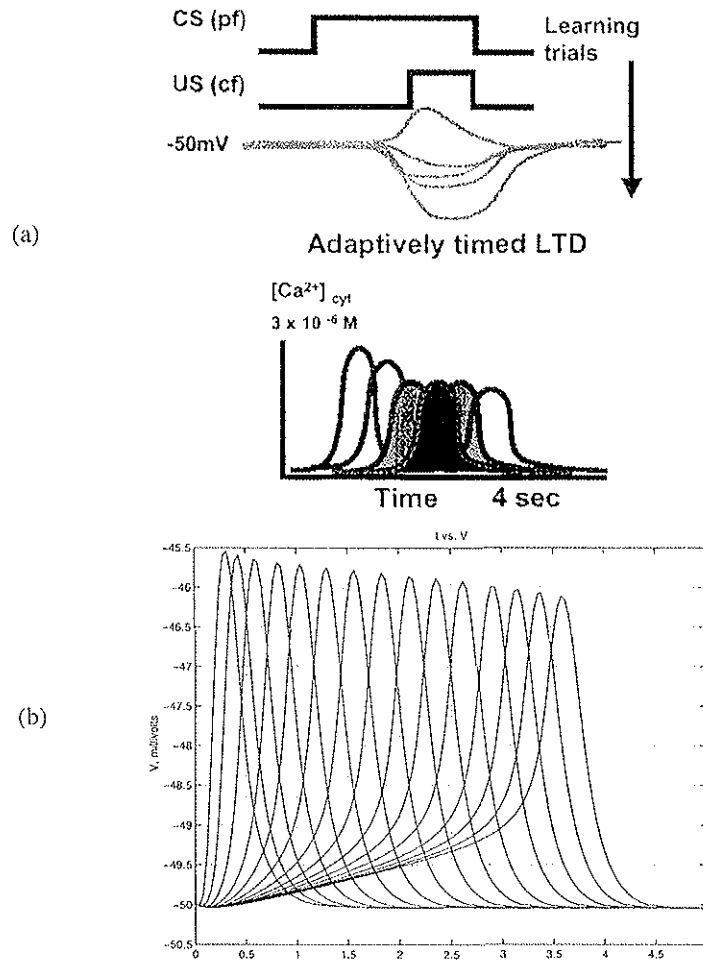


Fig. 8. (a) Purkinje cell spectrum (bottom) and adaptively timed Long Term Depression (LTD) over multiple CS-US pairings. As the unconditioned stimulus (US) arrives over multiple learning trials at a fixed interstimulus interval after the conditioned stimulus (CS), LTD occurs at those Purkinje cells which are active when the US arrives (shaded response curves). (b) Purkinje cell depolarization spectrum from Fiala et al. (1996) equations. Continuous glutamate input = 10 micromM. (Adapted with permission from Fiala et al., 1996.)

Fiala et al. (1996) utilized biochemical mechanisms of the metabotropic glutamate receptor (mGluR) system to simulate how learning of adaptively timed Long Term Depression, or LTD, of Purkinje cells occurs and causes disinhibition of cerebellar nuclei during classical conditioning. Fiala et al. (1996) showed that a Purkinje cell spectrum could learn to respond to two conditioned stimuli with different

interstimulus intervals (p. 3770). AVITEWRITE takes this approach one step further. Instead of learning one or two responses at discrete points in time, as in the conditioning task, it is hypothesized that the cerebellar adaptive timing mechanism can also learn a continuous response over time in sequential tasks like handwriting.

For a continuous handwriting task, different Purkinje cell spectra are activated by the commands corresponding to different muscle synergies. The climbing fiber unconditioned stimuli act as error-based signals that train the Purkinje cells to become hyperpolarized in specific temporal patterns that lead to correctly shaped writing movements. The level of depression of a given Purkinje cell determines the extent of cerebellar nucleus disinhibition during that Purkinje cell's activation and thus the learned gains for controlling a particular muscle synergy during a brief time window of movement. When these brief, individual movement commands are summed over the entire Purkinje cell population with staggered, overlapping cell activations, a continuously changing pattern of muscle synergy activations may be generated which can yield curved planned movements. In the AVITEWRITE model, this cerebellar adaptive timing module forms part of an integrated sequential learning and generation system (Figures 3 and 9) that also uses elements of VITE cortical and basal ganglia trajectory formation for visually reactive movements to targets and synergy-based spectral activation, as well as ideas from VITEWRITE about how working memories can build curved movements from overlapping synergies in a way that preserves shape-invariant volitional speed and size scaling.

This view of a cerebellar role in handwriting is consistent with data showing that there is cerebellar activity during drawing, and that the cerebellum is more active when lines are retraced than in new line generation because error detection (deviation from the lines) occurs during retracing but not new line generation (Jueptner & Weiller, 1998). Since the cerebellum is more active during error corrections, it is likely that climbing fibers (Figure 7) are signaling movement error, leading to Long-Term Depression or LTD of Purkinje cell-parallel fiber synapses (Gellman et al., 1985; Ito, 1991; Ito & Karachot, 1992; Oscarsson, 1969; Simpson et al., 1996). In a similar vein, the cerebellum may also be involved in a variety of complex sequential tasks. It is known that there is a cerebellar role in procedural memory. In a sequential button press task, lesions to the dentate nucleus cause deficits in learning and memory (Lu et al., 1998). Further, Doyon et al. (1998) demonstrated through studies using a sequential finger movement task that the cerebellum and striatum are involved in the automatization and long-term retention of motor sequence behavior.

In addition to showing how the cerebellum may be involved in learning a sequential handwriting task, the AVITEWRITE model also shows how the cerebellum may encode movement velocity. It is known that Purkinje cell simple spike discharge is direction- and speed-dependent (Coltz et al., 199a; Ebner, 1998). Simple spikes result from summation of excitatory postsynaptic potentials at parallel fiber-Purkinje cell synapses, across multiple Purkinje cell dendrites (Ghez, 1991, p. 631). AVITEWRITE assumes that movement context information, such as the movement direction and speed, is carried via the parallel fibers to the Purkinje cell populations controlling particular muscle synergies. Further, complex spike discharge of Purkinje cells is "spatially tuned and strongly related to movement kinematics" (Fu et al., 1997). A complex spike results when a single action potential is carried to a Purkinje

cell via a climbing fiber, triggering a large Purkinje cell action potential followed by a high-frequency burst of smaller action potentials (Ghez, 1991, p. 631). In AVITEWRITE, the climbing fiber inputs act as error-correcting signals which train Purkinje cells that control particular muscle synergies to become hyperpolarized at the appropriate times during movement. AVITEWRITE therefore assumes that the climbing fiber signal is dependent on the direction and amplitude of a required corrective movement. The required corrective movement is different from, and possibly in the opposite direction to, the actual movement of that particular muscle synergy, which is reflected in simple spike activity. In fact, Coltz et al. (1999b) have found that complex spike discharge is direction- and speed-dependent, and that it is related to directions opposite those of the corresponding simple spikes, and to speeds different from those of the simple spikes. This appears to be further evidence that climbing fibers transmit a movement error signal. The model suggests how, using a spectrum of phase-delayed Purkinje cell activations based on adaptive timing mechanisms, learned cerebellar outputs may code movement gain and velocity.

7. AVITEWRITE Model

AVITEWRITE uses visual spatial attention to determine where the hand will move to imitate a curve. Attention is modeled algorithmically since it is not the main focus of the present study. The model assumes that attention may be focused within a circular region around the present fixation point. Attention is initially focused around the current hand position on a template curve (Figure 9). Attention then shifts along the curve to another target (*TPV*: Target Position Vector) on the shape that lies within an attentional radius of the current hand position (*PPV*: Present Position Vector). How this is modeled will be more explicitly stated below.

In support of the model's use of spatial attention, experimental data suggest that superior frontal, inferior parietal, and superior temporal cortex are part of a network for voluntary attentional control (Hopfinger et al., 2000) which is critical for directing "unpracticed movements in man" (Richer et al., 1999, p. 1427). Jueptner et al. (1997a, 1997b) reported that the prefrontal cortex was activated in a finger movement-sequence learning task during new learning but not during automatic performance after learning. Further, the left dorsal prefrontal cortex was reactivated "when subjects paid attention to the performance of the prelearned sequence" (Jueptner et al., 1997b, p. 1313). Evidence for an interaction between parietal and frontal lobe activity and cerebellar activity was found by Arroyo-Anillo and Botez-Marquard (1998). The authors found that humans with olivopontocerebellar atrophy suffered deficits in copying a simple figure and in immediate visual spatial memory, "consistent with the hypothesis that the cerebellum is involved in visual spatial working memory... and that it modulates parietal lobe- and frontal lobe-mediated functions" (p. 52).

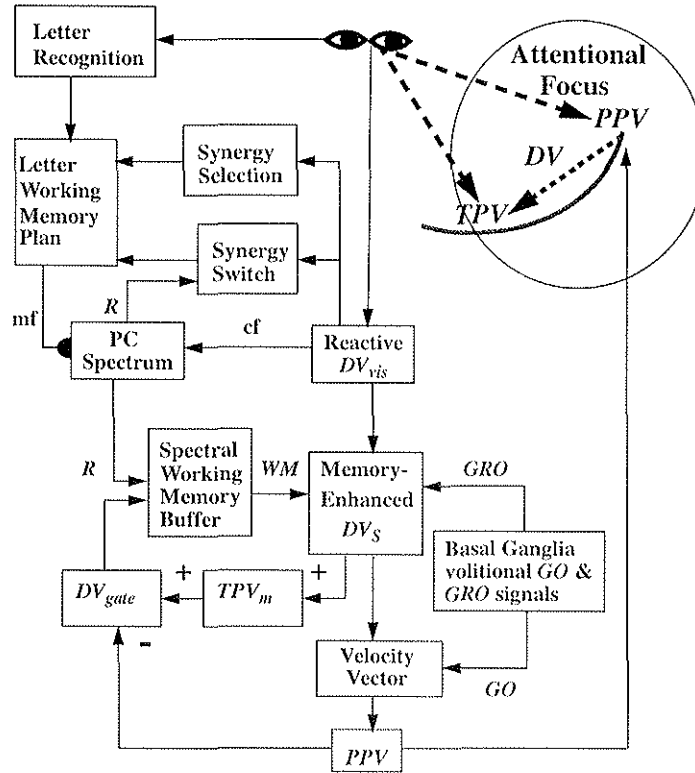


Fig. 9. AVITEWRITE architecture: cf = climbing fiber; DV_{smr} = Gating Difference Vector; DV_s = Size-scaled, memory-enhanced Difference Vector; DV_{vis} = Visual Difference Vector; GO = Volitional speed control signal; GRO = Volitional size control signal; mf = mossy fiber; PC = Purkinje cell; PPV = Present Position Vector; R = Adaptively timed cerebellar output; TPV = Target Position Vector; TPV_m = Memory-modulated Target Position Vector; WM = Spectral Working Memory Buffer output.

