



ELSEVIER

New Ideas in Psychology 22 (2004) 97–125

NEW IDEAS IN
PSYCHOLOGY

www.elsevier.com/locate/newideapsych

The cerebellum in thought and action: a fronto-cerebellar aging hypothesis

Michael J. Hogan*

Department of Psychology, National University of Ireland, Galway, Ireland

Available online 2 November 2004

Abstract

Normal aging is associated with deficits in both memory and executive control. While a number of theories of cognitive aging have proposed that decrements in frontally mediated executive control processes can account for many of the age-related changes observed, the models proposed to date have not adequately accounted for age changes in processing speed, intra-individual variability and automaticity of information processing. These basic aspects of information processing efficiency may be of central importance for our understanding of age-related cognitive changes and more elaborate neurological models are needed that incorporate explanatory mechanisms which account for their influence. In this paper, it is proposed that the dual role played by frontal and cerebellar degeneration and the disruption of fronto-cerebellar feedback and feedforward control loops may be of central importance for a model of age-related changes in processing speed, intra-individual variability, automaticity, and higher level cognitive functions like memory and executive control.

© 2004 Elsevier Ltd. All rights reserved.

1. Introduction

Normal aging is associated with deficits in both memory (see Craik & Jennings, 1992; Kausler, 1994; Light, 1991; Smith, 1996 for reviews) and executive control (see e.g., Anderson & Craik, 2000, Hasher & Zacks, 1988; Salthouse, 1996a, b; West, 1996). There are a number of influential theories that attempt to account for these

*Tel.: +353 91 524411 ext. 3455; fax: +353 91 521355.

E-mail address: michael.hogan@nuigalway.ie (M.J. Hogan).

age-related deficits in memory and executive control, the central notion being that decrements in frontally mediated executive control processes can account for many of the age-related changes observed. It has been proposed that the ability to manage one's thoughts, memories and actions in accordance with task-relevant goals involves executive control (Anderson & Craik, 2000). Component processes of executive control include working memory (Baddeley, 1986), attention switching (Kramer, Hahn, & Gopher, 1999; Meiran, Gotler, & Perlman, 2001), sustained attention (Posner & Peterson, 1990), inhibition (Shimamura, 1995), and goal maintenance (Duncan, 1995). Models of aging and memory propose that deficits in certain components of executive control (e.g. inhibition—Hasher & Zacks, 1988) act to reduce overall cognitive control. This reduction in cognitive control is assumed to result in the observed age-related memory deficits (see e.g. Anderson & Craik, 2000; Salthouse, 1996a, b; Hasher & Zacks, 1988).

Cognitive aging researchers have questioned whether or not the operation of various executive, memory, and reasoning processes is limited by the generalized capacity of the information processing system, and if so, how can this be modelled on a brain level. One of the most influential models of the causes of age-related decrements in cognitive ability in this regard is the general slowing model (Birren & Botwinick, 1955; Salthouse, 1991, 1996a, b). The effect of general slowing is indirect—it makes other elementary cognitive operations difficult to execute, leading to a decrement in the power and efficiency of working memory, which in turn causes an impairment in such higher order functions as attention, memory, and reasoning (Salthouse, 1996a, b). Thus, according to the general slowing model, age differences in executive control and memory do not reflect changes in these processes per se, but instead reflect age differences in the speed of processing (Balota, Dolan, & Duchek, 2000).

However, neurological models of aging need to account for other lower-level properties of information processing other than general slowing. In particular, research studies have consistently observed age-related increases in intra-individual variability using measures of reaction time (Myerson & Hale, 1993; Salthouse, 1993a, b) and sensorimotor and cognitive ability (Hertzog, Dixon, & Hulstsch, 1992; Li, Lindenberger, & Frensch, 2000; Rabbitt & Patrick, 2000). Infact, early theories (Crossman & Szafran, 1956; Welford, 1962) attributed the cause of cognitive aging deficits to age-related increase in neural noise in the central nervous system. More recently, neural network models of cognitive aging (Li & Lindenberger, 1998) suggest that an increase in the level of intra-network variability may be causally related to the patterns of cognitive decline typically observed in older adults, including processing speed. In relation to processing speed, both Eysenck (1982) and Jensen (1992) hold the view that RT medians/means are merely consequences of whatever basic process is reflected by RT SD. The particular process hypothesized by Eysenck is random errors in the transmission of information in the brain, or what might be called “neural noise”. Jensen (1992) argues that oscillation in response speed will cause a positive skew in the distribution of RTs pulling any measure of central tendency in the direction of skew. Hence RT mean or RT median could simply be derivatives of the phenomenon of temporal oscillations in reaction speed.

A central question now faced by researchers is whether or not the neurological models that account for age-related cognitive decline can provide an explanation for changes at the lower level (i.e., processing speed and variability) and at higher levels (i.e., executive control, memory and reasoning) of information processing efficiency. In this paper, it is proposed that existing frontal-lobe hypotheses (FLH) of aging cognition will benefit from the incorporation of specific hypotheses about the supportive role played by the cerebellum in the modulation of information processing (Schmahmann, 1996a, b; Schmahmann & Pandya, 1997; Ito, 1993). A more specific proposal made in this paper is that age-related degeneration of the cerebellum may be central for any understanding of lower level information processing changes associated with increased intra-individual variability and concomitant reductions in the speed and automaticity of cognitive operations.

2. The frontal lobes, disconnection and aging

Frontal areas have been linked to sustained attention (Posner & Peterson, 1990), working memory (Goldman-Rakic, 1992; Baddeley, 1986), the ability to carry out actions in accordance with goals (Duncan, 1995; Shallice, 2002), inhibitory control (Shimamura, 1995), and attention switching (Meiran et al., 2001). West (1996) provided a comprehensive review of the aging literature and of the frontal-lobe hypothesis of aging (FLH). He cited numerous studies suggesting that both neurophysiological and neuropsychological evidence indicate that the frontal lobes, and in particular, the dorso-lateral prefrontal cortices, are especially sensitive to increasing age. Structural evidence included that of differential reduction in the volume of the prefrontal cortex, reductions in neurotransmitter concentrations in the prefrontal cortex and an increase in the number of senile plaques, with greater concentrations in the frontal and temporal cortices, with increasing age. Functional imaging studies also indicate the occurrence of changes in metabolic rates and regional cerebral blood flow (rCBF) in the prefrontal cortex with age (West, 1996; Grady, 2000).

The central tenet of the FLH is that the cognitive abilities supported by the prefrontal cortex should therefore demonstrate signs of age-related decline at an earlier time and to a greater degree than cognitive abilities supported by other cortical and non-cortical structures. A large number of studies have found larger age-related decrements in tasks that are sensitive to frontal lobe function than in tasks sensitive to processing associated with other regions of the brain (Rabbitt & Lowe, 2000). West (1996) concluded that the prefrontal model of cognitive aging performs well in accounting for age-related changes in prospective memory, estimation of frequency of occurrence and source monitoring, as well as studies of age-related changes in attention. One area identified by West in which the frontal-lobe hypothesis did not adequately account for age-related findings was the age-related decline in recall and recognition. West asserts that this points to the need for a fuller neuropsychological model of cognitive aging which could include theories relevant to both frontally and temporally supported cognitive processes. Indeed,

reduced electrocortical efficiency associated with breakdown of neural network communication to temporal lobes is related to the memory decline seen in early Alzheimer's disease (Hogan et al., 2003).