AVITEWRITE uses spatial attention to constrain the choice of the target positions that drive imitative tracing of a curve. The model assumes that these targets are selected within an attentional "tube" that is swept out by shifts in attention around the curve (Figure 10). If there is no memory, or if movement deviates from the attentional radius around the curve being traced due to memory inaccuracy, then a new target is chosen on the curve. Each choice of a new TPV from the current PPV defines a visual Difference Vector, or DV_{vis} , that is constrained to point forward along the template curve and remain within an attentional radius (r_a) of it, or else return the hand to within a distance r_a of the curve if it has exceeded it. More details about the target selection algorithm are described below. The $TPVs$ are used to form difference vectors, DV_{vis} , that both drive the movement and act as teaching signals to train a cerebellar spectral memory via climbing fiber inputs

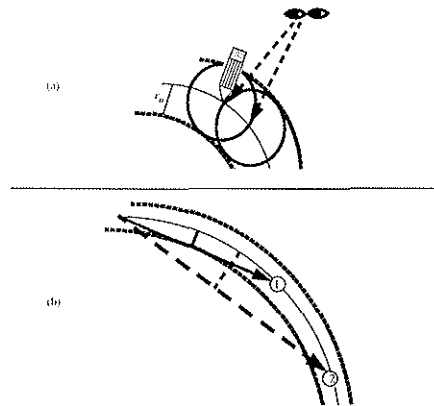


Fig. 10. Illustration of target selection: (a) Targets are chosen so as to keep the movement within an attentional radius, depicted as a circle around the current hand/pencil tip position, of the curve being traced. Superposition of these circular foci of attention as attention shifts across space generates an attentional "tube" around the template curve, shown as dotted lines. (b) Target 1 is possible because movement to it would not exceed the attentional radius, r_a , from the curve being traced, whereas Target 2 is invalid because r_a would be exceeded.

Once a target is chosen, vision provides direction and amplitude information, in the form of the difference vector, DV_{vs} , to a trajectory generator which can combine temporally overlapping muscle synergy activations to generate curved movements whose speed and size are volitionally controlled. Evidence for the use of visual difference vectors has been reported by several investigators. For example, in a study of human visuomanual pointing to a visual target on a horizontal plane, Vindras and Viviani (1998) found that final hand position appeared to be "coded as a vector represented in an extrinsic frame of reference centered on the hand" (p. 569). Similarly, in the Schwartz and Moran (1999) study of cell population vectors in motor and premotor cortex during drawing movements, "population vectors predicted direction (vector angle) and speed (vector length) throughout the drawing task" and that the "2/3 power law described for human drawing was also evident in the neural correlate of the monkey hand trajectory" (p. 2705).

Forming a visual difference vector to a target on the template curve includes activation of the appropriate muscle synergy to generate movement to that target. The trajectory generator then starts to integrate the memory-enhanced difference vector, DV_s , generating a velocity vector that drives movement to the target (Figure 9). At the beginning of learning, when there is not yet a memory contribution to movement control, DV_s equals DV_{vs} multiplied by a volitional size-scaling *GRO* factor. While movement towards the visual target is occurring, adaptively timed learning of the muscle synergy activations required to reach that target occurs. The cerebellum is activated by active muscle synergies. The model assumes that different synergies

activate different spectral memories to learn and store corrective movement commands. In the simulations (Figures 13), four separate spectral memories are formed for positive and negative, horizontal and vertical movement synergies, respectively. The use of separate synergy-activated spectral memories allows the model to learn a consistent movement despite the existence of variable errors on learning trials. It also allows muscle synergy-switching with independent control of each synergy.

A new synergy is activated at the start of movement and whenever there is a reversal in movement direction, requiring activation of a different synergistic set of muscles. Prior to learning, the synergies needed to begin a movement are determined by the value of DV_{vis} . For example, when starting the letter "U" when there is no prior memory of this letter, a DV_{vis} is formed which initially points in the negative y and positive x-directions. Purkinje cell spectra corresponding to the negative y and positive x-direction synergies therefore begin sampling the climbing fiber error/teaching signal. As memory starts to form, the model assumes that a visual representation of the letter is categorized by inferotemporal and prefrontal mechanisms in the "what" cortical processing stream, and that a visual cue is used to sample the appropriate synergies used to perform a given letter from memory (Figure 11). Although not modeled explicitly, AVITEWRITE assumes that a working memory, possibly in prefrontal cortex, forms a category representation of each letter which controls adaptive pathways to all the synergies. The letter category determines which cerebellar spectra, corresponding to the particular synergies needed to write that letter, are activated via mossy fiber inputs. Only those adaptive pathways that were modified due to prior learning will read-out nonzero values of the cerebellar spectral memory output, R . In order to initiate writing of a learned letter, the letter category triggers the initial spectra that control the synergies needed to start the movement. When writing the letter "U" for example, the letter category memory activates spectra corresponding to the negative y and positive x-direction synergies at the beginning of movement. The letter category representation also stores the identities of the other (the positive y) spectra involved in generating that particular letter. Their order of activation is determined automatically by the synergy switching rule described below.

Synergy switching is accomplished as follows in the model. If the total movement direction, determined by the sum of the reactive visual Difference Vector (DV_{vis}) and the cerebellar spectral memory (R) in Figure 9, changes sign, then a new synergy and Purkinje cell spectrum are activated. No new spectral components are activated in the spectrum from the prior synergy, although those components which are active at the time of the synergy switch continue to respond until they decay spontaneously. Such spectral behavior is supported by the responses of the biochemically-detailed Fiala et al. (1996) model to the sudden cessation of glutamate input to the Purkinje cells from the parallel fibers. In the Fiala et al. (1996) simulations, spectral components which are active at the time of input cessation remain active for a time while decaying spontaneously, whereas no new spectral components respond once the glutamate input has been shut off. The term spectral activity is here used to indicate the time-varying change in Ca^{2+} concentration and potential of a Purkinje cell following parallel fiber inputs. When writing a letter "U", a negative y-direction muscle synergy starts the movement. One Purkinje cell spectrum

would learn to correct all the negative y-synergy movement errors. At the bottom of the "U", the y-synergy would reverse, triggering activation of a new spectrum to learn to correct the positive y-synergy errors. At this point, input to the negative y-synergy spectrum would be stopped; e.g., by shutting off the glutamate input released from parallel fibers in the Fiala et al. (1996) model equations, and the spectra active at the time of the direction reversal would decay.

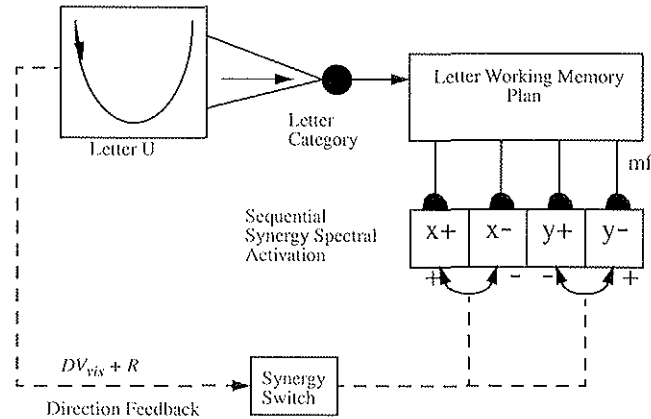


Fig. 11. Working Memory (*WM*) representation of a letter category that determines the sequential order of readout of synergy specific spectra for the positive and negative, *x* and *y* synergies, *x*+, *x*-, *y*+, and *y*-. Synergy switching is triggered by a change in sign of the total movement direction, $DV_{vix} + R$. *mf* = mossy fiber.

Error-driven movement learning is mediated by climbing fiber error signals, based on the Difference Vector $TPV-PPV$ between the target position and the present hand position. The climbing fiber signal modifies the parallel fiber/Purkinje cell synaptic efficacy by triggering patterns of Long Term Depression across the Purkinje cell populations that control the respective muscle synergies. As the Purkinje cells' activity becomes more depressed, their target cerebellar nucleus becomes disinhibited (Figure 7), thereby enhancing muscle synergy activation over time according to the temporal pattern of Purkinje cell population activity.

The AVITEWRITE model incorporates competition between reactive movement and memory-based movement control systems. The model hypothesizes that the cerebellar motor memory competes for control of movement with cortical areas that guide reactive movements based on visual input (Caminiti et al., 1999; Dagher et al., 1999; Jueptner et al., 1997a, 1997b; Jueptner & Weiller, 1998; Kawashima et al., 2000; Sadato et al., 1996). In the model, the reactive visual difference vector (DV_{vis}) and the learned output from cerebellar memory (R), transiently stored in a working memory buffer (*WM*) described below, are combined to form the Memory-Enhanced Difference Vector, DV_s . The DV_s is, in turn, multiplied by a volitional size-scaling *GRO* signal to yield the size-scaled, memory-enhanced Difference Vector, DV_s . When the memory contribution to DV_s is strong enough, then

the cerebellar memory determines DV_s and DV_{vis} decays to zero. A visual difference vector (DV_{vis}) will be formed to a target if either of two conditions is met:

First, if the memory is too small (below some threshold value), then the system waits for a brief period of time in case another memory is becoming active. If no memory grows beyond the threshold by the end of this time period, then a reactive visual DV_{vis} is formed in the manner described above. This DV_{vis} drives the reactive movement toward a target. Second, if an error is made due to a movement deviating from the attentional radius around the template curve, then a corrective visual DV_{vis} is formed which determines DV_s and drives a corrective movement. The difference between the target and present positions ($TPV-PPV$) generates a cerebellar teaching signal that updates the memory. Memory again takes over control once the trajectory re-enters the attentional focus around the template curve, at which time DV_{vis} decays to zero. Thus, on-line error correction occurs which automatically shuts off as the system successfully learns to generate the desired curve. As learning proceeds, error-prone movements become successively more accurate until no errors are made and memory alone controls the movement. Once memory can control the movement without errors, the learned movement can be correctly executed without visual feedback.

As in the original VITEWRITE model Bullock et al. (1993), a volitional *GO* signal scales movement speed in AVITEWRITE by altering the trajectory generator's rate of difference vector (DV_s) integration. However, the rate of predefined memory "planning vector" readout in VITEWRITE was a function of the movement's velocity. It is still unclear how such a rule can hold across learning trials during which initial variability in strokes and speeds eventually converges to a unimodal velocity profile.

When one turns to spectral learning to overcome this difficulty, one needs to face a different problem; namely, the rate with which cerebellar Purkinje cells can read out the synaptic weights that form their motor memory is limited. In other words, attempting to alter movement speed by changing the *GO* signal by a factor of 2.8 to match the range of human speeds (Wright, 1993) would not necessarily alter the rate at which the cerebellum reads out its stored motor commands by a comparable factor. AVITEWRITE hypothesizes that the rate at which the motor commands are retrieved from cerebellar long term memory defines the maximum possible rate at which error-free, memory-driven sequential handwriting movements can be made.