The FLH has been subject to many criticisms (see Greenwood, 2000; Rabbitt & Lowe, 2000) particularly regarding tests of frontal function. For example, it is not altogether clear what it is that classic "frontal" measures like the Stroop test (Stroop, 1935) are really measuring. While it is assumed that the test is a valid measure of inhibitory control, the test is a very complex one that also involves color processing, lexical processing, sustained attention, goal monitoring, and processing speed. There is growing acceptance amongst researchers that performance on classical frontal-lobe neuropsychological tests like the Stroop test is achieved by complex interactions between frontal areas and other cortical and subcortical areas (see e.g., Stuss, Floden, Alexander, Levine, & Katz, 2001). An additional problem with testing the FLH using neuropsychological tests of frontal function is that different frontal tests, assumed to rely on the integrity and efficiency of the same cortical region, are very poorly intercorrelated, with specific mechanisms like inhibition having poor construct validity (see Rabbitt & Lowe, 2000 for a discussion).

Given that there is no agreed-upon definition of the inhibition construct and poor construct validity for the operational definitions proposed to date (Shilling, Chetwynd, & Rabbitt, 2002), this poses problems for theories which propose that age-related differences from childhood to old age, in a variety of cognitive domains, can be interpreted as arising from ontogenetic differences in the efficiency of inhibitory processes that are supported by the pre-frontal cortex (Dempster, 1992; Hasher & Zacks, 1988). Furthermore, in the context of understanding age-related changes in lower-level information processing resources, PET studies of rCBF in the frontal lobes do not demonstrate consistent age-related differences in the magnitude or pattern of activation observed in response to cognitive demands, while demonstrating consistent declines in resting rate of rCBF (Gur, Gur, Obrist, & Skolnick, 1987; Warren, Butler, Katholi, & Halsey, 1985). To date, frontal-lobe theories of aging cognition have not offered an explanation for fundamental age-related cognitive phenomena like cognitive slowing (Salthouse, 1996a, b) and age-related increases in intra-individual variability (Myerson & Hale, 1993; Salthouse, 1993a, b; Hertzog et al., 1992; Li et al., 2000; Rabbitt & Patrick, 2000). Also, for many tasks sometimes associated with frontal functioning, age differences disappear once general slowing is taken into account (Verhaeghen & Cerella, 2002).

However, it should be noted that frontal-lobe theories of aging do not propose to explain every age-related cognitive phenomenon and the distributed nature of cognition is accepted by the majority of researchers and theorists who propose a central role for the frontal lobes in a model of aging cognition. For example, in his discussion of aging memory, West (1996) noted that the dorso-lateral prefrontal cortex probably does not store the actual representation used to guide behavior, but rather supports the maintenance of this representation stored in the temporal and parietal cortices through an interaction with sub-cortical structures (p. 280). Given the objections raised against the FLH and the likely involvement of sub-cortical structures in age-related memory changes, it appears that the next stage in the

development of models of aging cognition is to elaborate on how aging affects interactions between prefrontal and sub-cortical structures and the information processing mechanisms supported by such interactions.

Clues as to the importance of connectivity and interactions between multiple cortical and sub-cortical sites associated with age-related cognitive changes comes from studies of sub-cortical dementia or white-matter dementia (Albert, Feldman, & Willis, 1974; Filley, Heaton, Nelson, & Burks, 1989; Grafman, Weingartner, Newhouse, & Thompson, 1990; Gunning-Dixon & Raz, 2000; Junque, Pujol, Vendrell, & Bruna, 1990; Rao, Mittenberg, Bernardin, & Haughton, 1989). Albert et al. (1974) identified four behavioral features of sub-cortical damage: impaired memory, inability to manipulate previously acquired knowledge, emotional lability, and slowing of information processing. In addition, investigators have linked white-matter dementia impairments with frontal impairments (Filley et al., 1989). Research using magnetic resonance imaging (MRI) has indicated that increased damage to white matter is linked with cerebrovascular risk and with decreases in speed of information processing in normal older adults (Junque et al., 1990; Rao et al., 1989; Ylikoski, Ylikoski, Erkinjuntti, & Sulkava, 1993). In a meta-analysis examining the cognitive correlates of white-matter abnormalities in normal aging Gunning-Dixon and Raz (2000) found that degeneration of white matter was associated with attenuated performance on tasks of processing speed, immediate and delayed memory, executive functions and indices of global cognitive functioning.

Age-related sub-cortical white-matter degeneration may be a consequence of early onset degeneration either in sub-cortical structures like the cerebellum (Raz, Gunning-Dixon, Head, Williamson, & Acker, 2001) or the frontal lobes (see West, 1996; Grady, 2000 for reviews). However, it is possible that sub-cortical white-matter degeneration precedes and causes cell loss in both areas. Neither of these hypotheses has been tested in the neuroscience literature. Boone, Miller, Lesser, and Mehringer (1992) suggested that decline is evident in attention and select frontal-lobe functions only after a “threshold” of severity in WMH is observed. Mittenberg, Seidenberg, O’Leary, and DiGiulio (1989) speculated that the frontal-lobe disconnection syndrome caused by WMH might be a possible explanation for age-related changes in frontal-lobe function. Regardless of where neural damage is first seen, the existence of age-related white-matter degeneration suggests that an alternative explanation for the age-related deficits associated with both frontal and cerebellar degeneration (see below) is the disruption of fronto-cerebellar feedback and feedforward control loops and the efficiency of transmission between both areas (see Schmahmann, 1996a, b).

3. Cerebellar aging and models of cognitive control

Neuropsychological and neuroanatomical evidence suggests that the prefrontal cortex and lateral cerebellum are the last structures to develop during maturation and the first to undergo involution in later life (Haug & Eggers, 1991; West, 1996). The cerebellum is especially vulnerable to age-related dysfunction (Allman,

McLaughlin, & Hakeem, 1993; Raz et al., 2001). Although studies suggest that age-related shrinkage of the cerebellum may be sex-specific, it is unclear whether age-related decline is accelerated in women (Escalona, McDonald, & Doraiswamy, 1991; Raz, Dupuis, Briggs, McGavran, & Acker, 1998) or men (Oguro, Okada, Yamaguchi, & Kobayashi, 1998). In a well-controlled study of 190 healthy volunteers aged 18–81 years, Raz et al. (2001) assessed regional volumes of the cerebellar hemispheres using MRI. They found evidence for moderate age-related shrinkage of the cerebellum and lack of age-related differences in the ventral pons. The cerebellum and the pons were larger in men than in women.

While an examination of age-differences cerebellar volumes is useful, these studies tell us less about the possible functional role of the cerebellum in the patterns of age-related cognitive change observed. It should be noted that there has been very little emphasis on the role of the cerebellum in age-related reductions in information processing efficiency (see Raz et al., 2001 for a notable exception). There are a number of reasons for this. Firstly, functional imaging studies of aging performance rarely image, model or comment on cerebellar involvement (see Grady, 2000; Madden et al., 1999; Cabeza 2001, for reviews). This is an interesting omission given the evidence for cerebellar activity during a broad range of cognitive activities including; rule-based word-generation task (Petersen, Fox, Posner, & Mintun, 1989), mental imagery (Ryding, Decety, Sjoeholm, & Stenberg, 1993; Mellet, Tzourio, Denis, & Mazoyer, 1995; Parsons, Fox, Downs, & Glass, 1995), cognitive flexibility (Kim, Ugurbil, & Strick, 1994), sensory discrimination (Gao, Parsons, Bower, & Xiong, 1996), motor learning (Jenkins, Brooks, Nixon, & Frackowiak, 1994; Rauch, Baer, Cosgrove, & Jenike, 1995), verbal memory (Grasby, Frith, Friston, & Simpson, 1994), working memory (Klingberg, Roland, & Kawashima, 1995), and emotional states (Bench, Frankowiak, & Dolan, 1995; Mayberg & Solomon, 1995; see Schmahmann, 2000 for a review). Furthermore, electrophysiological studies of aging make the implicit assumption that topographical differences between younger and older adults reflect alteration in cortical dynamics even though it is widely recognized that electrophysiological manifestation on the cortex are the product of both cortical and subcortical activations (see Polich & Kok, 1995; Kok, 2000; Polich, 1996 for reviews). Findings from both fMRI and electrophysiological research are often used to support the frontal-lobe theory of cognitive aging (see e.g., Friedman, 2000; Grady, 2000 for reviews).

The central question of interest here is what role, if any, does the cerebellum play in age-related cognitive changes? In order to answer this question an examination of the functions of the cerebellum and age-related changes in these functions is necessary. However, we might want to firstly ask, why has the role of the cerebellum been largely ignored in the functional modelling of aging cognition?

One answer to this question could relate to underlying assumptions of the information processing approach to cognition. According to the information processing perspective human cognition can be understood by studying how it is that the brain, operating as a general purpose symbol processing system, acts to manipulate and transform symbols into other symbols that ultimately relate to things in the outside world (see e.g., Simon & Kaplan, 1989). Implicit in this

approach is the assumption that symbol processing and cognition are higher-level operations involving cortical structures. When elaborating cognitive models that deal in mental representations, semantic networks, productions system, propositional and imagistic codes, etc., one might fail to appreciate that information processing involves an elaborate web of cortical and subcortical interactions with common mechanisms and bi-directional pathways to parallel brain systems processing cognitive, sensory, and motor information (Ito, 1986, 1993; Leiner, Leiner, & Dow, 1986, 1989, 1993; Schmahmann, 1996a, b).

It is recognized that cognitive development during infancy and childhood is closely tied to sensory motor learning and development (e.g., Piaget, 1952). Unfortunately, these same theories assume that sensorimotor learning and processes are transformed into higher systems of thought, therefore deconstructing a more integrative sensorimotor–cognitive model of cognition and replacing it with a purely cognitive model (see Seitz, 2000, for an excellent analysis). In the next section, extensive evidence for the role of the cerebellum in information processing is presented. On the whole this evidence suggests that many of the most basic information processing mechanisms modulated by the cerebellum operate in parallel to modulate both sensorimotor and cognitive efficiency. Implications for the role of the cerebellum in a neurological model of aging cognition are discussed.

4. Functions of the cerebellum

4.1. The cerebellum as a modulator of both sensory–motor and cognitive functioning

It is now well established that the cerebellum plays a central role in the modulation of sensory and motor behavior (Holmes, 1939; Dow, 1942, 1949; Ito, 1986; Crispino, 1983). In addition to its role in motor functions, sensory maps of the cerebellum and the somatotopically organized cutaneous and kinesthetic inputs are well established (Snider, 1950; Snider & Eldred, 1951; Schmahmann, 1996a). Neocerebellar activity affects sensory modulation, and can enhance or inhibit brain stem, thalamic, hippocampal, and cerebral cortical responses to visual, auditory, and somatosensory stimulation (Crispino, 1983; Kitano & Ishida, 1976). According to Leiner et al. (1989), the number of neural connections between the cerebral cortex and the cerebellum became massive in humans during phylogeny. They note that the cerebellum receives from the cerebral cortex an input of about 20 million fibers on each side of the brain, in addition to the input it receives from other sources such as the spinocerebellar tracts. The output connections of the cerebellum are projected to the reticular formation and to the thalamus. Via the thalamus, the cerebellar projections can reach motor, cognitive, and language areas of the frontal lobe. Another important finding links the prefrontal cortex into the feedforward limb of the cerebrocerebellar circuit (see Schmahmann, 1996a, for an excellent review).

According to Ito (1986), the cerebellar cortex consists of numerous microzones, each of which is interconnected with a small cell group in a vestibular or cerebellar nucleus, forming a corticonuclear microcomplex. Ito (1993) postulates that the

structural unit of the cerebellum functions to encode errors in the performance of the system in which a given corticonuclear microcomplex is installed. Evidence for this error coding by the cerebellum has been available in various movement situations; for example, in smooth pursuit eye movements (Stone & Lisberger, 1990) and forearm movement (Wang, Kim, & Ebner, 1987). According to Ito (1993), signal transfer characteristics of the microzone and, accordingly, dynamic characteristics of the corticonuclear microcomplex are modified through long-term depression (LTD) toward minimization of control errors and the development of automaticity.

Leiner et al. (1989) concur with the idea of Ito (1986, 1993) that the cerebellum serves as an information processing mechanism, the circuitry of which generates rapid responses to the input that it receives. They further suggest that, because the circuitry of the lateral cerebellum consists of an assembly of longitudinal neural zones in which each zone of the cortex seems to be similar to every other zone (Ito, 1986), these similar zones seem able to perform similar processing operations on the information flowing to them from the cerebral cortex. The main difference between the zones seems to be the kind of information they receive (Schmahmann, 1996a) and the targets to which they send the results of their processing operations (Leiner, Leiner, & Dow, 1989, 1991, 1993).

According to Ito, the benefit conferred on the frontal motor areas is an increase of speed and skill in the control of muscle manipulation (Ito, 1986). Similarly, Leiner, Leiner, and Dow postulate that the benefit conferred on the prefrontal association areas may be an increased speed and skill in the control of mental manipulations (see e.g., Leiner et al., 1989, 1991, 1993). While the exact nature of cerebellar influence on either motor or non-motor behavior is yet to be established, the issues of error detection and automatization (Ito, 1993, Silveri, Leggio, & Molinari, 1994) have been discussed as critical mechanisms. Other hypotheses such as shifting attention (Akshoomoff & Courchesne, 1992), dynamic state monitoring (Paulin, 1993a, b), timing (Ivry & Keele, 1989), and sensory preprocessing of information (Bower, 1995), have all been proposed in relation to cerebellar involvement in both sensory–motor and cognitive functioning, and provide a theoretical basis for further modelling.

In a recent review focusing on neurological evidence for cerebellar involvement in cognition, Schmahmann (1996a) suggested that the net effect of the cerebrocerebellar feedforward and feedback loops is a cerebellar coordinate transformation integrating multiple internal representations with external stimuli and self-generated responses. According to Schmahmann, the cerebellar contribution to cognition is one of modulation rather than generation, with the modulation process of the cerebellum defined by an “oscillation dampener” which maintains function steadily around a homeostatic baseline, and smooths out performance. Schmahmann says

It is useful to consider cognitive performance, affect, and autonomic function in light of the understanding of cerebellar motor deficits which are characterised by abnormalities of rate, rhythm, and force of movements. Intact cerebellar function facilitates actions harmonious with the goal, appropriate to context, and judged accurately and reliably according to strategies mapped out prior to and during

behavior. When the cerebellar component of the distributed neural circuit is lost or disrupted, the oscillation dampener is removed, and there is no longer a smoothing out of behaviors around a homeostatic baseline. The consequence is “dysmetria of thought”. (p. 190)

Consistent with Schmahmann’s approach to systems neuroanatomy, cerebellar atrophy might be hypothesized to bring “chaos” into the information processing system, leading to reduced smoothness and efficiency of thought. Schmahmann concurs that this hypothesis is consistent with a quantifiable hypothesis of increased intra-individual variability in information processing. Intra-individual variability is an aspect of processing control that is central to recent models of age-related cognitive decline (Li et al., 2000).

4.2. The timing functions of the cerebellum

It has been suggested that the cerebellum provides timing for a number of tasks (Braitenberg, 1967, 1983, 1993; Ivry & Keele, 1989). Braitenberg (1967) drew attention to the striking regularity of the cerebellum as a possible mechanism for timing. Braitenberg (1983, 1993) suggests that the cerebellum utilizes its unique architecture to transform spatial signals into temporal information. Other models have been presented in which intervals above tenths of seconds could be stored by a group of oscillating neurons with different frequencies (Fujita, 1982a, b; Gluck, Reifnider, & Thompson, 1990).