How can learned movements be made across a wide range of speeds while keeping trajectory shape and velocity profiles relatively constant if the variability of the long term motor memory readout rate is limited? Van Galen (1991) suggested that working memory buffers between handwriting "processing modules" may "accommodate for time frictions between information processing activities in different modules" (p. 182). AVITEWRITE hypothesizes that a working memory system helps to write at a wide range of speeds even if the read-out rate of cerebellar spectra does not change. This working memory system, with movement speed-dependent motor command readout, is not to be confused with the prefrontal working memory assumed to store letter category representations discussed earlier but not explicitly modeled in AVITEWRITE. Experimental data support the idea that working memory function may influence movement speed. For example, several authors have found that lesions causing spatial working memory deficits also cause increased movement speed.

Ventral hippocampal lesions (Bannerman et al., 1999), cholinergic basal forebrain lesions (Waite et al., 1995), and NMDA receptor antagonism (Kretschmer & Fink, 1999) impair both spatial working memory and cause an increase in movement speed. Pleskacheva et al. (2000) found that voles with smaller hippocampal mossy fiber projections exhibited poorer spatial working memory and increased movement speed. Zhou et al. (1999) found that some neurons in the medial and lateral areas of the septal complex, which has close reciprocal connections with the hippocampus, display movement speed-related activity. Chieffi & Allport (1997) found support for the hypothesis that "short-term memory for a visually-presented location within reaching space" is represented in a "motoric code" (p. 244).

The AVITEWRITE model hypothesizes that the learned cerebellar movement commands are transiently stored in a working memory buffer (*WM* in Figure 9) which can read out those commands at a variable rate which is less than or equal to the rate at which motor commands are retrieved from the cerebellar spectral memory. The motor commands stored in the working memory are combined with the reactive visual difference vector (DV_{vis}) and scaled by the volitional, size-controlling *GRO* signal to form the memory-enhanced, size-scaled difference vector (DV_s) discussed above. A *memory-modulated* movement target (TPV_m) is generated from the memory-enhanced difference vector by adding DV_s to the current value of TPV_m . At the beginning of movement, TPV_m is initialized to the starting position of the hand; that is, to the initial value of the Present Position Vector (*PPV*).

When an animal is making sequential movements to a series of targets, it must read out the next target from working memory as it reaches the current target in order to continue the sequence. In AVITEWRITE, a subsequent motor command is loaded from working memory and executed only when the previous memory-modulated target (TPV_m) is reached. A memory-derived target has been reached when the present hand position (*PPV*) equals the position of TPV_m . The difference vector from *PPV* to TPV_m is defined as DV_{gmr} (Figure 9). Thus, when DV_{gmr} reaches zero or becomes negative, TPV_m has been reached and the next command is loaded from the working memory buffer (*WM*). (Alternatively, one could use a small, non-zero threshold value of DV_{gmr} to trigger *WM* readout.) The working memory of AVITEWRITE allows the volitionally controlled *GO* signal to alter movement speeds of both reactive and learned movements, while preserving trajectory shape and the shapes of the velocity profiles, by altering the rate of memory readout relative to the speed of the movement. The maximum speed at which a learned movement can be executed without error is determined by the rate of long term memory readout from the cerebellar spectral memory. In the model, removal of the cortical working memory buffer impairs the system's ability to decrease the speed of learned movements while preserving their kinematic features, such as shape and velocity profile invariance. The model hereby offers one possible explanation for the experimentally observed movement speed increases following spatial working memory impairment.

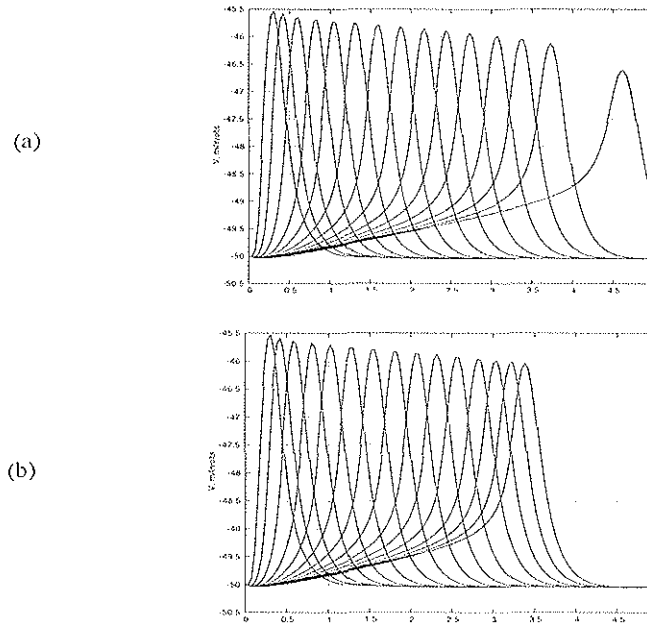


Fig. 12. (a) Purkinje cell depolarization spectrum from the Fiala et al. (1996) equations. Continuous glutamate input = 5 microM. (b) Continuous glutamate input = 25 microM. Note that the spectrum is more dense and spans a shorter time than in (a).

One consequence of decreasing movement speed and the rate of motor command readout from the working memory buffer is that visual error feedback will be delayed. If the Purkinje cells responsible for triggering the erroneous movement have returned to their baseline activity by the time that the error feedback arrives via climbing fibers, then the parallel fiber/Purkinje cell synaptic weights will not be modified and the error will be repeated on the next learning trial. Such late error feedback may "correct" the wrong synaptic weights if other Purkinje cells in the population are active at the time that the climbing fiber signal arrives. A corrective movement could still be learned by modifying the weights of the Purkinje cells which are active when the error signal arrives, but it could be too late for it to significantly improve the movement trajectory. Further, it might even worsen performance if the curvature of the template curve near the current position of the moving hand has changed since the time the error occurred and the corrective movement points away from the curve at the time it is made. AVITEWRITE proposes the following solution to the problem of delayed error feedback to the cerebellar Purkinje cell spectrum. This solution is consistent with the fact that increasing the conditioned stimulus intensity can "speed up the clock" in the rabbit nictitating membrane paradigm which earlier versions of spectral learning were used to model (Grossberg & Schmajuk, 1989, p. 93). In the model, the density of the Purkinje cell responses over time varies during learning as a function of the volitionally controlled *GO* signal that controls movement

speed. For learning at slow movement speeds, the density of Purkinje cell responses over time is decreased. This decreased density allows the activities of the Purkinje cells responsible for a given component of a movement synergy command to span a greater period of time so that more of them may be active at the time that the error feedback arrives. As speed increases, error feedback arrives sooner and Purkinje cell spectral density increases so that more cells are active sooner to sample the earlier error feedback. Simulations of the biochemically-predictive spectral timing model of Fiala et al. (1996) demonstrated that the rate of Purkinje cell response – that is, the spectral density – can be decreased by decreasing the amount of glutamate released at the parallel fiber/Purkinje cell synapse (Figure 12). By varying spectral density with speed in AVITEWRITE, successful learning may occur over a wider range of speeds. The mathematical equations and parameters that define the model are given in Grossberg and Paine (2000).

8. Model Simulations

Computer simulations illustrate the following model properties: (1) the model's ability to learn to generate cursive letters with realistic velocity profiles; (2) generation of an inverse relation between curvature and tangential velocity; (3) generation of a Two-Thirds Power Law relation between curvature and velocity; (4) the ability to vary the movement speed during learning, with a gradual increase in speed as learning proceeds; (5) variable speed performance of learned movements with preservation of the movement shape and the shape of the velocity profile; (6) the ability to vary the size of movements while maintaining isochrony as well as the shape of the velocity profiles; and (7) the ability to yield coarticulatory context effects, such as variation of letter size and downstroke duration due to adjacent letters.

Learning a Letter. Figures 13 and 14 illustrate the learning process as AVITEWRITE learns to write the cursive letter l by tracing a template curve for thirty-seven trials. On early trials, mistakes are made as the newly forming memory competes for control of the movement with visually reactive movements to targets on the curve. Memory control is initially poor and requires corrective reactive movements which yield a segmented trajectory and a velocity profile that consists of several discrete peaks. As learning proceeds over multiple trials, performance gradually improves and the writing time decreases until, on trial thirty-seven in this case, the memory representation of the synergy activations is able to drive an accurate, fast writing movement which does not deviate from the attentional radius around the template curve.

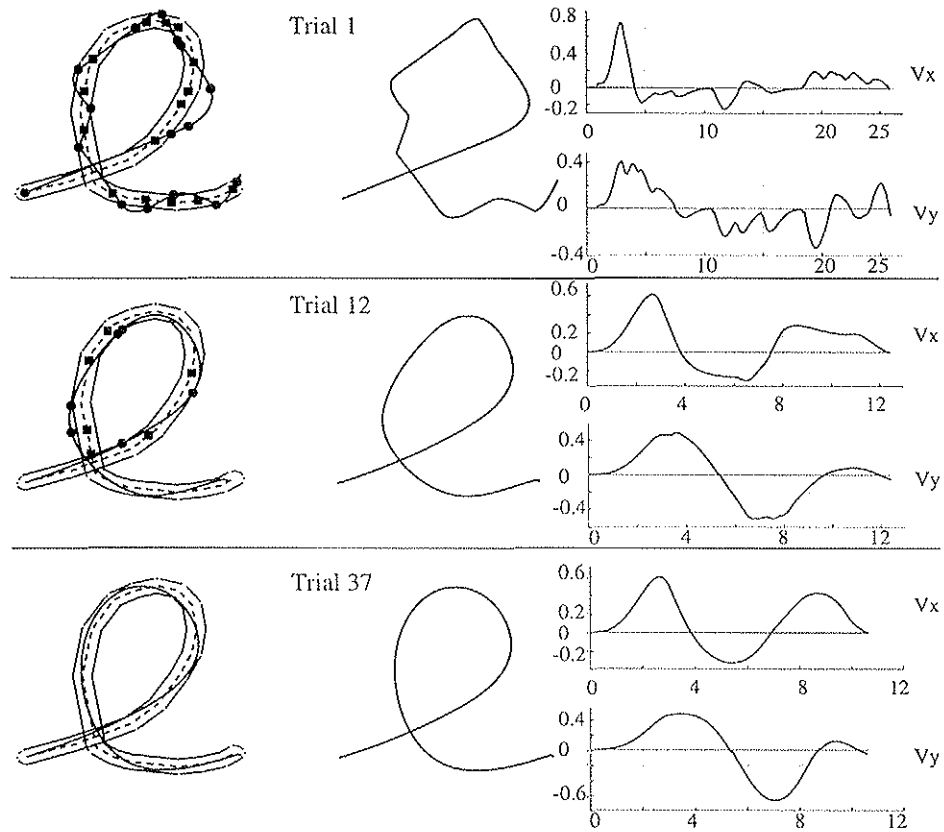


Fig. 13. Learning the letter *l*. *Left:* The attentional focus is illustrated by the tube around the dashed template curve. Circles indicate the *PPV* when a new target, marked by a square, is chosen, either because memory is too small or because the *PPV* has exceeded the distance, r_a , from the template curve. *Middle:* AVITEWRITE's *l* viewed in isolation. *Right:* *x* (top) and *y* (bottom) velocity profiles, V_x , V_y . (a) Learning trial 1; (b) Learning trial 12; (c) Final learning trial 37. The letter is now drawn without deviating from the attentional radius around the template curve. Note also that the writing time has decreased from over 25 to under 11 time units.