In addition to these theoretical ideas, derived primarily from neuroanatomical observations, various empirical phenomena have also suggested that the cerebellum may play a critical role in timing. For example, analysis of the EMG patterns of rapid arm movements in both monkeys (Soechting, Ranish, Palminteri, & Terzuolo, 1976; Vilis & Hore, 1980) and humans (Hallet et al., 1975) have suggested that cerebellar damage alters the timing of muscular activation patterns.

Cerebellar patients have been shown to be impaired in tasks of motor as well as perceptual timing, which required rhythmic tapping, or the judgment of intervals (Ivry & Baldo, 1992; Ivry & Keele, 1989; Ivry, Keele, & Diener, 1988). Ivry and Keele (1989) studied patients with Parkinson’s disease, cerebellar damage, cortical damage and peripheral nerve injury on two different tests of timing functions: the first measured the ability of the participants to produce and maintain a simple rhythm, and the second measured the ability of participants to discriminate differences between interval durations. In comparison with all the other groups, the cerebellar group showed marked deficits in both timing production and timing perception.

Ivry and Keele argue that classical conditioning of discrete, adaptive responses is precisely timed by the cerebellum. As in all forms of Pavlovian conditioning, the acquisition of eyelid responses is dependent on the interstimulus interval (ISI). The onset of the conditioned stimulus (CS) must precede the unconditioned stimulus (US) by at least 80 ms, but by no more than 2–3 s (Smith, Coleman, & Gormezano, 1969). Within this range the ISI also determines the timing of conditioned eyelid

responses—responses peak near the onset of the US (Levey & Martin, 1968). Studies also demonstrate that the ISI conditioned response is not determined by differential associative strength (Mauk & Ruiz, 1992). Thus the timing of Pavlovian eyelid responses is learned and appears to require a neural mechanism that is capable of temporal discrimination, that is, a timing mechanism. Indeed, it has been shown that while cerebellar cortex lesions do not abolish the conditioned response, the timing of the response is disrupted (McCormick & Thompson, 1984; Perrett, Ruiz, & Mauk, 1993).

Papka, Ivry, and Woodruff-Pak (1995), in a study of 140 normal adults, found that selective disruption of eyeblink classical conditioning (EBCC) was observed when performed concurrently with tapping, another cerebellar task (Ivry & Keele, 1989). It is unclear whether a cerebellar timing mechanism controlling the timing and variability of movement patterns, and the timing of responses in classical conditioning, also impacts on the timing and variability of other components of information processing. If one considers the timekeeping mechanism as being important in the coordination of inputs from various levels within the processing system, or in the timing of output from the cerebellum, then it is possible that a disruption in this system would lead to deficits across cognitive and non-cognitive tasks that demand such coordination. We will elaborate upon this proposal in more detail later.

4.3. The cerebellum and learning

Several early theories inspired by the synaptic organization of the cerebellum suggest that plasticity in the cerebellar cortex at granule cell-Purkinje cell synapses could mediate learning or adaptation of movement (Marr, Bayer, & Borchelt, 1969; Albus & Herz, 1972). Numerous studies have demonstrated that cerebellar lesions can abolish the acquisition, expression, and extinction of conditioned movements, and abolish the ability of the vestibular ocular reflex (VOR) to undergo adaptation (Robinson, Koth, & Ringenbach, 1976; McCormick & Thompson, 1984; Yeo, Hardiman, & Glickstein, 1984a,b; Yeo, 1991). Clinical studies have confirmed that eyelid conditioning is severely impaired in patients with cerebellar lesions (Daum, Channon, Polkey, & Gray, 1991; Solomon, Pomerleau, Bennett, & James, 1989a; Solomon, Stowe, & Pendlbeury, 1989b). Because classical conditioning has been interpreted as procedural learning (e.g., Solomon et al., 1989), it is important to assess the performance of cerebellar patients in other forms of procedural learning that do not concern motor performance per se and are of wider use in neuropsychology, such as perceptual or cognitive skill acquisition.

Patients with cerebellar damage have been found to perform worse than control participants on visuomotor prism adaptation tasks (Weiner, Hallett, & Funkenstein, 1983), and motor tracing tasks (Sanes, 1990). These studies demonstrate a contribution of the cerebellum to the acquisition of motor skills, that is, to adaptive, long-term processes of motor control and the integration of sensory inputs with motor demands.

4.4. *Processing speed and intelligence*

The models of cerebellar functioning proposed by Schmahmann, (1996a, b), Leiner et al. (1989), and Ito (1993) all make explicit a role for the cerebellum as a rapid modulatory information processor. In studies on the electrophysiology of trained simple visually initiated reaction-time movements in monkeys (Sasaki & Gemba, 1982; Sasaki, Gemba, & Tsujimoto, 1990), findings suggest that enough training for the movement recruits the cerebro-cerebellar interaction to activate the forelimb motor cortex via the neocerebellum and thalamus, and significantly shortens reaction times. To date, only a small number of studies have investigated RT in patients with cerebellar lesions (Botez, Botez, Elie, & Attig, 1989; Botez-Marquard & Botez, 1993; Canavan, Springelmeyer, Diener, & Hoemberg, 1994; Tachibana, Aragane, & Sugita, 1995).

Tachibana et al. (1995) measured event-related potentials (ERPs) and reaction times during semantic discrimination tasks in eight patients with cerebellar degeneration and in ten normal participants. The NA, N2 and P3 latencies were significantly longer in the patients, whereas N1 and P2 did not differ between groups (see Tachibana et al., 1995 for details). Botez et al. (1989) administered a battery of standard neuropsychological tests to a sample of 31 patients with cerebellar and brain-stem atrophy. Deficits were detected in verbal IQ, performance IQ, and full-scale IQ; poor performance occurred on the Stroop color-word interference test (a test normally sensitive to frontal-lobe dysfunction); and impairments were also seen on simple reaction-time tasks and on a dexterity test. There were no deficits, however, on tests of immediate or delayed recall of stories from the Wechsler Memory Scale. Apart from the verbal and Stroop effects, then, most of the poor performance could be attributed to motor deficits. Further, no definite conclusions could be drawn regarding the locus of impairments because of the widespread nature of the pathology in these patients.

Botez-Marquard & Botez (1993) evaluated the neuropsychological performance of a carefully chosen population of patients with olivopontocerebellar atrophy (OPCA) and Friedreich's ataxia, each patient being matched with a control participant. Botez and Botez were particularly interested in measuring information processing speed (IPS), in addition to visuospatial reasoning, organization and performance, by means of Raven's Standard Matrices Test (Raven, 1958), the Rey complex figure copying test, and the block design sub-test of the Wechsler Adult Intelligence Scale. IPS was measured by means of simple visual and auditory RT; movement time (MT) was also assessed. The results indicated a significant group effect based on the average of right and left hands measured together for visual reaction time, visual movement time, auditory reaction time and auditory movement time for OPCA and FA patients versus their controls. Both patient groups had lower performances on the Raven test and Rey complex figure-copying test. In relation to IPS, Botez and Botez concluded that intact sub-cortical functions, of which the cerebellum is a part, are necessary for normal RT performances.

Additional evidence for the role of the cerebellum in IPS comes from a study by Canavan et al. (1994). In this well-controlled investigation, eight patients with lesions

restricted to the cerebellum were compared in two experiments with a total of 25 age-matched controls in a reaction-time (RT) task. Simple and choice RTs were recorded, as well as RTs to abstract visual patterns signifying the particular movement to be performed. Canavan et al. noted that the pooled data implicate cerebellar lesion involvement in slowed RT independent of slowed movement time. Furthermore, whereas control participants displayed learning and speeded improvement in the complex abstract RT over series, the patients showed no learning at all (see Canavan for details). These findings are consistent with models of cerebellar functioning which highlight information processing speed, and the development of automaticity over trials, as key elements (e.g., Ito, 1993; Leiner et al., 1991).

4.5. The cerebellum and rapid attentional modulation

It has been suggested that the capacity of the cerebellum to modulate responses to sensory input may allow the neocerebellum to affect attention (Akshoomoff & Courchesne, 1992; Courchesne, Townsend, Akshoomoff, & Saitoh, 1994). It may do this via its connection with many of the areas that are believed to be involved in attentional processes (Heilman, Watson, & Valenstein, 1985; Mesulam, 1990; Posner & Peterson, 1990) including the reticular activating system, the posterior parietal cortex, the dorsolateral prefrontal cortex, the superior colliculus, the cingulate gyrus, and the pulvinar (Schmahmann, 1996a, b).

Courchesne et al. (1994) tested the hypothesis that the neocerebellum is involved in the dynamic adjustment of the direction of attention. They compared the performance of six patients with damage to the cerebellum with that of 13 control participants in two experiments. One experiment required the ability to rapidly shift the mental focus of attention between auditory and visual stimuli. This task was designed to dissociate voluntary mental shifts of attention from motor control functions of the cerebellum i.e., no motor action was necessary to re-position attention. The second task required the ability to continuously maintain a single focus of attention.

In the focus-attention experiment, the patients with damage to the cerebellum were normal in target-detection ability compared with the control participants. In contrast, the patients with damage to the cerebellum were severely impaired in the ability to rapidly shift their attention. Specifically, these patients were impaired in relation to the control participants in responding to the first randomly occurring target in the new focus of attention when it occurred 2.5 s or less after a cue to shift attention, but were successful when more time had elapsed. According to Courchesne et al., patients were not significantly impaired in responding to targets that occurred 2.5 s or less after a correctly detected target, as long as there was not a requirement to shift attention. Although attention shifting is typically thought to be a frontal-lobe function (Meiran et al., 2001), these results suggest that the cerebellum may be implicated in the speed of attention shifting.

4.6. Postural control and cognitive test performance

The role of the cerebellum in postural control mechanisms is well-established (Ayres, 1972; Diener, Dichgans, Guschlbauer, & Mau, 1984). If tests of postural control are a good behavioral indicator of cerebellar efficiency, then it might be expected that postural control be correlated with dimensions of cognitive efficiency. There is a body of research suggestive of a link between postural control and cognitive functioning. For example, Liemohn and Knapczyk (1974), in the context of a factor analytic study, reported correlations of .45 between monopodal static balance and intelligence, and correlations of .30 to .66 between intelligence and “hopping tasks” in an undifferentiated sample of mentally retarded children aged 5–14 years.

Singer (1968) arrived at the general conclusion that none of the motor and physical variables (including balance) which he explored correlated significantly with intelligence. However, Ismail and Kane (1969) carried out large-scale, systematic replicative investigations which showed that static as well as dynamic balance was significantly related to intelligence and reading ability in normal American and British pre-adolescents (aged 11–12 years). Also, Chissom (1971) found correlations between scholastic achievement, static balance, and gross motor coordination in normal first graders.

Jones, Calder, and Hughes (1975) reported significant linkages between academic and motor skills (including balance tests) in 6 to 7-year-old children, and Ghelfi (1975), in a sample of 200 Swiss high school students aged 13 to 18 years, demonstrated positive relationships between balance control and scholastic achievement in language and literature. The correlations however, turned out to be negative when marks in mathematics were used as the scholastic criteria. In the largest study hitherto carried out on the development of static balance ability ($N = 6979$, Japanese Research, 1982; reported in Kohen-Raz, 1988), significant relationships between monopodal standing (with eyes open) and academic achievement were found in age groups 7, 8, 10, 11, and 12 years. These and other studies (see Kohen-Raz, 1988 for details) are supportive of a link between the vestibulocerebellar-mediated tasks of postural control and higher-level cognitive ability, although methodological issues regarding sex differences, the sensitivity of assessment procedures used, and methods of statistical analysis have produced some ambiguity about the extent of the relationship.

5. Aging and the functions of the cerebellum

In order to propose that the age-related changes in the cerebellum have implications for observed reductions in information processing efficiency, it needs to be demonstrated that components of information processing which are known to be under the control of the cerebellum show age-related declines.

5.1. Timing

Evidence supporting an effect on aging on timing functions of the cerebellum has been somewhat mixed. However, as methodologies have evolved there is increased consensus that normal aging disrupts timing mechanisms. Using [Wing and Kristofferson's \(1973\)](#) formal quantitative model of rhythmic finger tapping, [Duchek, Balota, and Ferraro \(1994\)](#) extracted estimates of central timekeeping (clock delay) and response execution (motor delay) components of timing control from samples of young college students, older adults, non-demented individuals with Parkinson's disease (PD), and individuals with very mild senile dementia of the Alzheimer type (SDAT). Central timekeeping control was impaired only in the mild stage of SDAT, while the implementation of the timing response remained relatively unimpaired, even in mildly demented individuals. [Duchek et al. \(1994\)](#) reported no impairment in central or response execution components of timing as a function of normal aging (i.e., when healthy older controls were compared with college-age subjects). However, there was some impairment in response execution for the healthy controls over 80 years of age. These results were similar to those reported by [Green and Williams \(1993\)](#).

Evidence for age-related deficits in timing come a number of studies. Using a methodology similar to that employed by [Duchek et al. \(1994\)](#) and [Green and Williams \(1993\)](#), [Ivry and Keele \(1989\)](#) reported an impairment in clock delay for their older sample relative to younger controls. [Woodruff-Pak and Jaeger \(1998\)](#) were interested in examining predictors of the large age differences that exist in eyeblink classical conditioning in a sample of younger and older participants (age range of 20–89 years). Timed-interval tapping was used to assess cerebellar function, and blink reaction time and explicit learning and memory were also assessed. Age accounted for the largest proportion of the variance, but the cerebellar measure of timing also significantly predicted eyeblink conditioning. The researchers concluded that age-related effects in the cerebellum affect both timing and learning in normal adults. Using a sophisticated methodology, [Krampe, Engbert, and Kliegl \(2001\)](#) investigated performance of young and older amateur pianists on two rhythm tasks with either identical or variable internal successive keystrokes to test whether slowing of a central clock can explain age-related changes in timing variability. Age stability was found at the level of motor implementation, but there were age-related deficits for processes related to target-duration specification.

5.2. Classical conditioning

The cerebellum appears to be the site of the plasticity essential for learning and memory of the conditioned response ([Thompson, Donegan, & Lavond, 1988](#)). Early studies which compared young and very old participants (e.g., [Kimble & Pennypacker, 1963](#)) noted the relative inability of the older participants to acquire the conditioned eyeblink response. More recently, [Woodruff-Pak and Thompson \(1988\)](#) found that age differences in classical conditioning of the eyeblink response are large. In summary, participants in their 20s and 30s condition most rapidly and

to the highest level. In the decades of the 40s, 50s and 60s and older, participants condition progressively more slowly. They also achieve a progressively lower level of conditioning. Large age differences in conditioning do not appear abruptly in participants aged 60+. Rather, Woodruff-Pak and Thompson (1988) concluded that large age differences exist in the delay classical conditioning paradigm, and they first appear in age group 40–49. These results have been replicated by Solomon et al. (1989), and Woodruff-Pak and Jaeger (1998).