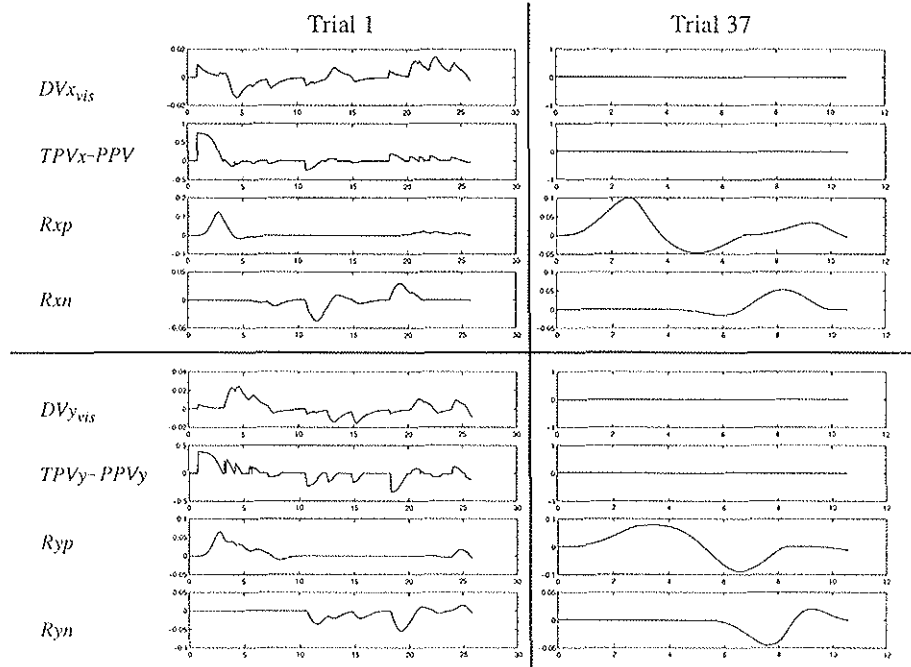


Fig. 14. Model components during learning of the letter *l* of Figure 3.12. *Left:* trial 1; *Right:* trial 37; *Top:* Positive and negative *x* synergies; *Bottom:* Positive and negative *y* synergies;

Figure 14 shows the dynamics of several model components during the learning process. The visual difference vector (DV_{vis}) from the present position (PPV) to a target (TPV) is integrated through time as it competes with memory, R , to control the movement. If R is less than a threshold value of ϵ or if movement exceeds a distance r_n from the template curve, then a target, TPV , is chosen and DV_{vis} grows toward the value of $TPV - PPV$. If $R > \epsilon$ and the PPV is within a distance r_n of the template curve, then DV_{vis} decays toward zero. The Purkinje cell population response, R , which forms the cerebellar memory output, is shaped by learning as the parallel fiber/Purkinje cell synaptic weights are modified based on the error signal $TPV - PPV$. Note that on trial 37 (right side of figure), memory alone controls movement and keeps it within the attentional radius r_n of the template curve. No errors are made and DV_{vis} and $TPV - PPV$ equal zero throughout the learned movement. Figure 15 shows the corresponding spectral activations during trial 37. Figure 16 shows a sample of how the model can learn all the letters of the alphabet.

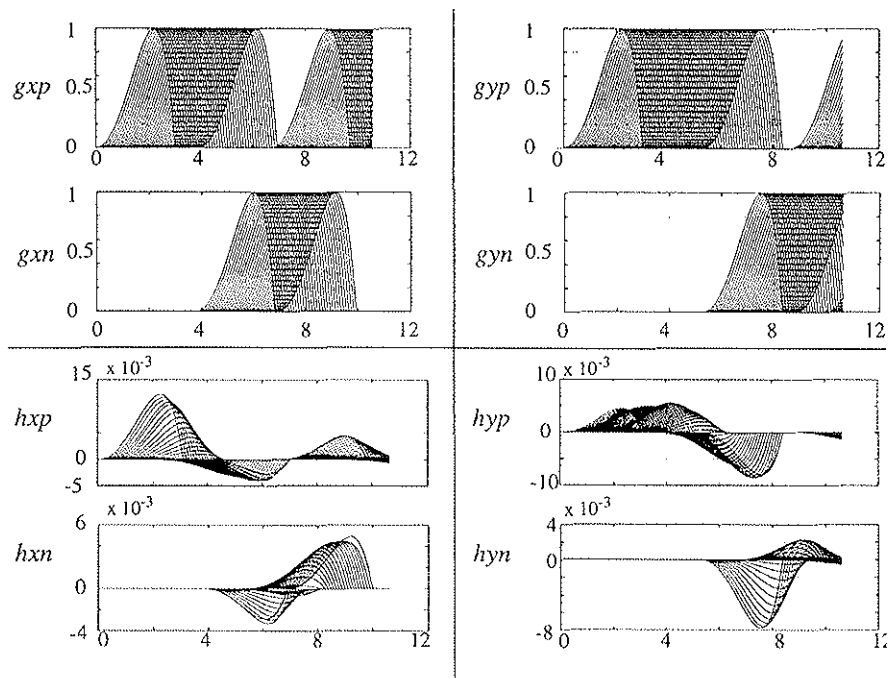


Fig. 15. Purkinje cell spectra during trial 37 of learning the letter *l*: *Top*: Spectrum of Purkinje cell responses (g) generated using Equation (2). Input to the spectrum of one synergy is shut off when the net movement direction, given by $DV_{ms} + R$, changes sign. A new synergy and Purkinje cell spectrum are then activated. Such synergy switching occurs at approximately times $t = 4$ and 7 in the positive and negative x synergies (left: gxp , gxn) and $t = 6$ and 9 in the positive and negative y synergies (right: gyp , gyn). *Bottom*: The pattern of learned Purkinje cell activations (h) formed when g is gated by the parallel fiber/Purkinje cell synaptic weights (z in Equation 3) formed during learning.

Inverse Relation between Curvature and Velocity. Figure 17 compares three letters learned by AVITEWRITE with similar letters written by adult human subjects (Edelman & Flash, 1987). Unimodal x and y velocity profiles are generated for each synergy by both humans and AVITEWRITE, as is the inverse relation between tangential velocity and curvature. The peaks in curvature near the ends of the simulated trajectories are the result of the x and y velocities (V_x , V_y) getting very small, with V_x and $V_y \ll 1$. The curvature:

$$C = \frac{(V_x \cdot A_y) - (V_y \cdot A_x)}{(V_x^2 + V_y^2)^{1.5}} \quad (1)$$

approaches infinity as the sum of V_x^2 and V_y^2 approaches zero. This effect is not seen in the human data shown in Figure 17 because the curvature has been truncated prior

to the end of the velocity profile where velocity reaches zero. Terms A_x and A_y are the x and y acceleration, respectively.

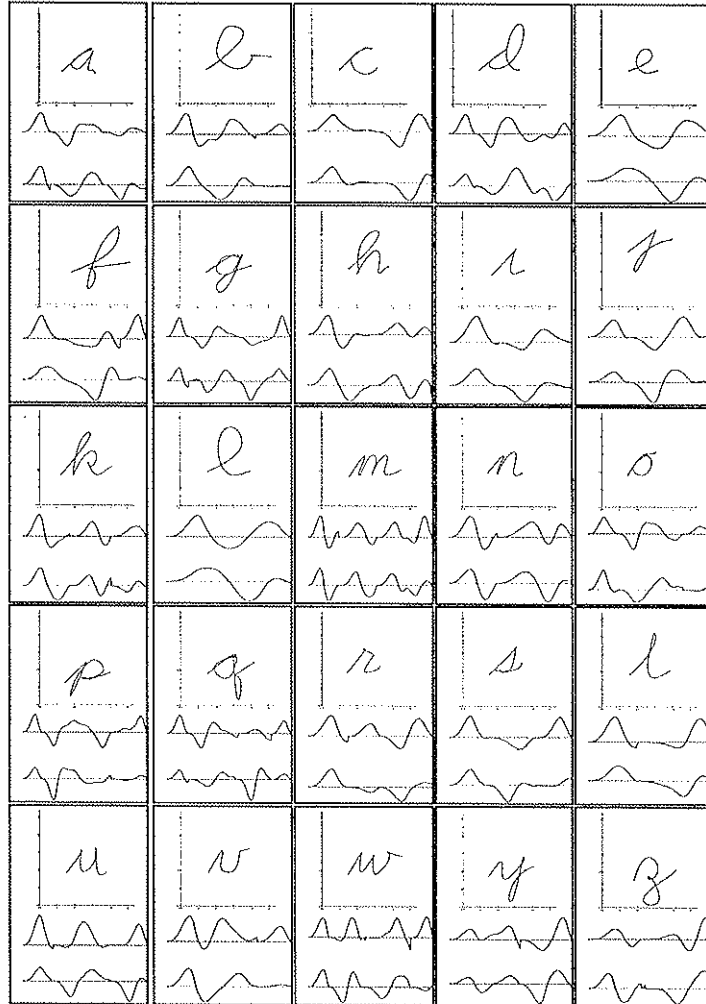


Fig. 16. The alphabet as learned by AVITEWRITE; Each panel contains a letter at the top with the x velocity profile in the middle and the y velocity profile at the bottom. All letters were learned at the relative scale shown here. The cross in the t , the letter x , and the dots on the i and j were omitted because they involved discontinuities in the movement, with lifting of the pen from the page and hand repositioning.