This finding is important, as it might suggest an early onset age-related cerebellar processing problem (see, Woodruff-Pak, Coffin, & Sasse, 1991 for a review). Learning, and the development of automaticity, has consequences for the speed and variability of performance (see Logan, 1988, 1990, 1992). Given that aging affects both speed and variability of performance, it might be speculated that the central functional role played by the cerebellum in the development of automaticity (Ito, 1993) might reduce the efficiency of information processing by mediating not only learning rate, but also the speed and variability of processing. There is extensive evidence that information processing not only slows with increasing age (see Salthouse, 1996a, b) but that older adults do not improve as much as younger adults with extended practice on performance tasks (Czaja & Sharit, 1993; Fisk, Cooper, Hertzog, & Anderson-Garlach, 1995; Fisk & Warr, 1998; Jenkins & Hoyer, 2000; Rogers, Fisk, & Hertzog, 1994; Rogers, Hertzog, & Fisk, 2000; Salthouse, 1994; Fisk & Fisher, 1994; Jenkins, Myerson, Joerding, & Hale, 2000). Although neurological models of aging cognition have been more confident in naming the frontal lobes as critical for age-related declines in inhibition, working memory, and prospective memory, the possible role played by the cerebellum in slowing of information processing, increased intra-individual variability and reduced efficiency in the development of automaticity during learning has not been emphasized.

5.3. *Cerebellum-controlled visual functions*

Research has found age-related changes using caloric testing of the VOR (Bruner, 1971), and age-related changes in pursuit-tracking ability (Sharpe & Sylvester, 1978; Spooner, Sakala, & Bahol, 1980), and in responses to constant-velocity optokinetic stimuli (Magnusson, Padoan, & Oernhagen, 1989). Peterka, Black, and Schoenhoff (1990) found both VOR time constant and OKR gain constant increased slightly in participants up to about 30 years and then decreased with increasing age. Demer (1994) has confirmed these findings. If this increased time delay is representative of general age-related changes in the feedback efficiency of the cerebellum, then any speeded processing task which makes use of the cerebellum (Ito, 1993; Leiner et al., 1989; Akshoomoff & Courchense, 1992) may be influenced by age.

5.4. *Postural control*

Sheldon (1963) investigated the control of quiet stance across the life span. He found that postural stability was directly proportional to age until adolescence; then postural sway appeared to be very similar across age groups in adults up to the fifth

decade, at which point postural stability became inversely proportional to age (see Pyykko & Jantti, 1988, for similar findings). Studies have shown that older adults are highly susceptible to instability during standing when sensory information related to balance control is reduced or distorted (Manchester, Woollacott, Zederbauer-Hylton, & Marin, 1989; Woollacott & Jensen, 1996). These findings suggest that deterioration in the visual, vestibular, and somatosensory sub-systems may have a great impact on balance-control abilities in the older adult. On the other hand, while age-related changes such as diminution of the axon population in the optic nerves, and loss of visual acuity (particularly in the periphery; Sekuler, Hutman, & Owsley, 1980), higher proprioceptive thresholds and decreased position sense (Lord, Clark, & Webster, 1991), and decreased muscular strength (Anstey, Lord, & Williams, 1997; Lord et al., 1991), have been studied in connection with the maintenance of postural control in old age (see Alexander, 1994, for a recent review), attempts to predict balance control using sensory and motor tests have yielded poor results (see, e.g., Lord et al., 1991).

Stelmach, Teasdale, DiFabio, and Phillips (1989) have found evidence that age changes in higher-level sensory integrative mechanisms necessary to reorganize the available sensory information may be an important causal factor in age-related degeneration of postural control mechanism (see also Teasdale, Stelmach, & Breunig, 1991). Older adults appear to have delayed latency of postural responses when compared with young control participants (cf. Woollacott & Jensen, 1996). This delayed postural latency may be a specific example of how the cerebellum modulates processing speed within the brain (see e.g., Canavan et al, 1994; Botez-Marquard & Botez, 1993).

Only recently have cognitive aging researchers begun to recognize more fully that age-related individual differences in sensory and motor functioning are not only peripheral phenomena but also reflect age-based changes in the central nervous system (cf. Fozard, 1990). Lindenberger and Baltes (1994) suggested that if sensory measures provide a more reliable and direct measure of age-associated changes in the brain than do measures of cognitive functioning, then, the former should mediate a large proportion of the age-related variance in the latter. Using data from the Berlin Aging Study (BASE), they examined relations among age, sensory functions (i.e., visual and auditory acuity), and intelligence in a heterogeneous, age-stratified sample of old and very old individuals ($N = 156$, M age = 84.9 years, age range = 70–103). Intelligence was assessed by 14 tests measuring five cognitive abilities (speed, reasoning, memory, knowledge, and fluency; see Lindenberger & Baltes, 1994 for details). Using structural equation modelling, Lindenberger and Baltes found that age accounted for 40.8% of the variance in intelligence, vision for 41.3%, and hearing for 34.5%. Taken together, age, vision, and hearing accounted for 52.0% of the variance in intelligence. Only 2.8% of the total variance in intelligence was uniquely related to age. Together, visual and auditory acuity accounted for 49.2% of the total and 93.1% of the age-related reliable variance in intelligence. Lindenberger and Baltes (1994) also assessed balance-gait ability using three measures. The composite balance-gait measure accounted for 41.2% of the variance in intelligence ($p < .001$), shared 88.6% of its predictive variance for intelligence with vision and

hearing, and predicted a significant portion of variance (3.6%, $p < .05$) over and above that explained by age, vision and hearing. This finding that balance-gait performance predicts cognitive performance independent of age is consistent with previous research (e.g., Kohen-Raz, 1988) that has found measures of postural control correlate with cognitive performance in younger adults also.

Given that posture control and the measures of balance-gait used by Lindenberger and Baltes (1994) reflect complex multisensory integrative processes which are controlled to a large extent by the cerebellum (Schmahmann, 1996a, b), it might be hypothesized that the common cause involved in intellectual and sensory decline with age is an age-related decline in the information processing mechanisms common to both sensory–motor integration and cognition. Sensory–motor integration has been hypothesized to be associated with cognitive ability throughout development in the past (Ayres, 1972). For example, Ayres (1972) suggested a strong theoretical link between cerebellar functioning, sensory–motor integration and cognitive efficiency during early development.

The research and theories reviewed above provide insight into the ways in which the cerebellum modulates information processing efficiency throughout development and into old age. In the next section a series of tentative hypotheses regarding the role of the cerebellum in information processing efficiency throughout development is introduced.

6. A tripartite model of cerebellar information processing efficiency with implications for models of aging cognition

Consistent with the models of cerebellar functioning that are currently available it can be assumed that across the life span *the cerebellum supports the functions of the frontal and prefrontal cortex and plays a basic modulatory role in cognitive processing at the level of information-processing efficiency* (see e.g., Schmahmann, 1996a; Ito, 1993). Theoretical models of human development (Fiske & Rice, 1955; Kraemer & Gullion, 1994; Nesselroade & Featherman, 1994) and adult aging (Schroots, 1995) suggest that the regulation of intra-individual variability is critical for adaptation during early development and resilience into old age. The modulation of variability in basic aspects of information processing is central to models of cognition and intelligence (Eysenck, 1982, 1987; Jensen, 1992). A role for the cerebellum in the modulation of information processing variability is a direct prediction of recent theories of cerebellar function (Schmahmann, 1996a; Ito, 1993). A more specific proposal made in this paper is that age-related degeneration of the cerebellum may increase intra-individual variability in information processing.