The Two-Thirds Power Law. As curvature increases, the angular velocity required to move through the curve in a given amount of time also increases. Thus, angular velocity is a function of the curvature. This relation is quantified by the Two-Thirds

Power Law, which states that the angular velocity is proportional to the curvature raised to the two-thirds power (Lacquaniti et al., 1983):

$$A = kC^{\frac{2}{3}}, \quad (2)$$

where A = angular velocity, C = curvature, and k is a proportionality constant. Equivalently,

$$V_{\text{tan}} = kr^{\frac{1}{3}}, \quad (3)$$

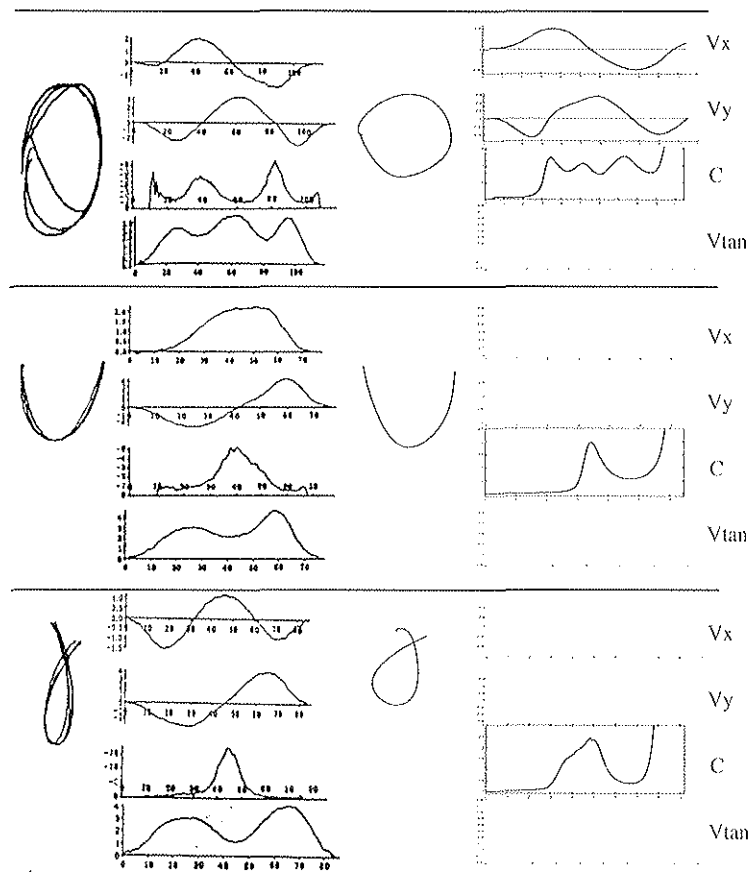


Fig. 17. *Left:* Human writing with x and y velocity profiles (V_x, V_y), movement curvature (C), and tangential velocity (V_{tan}) (Reproduced with permission from Edelman & Flash, 1987). *Right:* Similar shapes learned by AVITWRITE.

where V_{tan} = tangential velocity, r = radius of curvature ($1/C$), and k is a proportionality constant. The law was originally reported to hold mainly for elliptical movements (Lacquaniti et al., 1983). Since then, others (Wann et al., 1988, p. 635) have reported that the law holds for handwriting movements at fast speeds. The law is violated when "size differences and translation are combined in a word" (Thomassen & Teulings, 1985, p. 260). Nevertheless, the law holds under many conditions in human handwriting movements. The Two-Thirds Power Law relation emerges from the learning process described in the current model (Figure 18). The Two-Thirds Power Law prediction of tangential velocity becomes unrealistically large as the curvature of the movement becomes very small ($C \ll 1$), as may occur near the beginning and end of a movement (Figure 17), causing the large spikes in the power law predictions in Figure 18. Smoothing the acceleration, as would be done by the motor plant, reduces the number of these spikes.

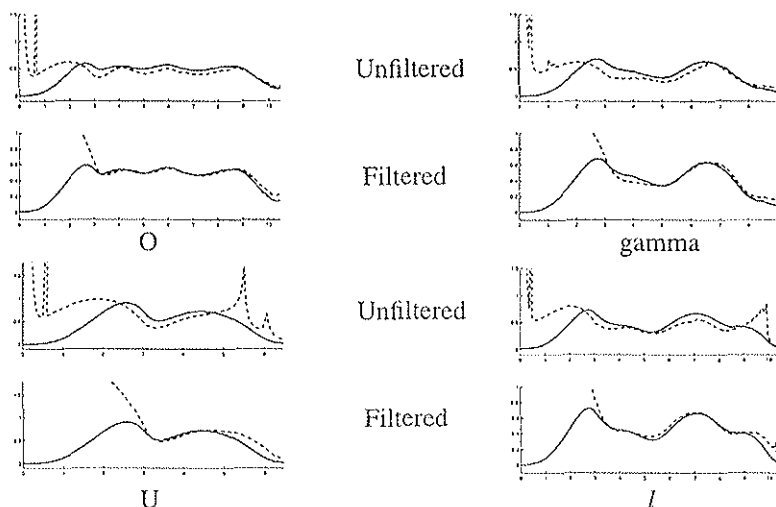


Fig. 18. Two-Thirds Power Law predictions (dotted lines) of tangential velocity compared to the actual tangential velocity (solid lines) of AVITEWRITE for the letters O, U, gamma, and *l*. For each letter, the top panel shows the power law prediction calculated using the unfiltered model acceleration profile, and the bottom panel with filtered outputs.

Variable Speeds During Learning. A task must usually be performed more slowly during the early stages of learning than at later stages. Increasing the speed of performance before the motor system has adequately learned the task results in more errors. Such a gradual speed increase occurs while learning to play musical instruments or a new language. A similar phenomenon occurs during the learning of handwriting movements (Alston & Taylor, 1987, p. 115; Burns, 1962, pp. 45-46; Freeman, 1914, pp. 83-84).

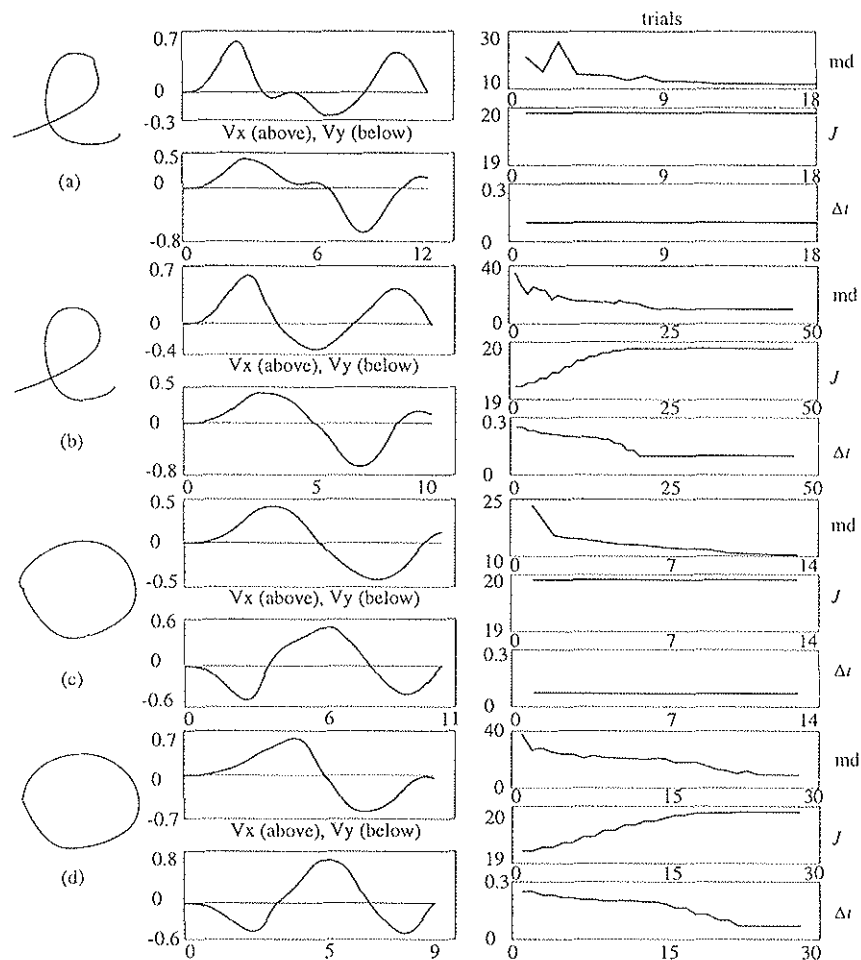


Fig. 19. Letters learned with variable speed compared to learning at a constant, fast speed. In (a) and (c), the *GO* signal (J) and spectral density (calibrated by $\bullet t$) were held constant ($J = 20$, $\bullet t = 0.1$). In (b) and (d), the *GO* signal and spectral density were incrementally increased every two trials (starting at $J = 19.25$, $\bullet t = 0.25$; ending at $J = 20$, $\bullet t = 0.1$). The result was an increase in the range of movement durations. (a) through (d): *Left*: Letter learned by AVITEWRITE; *Middle*: x and y velocity profiles, V_x , V_y ; *Right*: (top) trials versus movement duration (md); (middle) J over the course of learning; (bottom) $\bullet t$ over the course of learning.

Figure 19 shows that this gradual decrease of movement duration over multiple learning trials is a feature of AVITEWRITE's learning as well. The decrease in movement duration over the course of learning in AVITEWRITE may occur for two reasons: (1) In the early trials, the memory is not yet fully developed. As a result, the movement repeatedly deviates from the attentional radius around the template curve being traced, and the total distance moved may exceed the length of the

template curve (Figure 13a). As learning progresses, the movement remains within the attentional radius more and more, so the total movement distance may decrease (Figures 13b, and 13c). (2) Since fewer DV_{vis} 's contribute to forming the memory at earlier trials (the memory forms a cumulative representation of all the DV_{vis} 's over all past learning trials), the size of the memory signal R may be smaller at a given time for earlier trials as compared to later trials. Movement velocity scales with the size of the cerebellar memory output, R . This increase in the size of the memory signal over the course of learning can also lead to a speed increase and a decrease in movement duration as learning progresses.

In addition to a decrease of movement duration resulting from the learning mechanism described above, a person may also voluntarily alter the speed of a movement. The model allows for such speed scaling during learning by varying the volitional GO signal along with the density of the cerebellar spectra which are sampling the movement error signals. Altering spectral density can also alter the size of the memory signal, R , generated at a given time. Since the movement velocity is proportional to the size of R , the speed is altered both by changes in the GO signal and by changes in the spectral density. If the execution rate of movement commands stored in the working memory is reduced by decreasing movement speed via the GO signal, error feedback to the cerebellum is delayed.

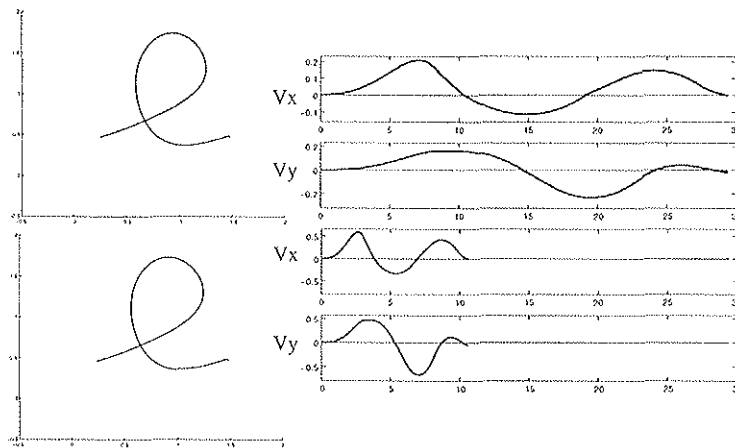


Fig 20. Speed scaling of the letter l with preservation of the letter shape and the shape of the x and y velocity profiles, V_x , V_y . *Top:* Letter l with the GO signal input $J = 7$. *Bottom:* Letter l with the GO signal input $J = 20$.