In relation to cognitive aging, early theories (Crossman & Szafran, 1956; Welford, 1962) attributed the cause of cognitive aging deficits to age-related increase in neural noise in the central nervous system. Neural network models of cognitive aging (Li & Lindenberger, 1998) suggest that an increase in the level of intra-network variability may be causally related to the patterns of cognitive decline typically observed in older adults (Schaie, 1996). Surprisingly, very few studies have tested this

hypothesis. A small number of studies have consistently observed age-related increases in intra-individual variability using measures of reaction time (Myerson & Hale, 1993; Salthouse, 1993a, b; Hogan, 2004) and sensorimotor and cognitive ability (Hertzog et al., 1992; Li et al., 2000; Rabbitt & Patrick, 2000). Theories of cerebellar functioning (Ito, 1993; Schmahmann, 1996a) that highlight cerebellar “modulation”, “control”, and “oscillation dampening” may help to explain these findings by reference to a link between information processing variability and cerebellar efficiency. It may be that the aging cerebellum increases the variability in the speed of feedforward and feedback control loops (Schmahmann, 1996a), thus reducing the efficiency of error feedback mechanisms (Ito, 1993) and disrupting the consistency of the consolidation process during learning (Woodruff-Pak & Jaeger, 1998). Recent computational models of aging cognition predict that an increase in intra-individual variability disrupts the development of automaticity (see e.g., Li & Lindenberger, 1998; Li et al., 2000). Another possible consequence of normal age-related decline in the functioning of the cerebellum is that *previously* automatic processes (e.g., postural control) will become increasingly less automatic and require additional cognitive control, thus reducing the overall efficiency of the cognitive system (see e.g., Teasdale et al., 1991, for a similar hypothesis).

Elaborating on the role played by the cerebellum in a model of lifespan information processing efficiency, it can be stated that *the cerebellum acts as a multimodal resource modulator for sensory, motor and cognitive functions* (Schmahmann, 1996a). Given the evidence reviewed above, the availability of resources that are supported by functioning of the cerebellum can be understood by reference to at least three components of information processing: timing, speed of processing, and automaticity components. Aging of the cerebellum and/or disconnection between the cerebellum and the pre-frontal lobe areas will reduce the efficiency of working memory and executive control by reducing the capacity base supported by the functions of timing, processing speed, and automaticity.

Assuming that the cerebellum plays a role in cognitive, sensory and motor integration, creating a cerebellar coordinate transformation integrating multiple internal representations with external stimuli and self-generated responses, then it can be hypothesized that these distributed elements must be integrated in time. Duchek et al. (1994) have noted that many actions require the coordination of multiple cognitive elements. Therefore, if we assume that the execution of a particular response requires timed coordination between two successive cognitive elements (Element A and Element B), if there is a disruption in a central timing mechanism, it is quite possible that on some occasions Element B would start before Element A was completed, and thus some competition between elements might disrupt aspects of performance.

If the cerebellum modulates the relative timing and competition between processing elements then timing functions may be of central importance when modelling both the speed and variability of information processing during tasks which require coordination of two or more component elements. One hypothesis is that the cerebellar timing component (see Keele & Ivry, 1990 for details) located in the lateral cerebellum supports the relative timing of information processing

operations during the sensory–motor–cognitive integration process. A timing component designed to synchronize information processing within a parallel distributed, information-processing framework is not inconsistent with recent models of the reaction time process (McClelland & Rummelhart, 1981; Balota & Ferraro, 1993; Duchek et al., 1994) and is proposed here to be an important aspect of variability modulation. Synchronized timing of processes within a network with multiple information elements leads to smooth, efficient processing, with minimal variability between trials (Duchek et al., 1994; Ito, 1993), and a reduction of inter-process interference. The direct link between a cerebellar timing mechanism and the speed and variability of information processing has not yet been established. However convergent evidence reviewed above does suggest that cerebellar lesions produce reductions in both speed-of-processing and timing functions. The research reviewed here also provides strong and consistent evidence for age-related slowing and an age-related increase in intra-individual variability. It is possible that normal aging in the cerebellum is causally related to these age-related behavioral changes.

Consistent with research evidence reviewed earlier, the lifespan model of cerebellar efficiency proposes that the basic speed of cerebro–cerebellar feedback and feedforward transfer is important for the efficiency of information processing in general. It has been proposed that the rapid information-processing feedback loops located in the Purkinje-cell microcomplexes of the cerebellar cortex play a central role in speed of information exchange between the cortex and the cerebellum (see Botez & Botez, 1993; Ito, 1993; Schmahmann, 1996a, b). The feedback loop of the cerebro–cerebellar network provides the cerebellum with distributed sensory, motor and cognitive codes from the cortex, whereby the cerebellum, integrating multiple internal representations with external stimuli and self-generated responses, returns information to the cortex via the feedforward loop of the cerebro–cerebellar network (see Schmahmann, 1996a). Information intended for the frontal lobes is then re-integrated with cognitive codes, e.g., the goals of processing. At this stage response initiation or continued cognitive processing occurs.

If the cerebro–cerebellar feedback and feedforward network is involved in information processing, then it can be assumed that many cognitive acts will involve multiple feedback and feed-forward cycles in the cerebro–cerebellar network before integrated codes are available for response initiation to occur. Furthermore, it can be assumed that the number of feedback–feedforward cycles will reduce with practice as integrated perception, thought, and action become consolidated through repetition or as processing shifts from algorithmic to direct retrieval (see Logan, 1992). Therefore, in the context of a model of information processing efficiency that includes the cerebellum within a distributed network, the overall speed and variability of processing measured using behavioral tests of information processing, like reaction time (RT) tasks, will reflect three aspects of cerebro–cerebellar interaction: (a) the basic speed of the cerebro–cerebellar cycle (see Leiner et al., 1991; Ito, 1993), (b) the distribution of number of cerebro–cerebellar cycles (i.e., variability in number of feedback–feedforward cycles needed for response initiation from trial to trial), and (c) the amount of practice received on the particular RT task. Furthermore, it can be assumed that the speed of an average cerebro–cerebellar cycle

is dependent on at least two factors: (a) the efficiency of the cerebellar timing component (i.e., synchronization and integration of cognitive–sensory–motor information in the cerebellum is necessary before the feedforward leg of processing can occur) and (b) the integrity of subcortical white-matter interconnecting the cortex with the cerebellum. Overall the benefit accrued from both the timing and speed of processing components is enhanced efficiency and control within the information processing system which allows for larger, more complex computations to be processed successfully within a shorter time-span (see [Lehrl & Fischer, 1988, 1990](#), for a similar prediction in relation to computational span).

In the tentative model outlined here, timing and processing speed are intimately related to the third component of cerebellar efficiency, the automaticity component. A learning centre is also located in the Pukinje-cell microcomplexes ([Ito, 1993](#)) where regularly occurring feedback patterns are stored for later use, and used in an automatic-feedforward manner, so reducing the total resources necessary for information-processing computations. Just as timing and speed of processing work in concert to produce fast, efficient information processing, the development of automaticity also works to improve the total capacity of information-processing resources available by (1) refining and regularizing the timing of individual processing components over trials of learning which reduces variability in processing speed (see [Logan, 1990, 1992](#)), (2) automatizing the individual algorithmic processing computations whereby feedforward mechanisms provide computation outputs with increasing speed and, eventually, with an asymptotic minimal time when they are automatically computed/retrieved (see [Logan, 1988, 1992](#)). Enhanced timing within a network of processing elements and a shift from algorithmic processing to retrieval of individual-process computations serves to enhance the resources available for additional processing. It is predicted that the resource benefits induced through practice will be narrowly transferable and be task- or domain-specific (see, [Logan, 1992](#)).