Speed-Scaling of a Learned Movement. Previously learned movements can be written at a wide range of speeds with relatively little distortion of the shape of the movement or the velocity profiles. Wright (1993) has shown that the speed of handwriting movements can be varied by a factor of about 2.8 (a range of 0.6 to 1.66 times the baseline speed) without significantly altering the letter shape. Presumably, no new learning takes place during such speed-scaling since the letters have been written by the subjects for years.

The model yields speed-scaling by a comparable factor without shape or velocity profile distortion, as shown in Figure 20. These results are obtained through the use of a working memory buffer which transiently stores the outputs of the cerebellar long term memory and sends them on to the motor apparatus at a rate which can be decreased relative to the rate of cerebellar readout (Figure 9). Speed is altered by varying the size of the *GO* signal.

If learning has been completed at some final spectral density, altering spectral density thereafter can result in distortions of the movement and its velocity profile. Thus, attempting to control the speed of learned movements by altering spectral density alone may trigger new movement errors. Instead, AVITEWRITE uses the volitional *GO* signal in conjunction with the working memory system to yield speed scaling with shape invariance. Since no new learning is required, and hence no delayed error feedback, the spectral density is kept constant at the value reached on the last learning trial at which error-free movement was achieved. The model assumes that an attentional gate couples the *GO* signal and spectral density during attentive imitation, but that they are decoupled during automatic performance of a previously learned letter.

Size Scaling and Isochrony. Size can be scaled in the model by varying the volitional *GRO* signal in Figure 9. Using the same *GRO* value for both horizontal and vertical directions will uniformly alter the size of a letter without altering the ratio of height to width (Figure 21). However, Wann and Nimmo-Smith (1990) have shown that humans do alter this ratio when scaling letter sizes; that is, vertical and horizontal sizes can be scaled independently. In their experiment of size scaling, subjects were found to increase the horizontal (*x*) component of movement by 46% and the vertical (*y*) component by 78% (p. 111). Figure 22 shows the result of a simulation in which different *GRO* values are used for the horizontal and vertical directions, with the *x* synergies' *GRO* signal *S_x* increased 46% and *S_y* by 78%, relative to the value used during learning.

Human handwriting exhibits isochrony; namely, the tendency for shapes of different sizes to be drawn in the same amount of time. Isochrony is also a feature of the model's performance, as seen in Figures 21 and 22. Isochrony in humans is observed at small sizes, but it fails at large sizes; that is, the isochrony principle is valid within the "neighborhood of normal letter heights (approx. 0.5 cm) [but the] writing time will increase at some point where force demands become too high" (Thomassen & Teulings, 1985, p. 255). "Writing time is not invariant across changes in writing size, but increases by a small amount" (Wright, 1993, p. 49). These limits of isochrony may be due to the physical limitations of the hand/arm system and/or limits of the central force-control mechanisms of the brain, as exemplified in the extreme case of Parkinson's disease patients who appear to have a "reduced capability to maintain a given force level for the [prolonged] stroke time periods" required when letter size is greatly increased (Van Gemmert et al., 1999, p. 685).

Coarticulatory Context Effects in Handwriting. How a cursive letter is written may be affected by adjacent, connected letters. Thomassen and Schomaker (1986) demonstrated context effects which they assume are due to coarticulation; that is,

"anticipatory and overlapping instructions to the motor system" (p. 257). Different sets of muscles with separate goals can be working simultaneously, or the same set of muscles can be receiving motor commands to carry out separate goals. In the latter case, the muscles' movements may be a summation or averaging of the commands they receive. If conflicting commands are received, some muscles in a group which usually work together toward a common goal may carry out one command while other muscles in the group carry out other commands (Ohman, 1965, pp. 166, 168; Fowler et al., 1993, p. 179).

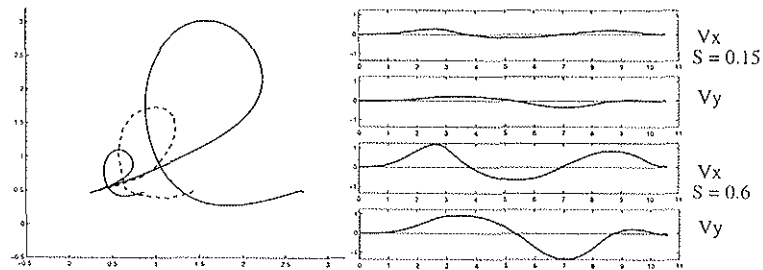


Fig. 21. Size scaling with isochrony. The dashed letter l is the template curve traced during learning with a baseline, size-scaling GRO signal $S = 0.3$. $S = 0.15$ for the smaller, solid l written by AVITEWRITE, and $S = 0.6$ for the larger, solid l . Both the large and the small l are written in the same amount of time, as seen in the x and y velocity profiles, V_x , V_y .

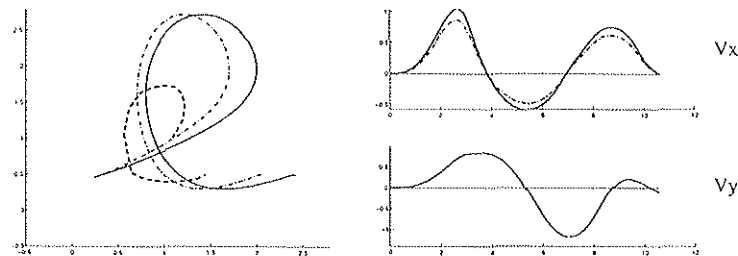


Fig. 22. Independent scaling of horizontal and vertical components of size. The small, dashed letter l is the template curve traced during learning with a baseline, size-scaling GRO signal parameters $S_x = S_y = 0.3$. The two larger l 's both have a y GRO signal parameter $S_y = 0.53$. The large, dash-dotted l has an x GRO signal of $S_x = 0.44$ corresponding to the dotted x velocity profile, V_x , while the large, solid l has $S_x = 0.53$ with a solid x velocity profile.

Thomassen and Schomaker (1986) found that "more rapid writers... display stronger context effects than slower writers" (p. 257). This finding is consistent with the observed increase in speech *carryover coarticulation* with increases in speaking rate. "Carryover" ("perseverative", "left to right") coarticulation occurs when new motor commands are given before the previous commands have been fully executed.

Muscles then begin contracting in a new pattern before the previous pattern of muscle contractions has been completed (Ostry et al., 1996).

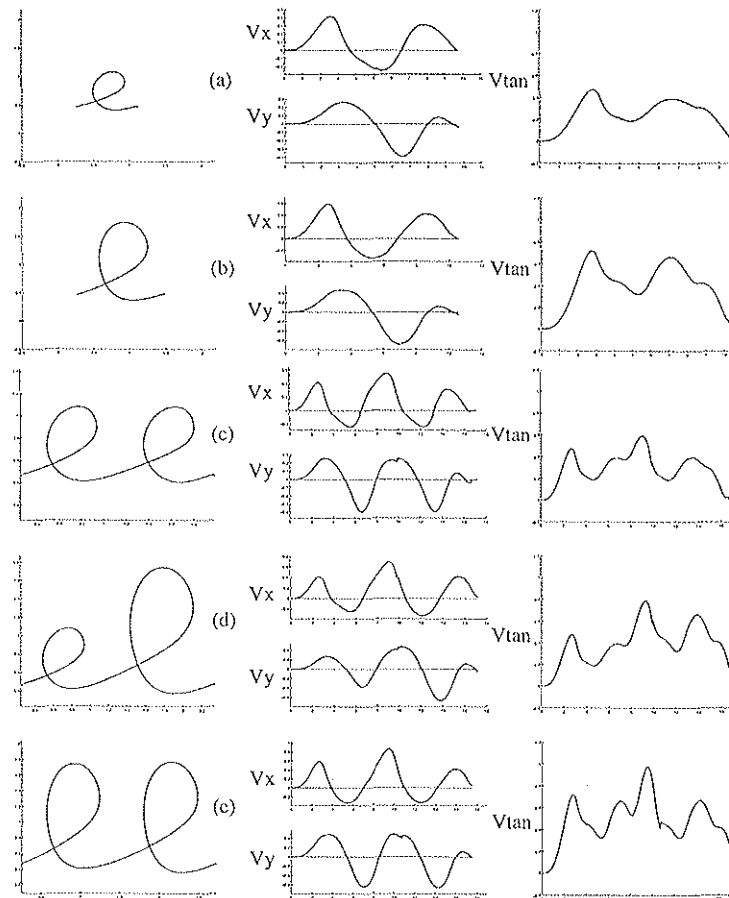


Fig. 23. Simulated combinations of the letters *e* and *l*. *Left:* The letters; *Middle:* *x* and *y* velocity profiles, V_x , V_y ; *Right:* Tangential velocity, V_{tan} .

The idea that some of the observed context effects in handwriting are due to carryover coarticulation was tested as follows. Connected letters were simulated with varying degrees of overlap of the corresponding spectral memories. In other words, the degree of superposition between adjacent letters was varied. The letters *e* and *l* were learned by the modeled system (Figures 23). The learned memory traces were then read out successively with varying degrees of overlap. Some of the downstroke duration and size effects observed by Thomassen and Schomaker (1986) were replicated by varying the degree of superposition between adjacent letters. In the simulation of the word *eele*, shown in Figure 24, the relative timing of the loading of the previously learned letter memories was varied and the sizes of the letters were

compared. The second *e* becomes smaller than the other *e*'s when its superposition increases with the large vertical upstroke of the following *l*, thereby canceling a large part of the *e* downstroke (Figures 24b and 24c). Increasing the time separation between letters can eliminate the coarticulatory size effects in the model, as seen in Figure 24a.

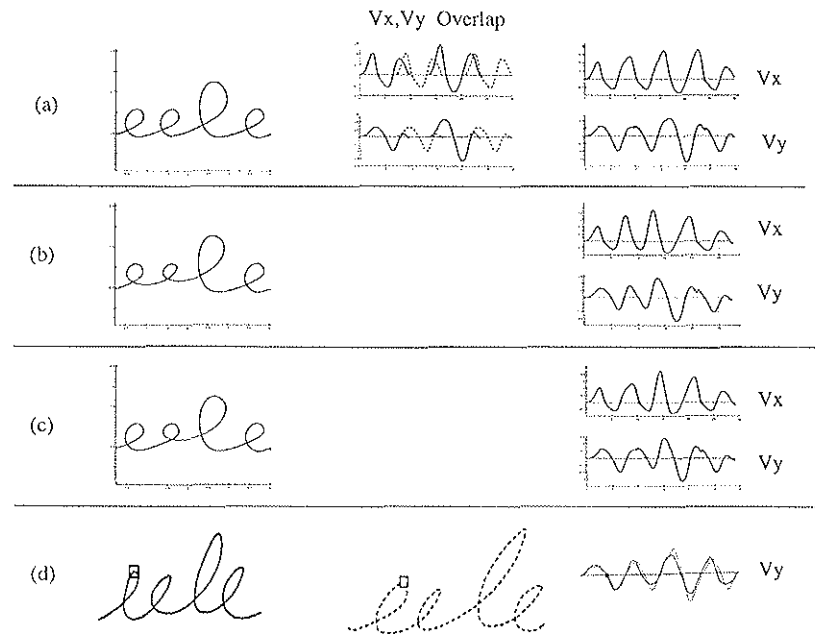


Fig. 24. Simulations of coarticulation: (a) through (c): Simulated *eele* with varying degrees of overlap between the letters. Timing relations are as follows. (a) 6.6, 6.6, 7 (The second letter begins 6.6 time units after the first; the third starts 6.6 after the second, and the fourth starts 7 time units after the third, corresponding to the second V_x zero crossings shown in V_x Overlap.) V_x, V_y Overlap show the overlapping velocity profiles of the individual letters. (b) 5, 5, 7; (c) 6.6, 5, 7; (d) Human writing of *eele* by two subjects (Figure (d) reproduced with permission from Thomassen & Schomaker, 1986). The dotted y velocity profile, V_y , corresponds to the dotted *eele*.

9. Conclusion

The AVITEWRITE model clarifies aspects of how a person learns to make curved handwriting movements. This model incorporates elements of two previous groups of models: spectral timing models that analyze cerebellar learning (Fiala, Grossberg, & Bullock, 1996; Grossberg & Merrill, 1992; Grossberg & Schmajuk, 1989) and the VITE and VITEWRITE models of how the cerebral cortex and basal ganglia work together to control the read-out of trajectory commands (Bullock & Grossberg, 1988a, 1988b, 1991; Bullock, Grossberg & Mannes, 1993). The AVITEWRITE model hereby seeks to clarify how the cerebral cortex, cerebellum, and basal ganglia may interact

during complex learned movements. There is both cooperation and competition between reactive vision-based imitation and planned memory readout. The cooperation includes interactions between cortical difference vectors and cerebellar learning. The competition arises between cerebellar control of learned movements and error-driven, cortical control of reactive movements to attentionally chosen visual targets. The model suggests that there is an automatic shift in the balance of movement control between these cortical and cerebellar processes during the course of learning. Reactive movements are made to attentionally chosen targets on a curve at the same time as movement error signals are generated which allow the cortico-cerebellar system to learn how to draw the curve. Memory-based movements gradually supersede visually-driven movements as learning progresses. Finally, the model shows how challenging psychophysical properties of planar hand movements may emerge from this cortico-cerebellar-basal ganglia interaction.

References

- Abend, W., Bizzi, E., Morasso, P. (1982). Human arm trajectory formation. *Brain*. 105, 331-348.
- Alston, J., Taylor, J. (1987). *Handwriting: Theory, research, and practice*. New York: Nichols.
- Andersen, R., Essick, G., Siegel, R. (1985). Encoding of spatial location by posterior parietal neurons. *Science*. 230, 456-458.
- Andersen, R. (1995). Encoding of intention and spatial location in the posterior parietal cortex. *Cerebral Cortex*. 5, 457-469.
- Arroyo-Anillo, E.M., Botz-Marquard, T. (1998). Neurobehavioral dimensions of olivopontocerebellar atrophy. *Journal of Clinical and Experimental Neuropsychology*. 20, 52-59.
- Bannerman, D.M., Yee, B.K., Good, M.A., Heupel, M.J., Iversen, S.D., Rawlins, J.N. (1999). Double dissociation of function within the hippocampus: a comparison of dorsal, ventral, and complete hippocampal cytotoxic lesions. *Behavioral Neuroscience*. 113, 1170-1188.
- Bartha, G.T., Thompson, R.F., Gluck, M.A. (1991). Sensorimotor learning and the cerebellum. In M. Arbib, J. Ewert (Eds.). *Visual structures and integrated functions*. Berlin: Springer.
- Berardelli, A., Hallett, M., Rothwell, J.C., Agostino, R., Manfredi, M., Thompson, M., Thompson, P.D., Marsden, C.D. (1996). Single-joint rapid arm movements in normal subjects and in patients with motor disorders. *Brain*. 119, 661-674.
- Bernstein, N. (1967). *The coordination and regulation of movements*. London: Pergamon Press.
- Bizzi, E., Saltiel, P., Tresch, M. (1998). Modular organization of motor behavior. *Zeitschrift für Naturforschung [C]*. 53, 510-7.
- Buchanan, T.S., Almdale, D.P.J., Lewis, J.L., Rymer, W.Z. (1986). Characteristics of synergic relations during isometric contractions of human elbow muscles. *Journal of Neurophysiology*. 56, 1225-1241.
- Bullock, D., Cisek, P., Grossberg, S. (1998). Cortical networks for control of voluntary arm movements under variable force conditions. *Cerebral Cortex*. 8, 48-62.
- Bullock, D., Fiala, J.C., Grossberg, S. (1994). A neural model of timed response learning in the cerebellum. *Neural Networks*. 7, 1101-1114.
- Bullock, D., Grossberg, S. (1988a). The VITE model: A neural command circuit for generating arm and articulator trajectories. In J. Kelso, A. Mandell, M. Shlesinger (Eds.). *Dynamic patterns in complex systems*. Singapore: World Scientific.

- Bullock, D., Grossberg, S. (1988b). Neural dynamics of planned arm movements: Emergent invariants and speed-accuracy properties during trajectory formation. *Psychological Review*. 95, 49-90.
- Bullock, D., Grossberg, S. (1991). Adaptive neural networks for control of movement trajectories invariant under speed and force rescaling. *Human Movement Science*. 10, 3-53.
- Bullock, D., Grossberg, S., Mannes, C. (1993). A neural network model for cursive script production. *Biological Cybernetics*. 70, 15-28.
- Buonomano, D.V., Mauk, M.D. (1994). Neural network model of the cerebellum: Temporal discrimination and the timing of motor responses. *Neural Computation*. 6, 38-55.
- Burns, P.C. (1962). Improving handwriting instruction in elementary schools. Minneapolis (pp. 45-46). Minneapolis, MN: Burgess Publishing Co.
- Caminiti, R., Genovesio, A., Marconi, B., Mayer, A.B., Onorati, P., Ferraina, S., Mitsuda, T., Giannetti, S., Squatrito, S., Maioli, M.G., Molinari, M. (1999). Early coding of reaching: Frontal and parietal association connections of parieto-occipital cortex. *European Journal of Neuroscience*. 11, 3339-3345.
- Chapeau-Blondeau, F., Chauvet, G. (1991). A neural network model of the cerebellar cortex performing dynamic associations. *Biological Cybernetics*. 65, 267-279.
- Chieffi, S., Allport, D.A. (1997). Independent coding of target distance and direction in visuo-spatial working memory. *Psychological Research*. 60, 244-250.
- Coltz, J.D., Johnson, M.T.V., Ebner, T.J. (1999a). Cerebellar Purkinje cell simple spike discharge encodes movement velocity in primates during visuomotor arm tracking. *The Journal of Neuroscience*. 19, 1782-1803.
- Coltz, J.D., Johnson, M.T.V., Ebner, T.J. (1999b). Cerebellar Purkinje cell complex spike discharge during visuomotor arm tracking in primates: Relationships to movement parameters and comparisons to simple spike discharge. *Society for Neuroscience Abstracts*. 25, 372.
- Dagher, A., Owen, A.M., Boecker, H., Brooks, D.J. (1999). Mapping the network for planning: a correlational PET activation study with the Tower of London task. *Brain*. 122, 1973-1987.
- Doyon, J., LaForce Jr., R., Bouchard, G., Gaudreau, D., Roy, J., Poirier, M., Bedard, P., Bedard, F., Bouchard, J. (1998). Role of the striatum, cerebellum and frontal lobes in the automatization of a repeated visuomotor sequence of movements. *Neuropsychologia*. 36, 625-641.
- Ebner, T.J. (1998). A role for the cerebellum in the control of limb movement velocity. *Current Opinion in Neurobiology*. 8, 762-769.
- Edelman, S., Flash, T. (1987). A model of handwriting. *Biological Cybernetics*. 57, 25-36.
- Fiala, J., Grossberg, S., Bullock, D. (1996). Metabotropic glutamate receptor activation in cerebellar Purkinje cells as substrate for adaptive timing of the classically conditioned eye-blink response. *The Journal of Neuroscience*. 16, 3760-3774.
- Fowler, C., Saltzman, E. (1993). Coordination and coarticulation in speech production. *Language and Speech*. 36, 171-195.
- Freeman, F.N. (1914). The teaching of handwriting (pp. 83-84). Boston, MA: Houghton-Mifflin, The Riverside Press Cambridge.
- Freeman, J.A. (1969). The cerebellum as a timing device: an experimental study in the frog. In R. Llinas (Ed.). *Neurobiology of cerebellar evolution and development*, pp. 397-420. Chicago: American Medical Association.
- Fu, Q.G., Mason, C.R., Flament, D., Coltz, J.D., Ebner, T.J. (1997). Movement kinematics encoded in complex spike discharge of primate cerebellar Purkinje cells. *Neuroreport*. 8, 523-529.

- Gellman, R., Gibson, A.R., Houk, J.C. (1985). Inferior olivary neurons in the awake cat: Detection of contact and passive body displacement. *Journal of Neurophysiology*. 54, 40-60.
- Georgopoulos, A.P., DeLong, M.R., Crutcher, M.D. (1983). Relations between parameters of step-tracking movements and single cell discharge in the globus pallidus and subthalamic nucleus of the behaving monkey. *The Journal of Neuroscience*. 3, 1586-1598.
- Georgopoulos, A.P., Kalaska, J.F., Caminiti, R., Massey, J.T. (1982). On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *The Journal of Neuroscience*. 2, 1527-1537.
- Georgopoulos, A.P., Lurito, J.T., Petrides, M., Schwartz, A.B., Massey, J.T. (1989). Mental rotation of the neuronal population vector. *Science*. 243, 234-236.
- Georgopoulos, A.P., Taira, M., Lukashin, A. (1993). Cognitive neurophysiology of the motor cortex. *Science*. 260, 47-52.
- Ghez, C. (1991). The Cerebellum. In E.R. Kandel, J.H. Schwartz, T.M. Jessel (Eds.). Principles of neural science, pp. 626-646. New York: Elsevier Science Publishers.
- Greer, K., Green, D. (1983). Context and motor control in handwriting. *Acta Psychologica*. 54, 205-215.
- Grossberg, S., Merrill, J. (1992). A neural network model of adaptively timed reinforcement learning and hippocampal dynamics. *Cognitive Brain Research*. 1, 3-38.
- Grossberg, S., Merrill, J. (1996). The hippocampus and cerebellum in adaptively timed learning, recognition, and movement. *Journal of Cognitive Neuroscience*. 8, 257-277.
- Grossberg, S., Paine, R. (2000) A neural model of corticocerebellar interactions during attentive imitation and predictive learning of sequential handwriting movements. *Neural Networks*. in press.
- Grossberg, S., Schmajuk, N. (1989). Neural dynamics of adaptive timing and temporal discrimination during associative learning. *Neural Networks*. 2, 79-102.
- Hallett, M., Khoshbin, S. (1980). A physiological mechanism of bradykinesia. *Brain*. 103, 301-314.
- Hertrich, I., Ackermann, H. (1995). Coarticulation in slow speech: Durational and spectral analysis. *Language and Speech*. 38, 159-187.
- Hollerbach, J.M., Flash, T. (1982). Dynamic interactions between limb segments during planar arm movement. *Biological Cybernetics*. 44, 67-77.
- Hopfinger, J.B., Buonocore, M.H., Mangun, G.R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*. 3, 284-291.
- Horak, F.B., Anderson, M.E. (1984a). Influence of globus pallidus on arm movements in monkeys, I. Effects of kainic acid-induced lesions. *Journal of Neurophysiology*. 52, 290-304.
- Horak, F.B., Anderson, M.E. (1984b). Influence of globus pallidus on arm movements in monkeys, II. Effects of stimulation. *Journal of Neurophysiology*. 52, 305-322.
- Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*. 286, 2526-2528.
- Ito, M. (1984). The cerebellum and neural control (pp. 325-349). New York: Raven.
- Ito, M. (1991). The cellular basis of cerebellar plasticity. *Current Opinion in Neurobiology*. 1, 616-620.
- Ito, M., Karachot, L. (1992). Protein kinases and phosphatase inhibitors mediating long-term desensitization of glutamate receptors in cerebellar Purkinje cells. *Neurosciences Research*. 14, 27-38.
- Jaffe, S. (1992). A neuronal model for variable latency response. In F.H. Eeckman (Ed.). Analysis and modeling of neural systems. Boston: Kluwer Academic Publishers.

- Jueptner, M., Frith, C.D., Brooks, D.J., Frackowiak, R.S., Passingham, R.E. (1997a). Anatomy of motor learning. II. Subcortical structures and learning by trial and error. *Journal of Neurophysiology*. 77, 1325-1337.
- Jueptner, M., Stephan, K.M., Frith, C.D., Brooks, D.J., Frackowiak, R.S., Passingham, R.E. (1997b). Anatomy of motor learning. I. Frontal cortex and attention to action. *Journal of Neurophysiology*. 77, 1313-1324.
- Jueptner, M., Weiller, C. (1998). A review of differences between basal ganglia and cerebellar control of movements as revealed by functional imaging studies. *Brain*. 121, 1437-1449.
- Kalaska, J.F., Cohen, D.A.D., Prud'homme, M.J., Hyde, M.L. (1990). Parietal area 5 neuronal activity encodes movement kinematics, not movement dynamics. *Experimental Brain Research*. 80, 351-364.
- Kawashima, R., Okuda, J., Umetsu, A., Sugiura, M., Inoue, K., Suzuki, K., Tabuchi, M., Tsukiura, T., Narayan, S.L., Nagasaka, T., Yanagawa, I., Fujii, T., Takahashi, S., Fukuda, H., Yamadori, A. (2000). Human cerebellum plays an important role in memory-timed finger movement: an fMRI study. *Journal of Neurophysiology*. 83, 1079-1087.
- Kelso, J.A.S. (Ed.) (1982). Human motor behavior. Hillsdale, NJ: Lawrence Erlbaum.
- Kretschmer, B.D., Fink, S. (1999). Spatial learning deficit after NMDA receptor blockade and state-dependency. *Behavioural Pharmacology*. 10, 423-428.
- Lacquaniti, F., Terzuolo, C., Viviani, P. (1983). The law relating the kinematic and figural aspects of drawing movements. *Acta Psychologica*. 54, 115-130.
- Lu, X., Hikosaka, O., Miyachi, S. (1998). Role of monkey cerebellar nuclei in skill for sequential movement. *Journal of Neurophysiology*. 79, 2245-2254.
- Moore, J.W., Desmond, J.E., Berthier, N.E. (1989). Adaptively timed conditioned responses and the cerebellum: A neural network approach. *Biological Cybernetics*. 62, 17-28.
- Morasso, P. (1981). Spatial control of arm movements. *Experimental Brain Research*. 42, 223-227.
- Morasso, P. (1986). Understanding Cursive Script as a Trajectory Formation Paradigm. In H. Kao, G. van Galen, R. Hoosain (Eds.). *Graphonomics: Contemporary research in handwriting*, pp. 137-167. New York: Elsevier Science Publishers.
- Morasso, P., Mussa Ivaldi, F.A., Ruggiero, C. (1983). How a discontinuous mechanism can produce continuous patterns in trajectory formation and handwriting. *Acta Psychologica*. 54, 83-98.
- Mussa-Ivaldi, F. (1988). Do neurons in the motor cortex encode movement direction? An alternative hypothesis. *Neuroscience Letters*. 91, 106-111.
- Ohman, S. (1965). Coarticulation in VCV utterances: spectrographic measurements. *Journal of the Acoustical Society of America*. 39, 151-168.
- Oscarsson, O. (1969). Termination and functional organization of the dorsal spino-olivocerebellar path. *The Journal of Physiology (London)*. 200, 129-149.
- Ostry, D., Gribble, P., Gracco, V. (1996). Coarticulation of jaw movements in speech production: is context sensitivity in speech kinematics centrally planned? *The Journal of Neuroscience*. 16, 1570-1579.
- Perrett, S.P., Ruiz, B.P., Mauk, M.D. (1993). Cerebellar cortex lesions disrupt learning-dependent timing of conditioned eyelid responses. *The Journal of Neuroscience*. 13, 1708-1718.
- Plamondon, R., Alimi, A. (1997). Speed/accuracy trade-offs in target-directed movements. *Behavioral and Brain Sciences*. 20, 279-349.
- Pleskacheva, M.G., Wolfer, D.P., Kupriyanova, I.F., Nikolenko, D.L., Scheffrahn, H., Dell'Omo, G., Lipp, H.P. (2000). Hippocampal mossy fibers and swimming navigation learning in two vole species occupying different habitats. *Hippocampus*. 10, 17-30.

- Richer, F., Chouinard, M.J., Rouleau, I. (1999). Frontal lesions impair the attentional control of movements during motor learning. *Neuropsychologia*. 37, 1427-1435.
- Sadato, N., Ibanez, V., Deiber, M.P., Campbell, G., Leonardo, M., Hallett, M. (1996). Frequency-dependent changes of regional cerebral blood flow during finger movements. *Journal of Cerebral Blood Flow and Metabolism*. 16, 23-33.
- Schillings, J., Meulenbroek, R., Thomassen, A. (1996). Limb segment recruitment as a function of movement direction, amplitude, and speed. *Journal of Motor Behavior*. 28, 241-254.
- Schwartz, A.B., Moran, D.W. (1999). Motor cortical activity during drawing movements: Population representation during lemniscate tracing. *Journal of Neurophysiology*. 82, 2705-2718.
- Simpson, J.I., Wylie, D.R., De Zeeuw, C.I. (1996). On climbing fiber signals and their consequence(s). *Behavioral and Brain Sciences*. 19, 384-398.
- Soechting, J., Terzuolo, C. (1987). Organization of arm movements. Motion is segmented. *Neuroscience*. 23, 39-51.
- Stelmach, G., Mullins, P., Teulings, H. (1984). Motor programming and temporal patterns in handwriting. In J. Gibbon, L. Allan (Eds.). *Timing and Time Perception, Annals of the New York Academy of Sciences*. 423, 144-157.
- Thomassen, A., Schomaker, L. (1986). Between-letter context effects in handwriting trajectories. In H. Kao, G. van Galen, R. Hoosain (Eds.). *Graphonomics: Contemporary research in handwriting*, pp. 253-272. New York: North-Holland: Elsevier Science Publishers.
- Thomassen, A., Teulings, H. (1985). Time, size and shape in handwriting: Exploring spatio-temporal relationships at different levels. In J. Michon, J. Jackson, (Eds.). *Time, mind, and behavior*, pp. 253-263. Berlin: Springer-Verlag.
- Turner, R.S., Anderson, M.E. (1997). Pallidal discharge related to the kinematics of reaching movements in two dimensions. *Journal of Neurophysiology*. 77, 1051-1074.
- Turner, R.S., Grafton, S.T., Votaw, J.R., Delong, M.R., Hoffman, J.M. (1998). Motor subcircuits mediating the control of movement velocity: A PET study. *Journal of Neurophysiology*. 80, 2162-2176.
- Turvey, M.T. (1990). Coordination. *American Psychologist*. 45, 938-953.
- van Galen, G.P. (1991). Handwriting: Issues for a psychomotor theory. *Human Movement Science*. 10, 165-191.
- van Galen, G.P., Weber, J. (1998). On-line size control in handwriting demonstrates the continuous nature of motor programs. *Acta Psychologica*. 100, 195-216.
- van Gemmert, A.W., Teulings, H.L., Contreras-Vidal, J.L., Stelmach, G.E. (1999). Parkinson's disease and the control of size and speed in handwriting. *Neuropsychologia*. 37, 685-694.
- Vindras, P., Viviani, P. (1998). Frames of reference and control parameters in visuomanual pointing. *Journal of Experimental Psychology: Human Perception and Performance*. 24, 569-591.
- Waite, J.J., Chen, A.D., Wardlow, M.L., Wiley, R.G., Lappi, D.A., Thal, L.J. (1995). 192 immunoglobulin G-saporin produces graded behavioral and biochemical changes accompanying the loss of cholinergic neurons of the basal forebrain and cerebellar Purkinje cells. *Neuroscience*. 65, 463-476.
- Wann, J., Nimmo-Smith, I., Wing, A. (1988). Relation between velocity and curvature in movement: equivalence and divergence between a power law and a minimum-jerk model. *Journal of Experimental Psychology: Human Perception and Performance*. 14, 622-637.
- Wann, J.P., Nimmo-Smith, I. (1990). Evidence against the relative invariance of timing in handwriting. *The Quarterly Journal of Experimental Psychology*. 42A, 105-119.

- Wright, C.E. (1993). Evaluating the special role of time in the control of handwriting. *Acta Psychologica*. 82, 5-52.
- Zhou, T.L., Tamura, R., Kuriwaki, J., Ono, T. (1999). Comparison of medial and lateral septal neuron activity during performance of spatial tasks in rats. *Hippocampus*. 9, 220-234.
- Zipser, D. (1986). A model of hippocampal learning during classical conditioning. *Behavioral Neuroscience*. 100, 764-776.