In the context of a lifespan model of cerebellar efficiency, it is assumed that age-related reductions in the efficiency of the cerebellum or a relative disconnection between the cerebellum and the cortex will help to account for age-related slowing, increased intra-individual variability and reduced learning rate. Furthermore, domain-specific ([Lima, Hale, & Myerson, 1991](#)), and process-specific ([Fisk & Fisher, 1994](#)) slowing with age will be observed to the extent that individual differences in domain-specific and process-specific automaticity can be statistically controlled or experimentally manipulated. When automaticity is lost through either degeneration or disuse the total capacity of the processing system will be reduced due to the need for a compensatory re-distribution of available processing resources. One consequence of cerebellar aging is a decoupling of previously automatic functions (e.g., postural control). Although decoupling of automatic feedforward and feedback networks reduces overall efficiency, the sustained activation of these networks through practice mediates and limits the breakdown. A cerebellar model of information processing efficiency subsumes both unitary and multiple resources theories within a global resource theory, whereby timing and processing speed components provide a basic resource for all information processing within multiple

domains, while automaticity acts to produce increased differentiation and resource specialization throughout development. This may help to account for the observed increase in inter-individual variability observed with increasing age (see Morse, 1993).

Ongoing work in our laboratory suggests that variability in the amplitude of the ERP signal is, much like variability in RTs, sensitive to aging. An interesting avenue for future investigations, which seeks to clarify the role of the cerebellum in a life span model of cognitive efficiency, is to combine MR measures with EEG assessments to ascertain whether or not individual and age-related differences in the size or functional activation of the cerebellum are correlated with timing-, variability-, or learning-related changes in components of the EEG. EEG methods have excellent temporal resolution and provide, perhaps, the best way to examine these changes. For example, we might look to properties of the EEG signal such as the relative timing of N1, N2, P3, and N4 components of ERPs, variability in latency and amplitude these components, fluctuations in coherence from trial to trial, or learning related changes in ERPs, event-related spectral power, and coherence. If the concept of neural noise (Li et al., 2000) is to have any explanatory power, and be included in theories of aging cognition, an operational definition or series of operational definitions will have to be proposed for the construct.

In conclusion, there is growing interest in the role of the cerebellum as a modulator of sensory–motor and cognitive activity. In this paper we reviewed evidence supporting a role for the cerebellum in the speed, variability, and automaticity of processing operations. Furthermore, it was suggested that these very same aspects of information processing efficiency, so central in models of age-related cognitive decline, might be explained by reference to age-related changes in cerebellar efficiency or disconnection in the critical cerebro–cerebellar networks. Further research is necessary before it can be said that the fronto-cerebellar aging hypothesis introduced here can add significantly to the currently popular and widely discussed frontal-lobe hypothesis of aging.

References

- Akshoomoff, N. A., & Courchesne, E. (1992). A new role for the cerebellum in cognitive operations. *Behavioral Neuroscience*, *106*(5), 731–738.
- Albert, M. L., Feldman, R. G., & Willis, A. L. (1974). The “subcortical dementia” of progressive supranuclear palsy. *Journal of Neurology, Neurosurgery and Psychiatry*, *37*(2), 121–130.
- Albus, K., & Herz, A. (1972). Inhibition of behavioural and EEG activation induced by morphine acting on lower brain-stem structures. *Electroencephalography and Clinical Neurophysiology*, *33*(6), 579–590.
- Alexander, N. B. (1994). Postural control in older adults. *Journal of the American Geriatrics Society*, *42*(1), 93–108.
- Allman, J. M., McLaughlin, T., & Hakeem, A. (1993). Brain structures and life-span in primate species. *Proceedings of the National Academy of Sciences USA*, *90*(8), 3559–3563.
- Anderson, N. D., & Craik, F. I. M. (2000). Memory in the aging brain. In Tulving, E., & Craik, F. I. M. (Eds.), *The Oxford handbook of memory* (pp. 421–452). Oxford: Oxford University Press.
- Anstey, K. J., Lord, S. R., & Williams, P. (1997). Strength in the lower limbs, visual contrast sensitivity, and simple reaction time predict cognition in older women. *Psychology and Aging*, *12*(1), 137–144.

- Ayres, A. J. (1972). Types of sensory integrative dysfunction among disabled learners. *American Journal of Occupational Therapy*, 26(1), 13–18.
- Baddeley, A. (1986). *Working memory*. Oxford: Oxford University Press.
- Balota, D. A., & Ferraro, R. F. (1993). A dissociation of frequency and regularity effects in pronunciation performance across young adults, older adults, and individuals with senile dementia of the Alzheimer type. *Journal of Memory and Language*, 32, 573–592.
- Balota, D. A., Dolan, P. O., & Duchek, J. M. (2000). Memory changes in healthy older adults. In Tulving, E., & Craik, F. I. M. (Eds.), *The Oxford handbook of memory* (pp. 395–409). Oxford: Oxford University Press.
- Bench, C. J., Frankowiak, R. S. J., & Dolan, R. J. (1995). Changes in regional cerebral blood flow on recovery from depression. *Psychological Medicine*, 25(2), 247–261.
- Birren, J. E., & Botwinick, J. (1955). Speed of response as a function of perceptual difficulty and age. *Journal of Gerontology*, 10, 433–436.
- Boone, K. B., Miller, B. L., Lesser, I. M., Mehlinger, M., et al. (1992). Neuropsychological correlates of white-matter lesions in healthy elderly subjects: A threshold effect. *Archives of Neurology*, 49(5), 549–554.
- Botez, M.-I., Botez, T., Elie, R., & Attig, E. (1989). Role of the cerebellum in complex human behavior. *Italian Journal of Neurological Sciences*, 10(3), 291–300.
- Botez-Marquard, T., & Botez, M. -I. (1993). Cognitive behavior in heredodegenerative ataxias. *European Neurology*, 33(5), 351–357.
- Bower, J. M. (1995). Reverse engineering in the nervous system: An in vivo, in vitro, in computo approach to understanding the mammalian olfactory system. In Zornetzer, S. F., & Davis, J. L. (Eds.), *An introduction to neural and electronic networks*, (2nd ed.) (pp. 3–29). San Diego, CA, USA: Academic Press Inc.
- Braitenberg, V. (1967). Is the cerebellar cortex a biological clock in the millisecond range? *Progress in Brain Research*, 25, 334–346.
- Braitenberg, V. (1983). The cerebellum revisited. *Journal of Theoretical Neurobiology*, 2, 237–241.
- Braitenberg, V. (1993). The cerebellar network: Attempt at a formalization of its structure. *Network*, 4, 11–17.
- Bruner, A. (1971). Age related changes in caloric nystagmus. *Acta Otolaryngologia*, 282, 1–24.
- Cabeza, R. (2001). Cognitive neuroscience of aging: contributions of functional neuroimaging. *Scandinavian Journal of Psychology*, 42(3), 277–286 (Review).
- Canavan, A. G. M., Springelmeyer, R., Diener, H. C., & Hoemberg, V. (1994). Conditional associative learning is impaired in cerebellar disease in humans. *Behavioral Neuroscience*, 108(3), 475–485.
- Chissom, B. S. (1971). A factor-analytic study of the relationship of motor factors to academic criteria for first- and third-grade boys. *Child Development*, 42(4), 1133–1143.
- Courchesne, E., Townsend, J., Akshoomoff, N. A., Saitoh, O., et al. (1994). Impairment in shifting attention in autistic and cerebellar patients. *Behavioral Neuroscience*, 108(5), 848–865.
- Craik, F. I. M., & Jennings, J. J. (1992). Human memory. In Craik, F. I. M., & Salthouse, T. A. (Eds.), *The handbook of aging and cognition* (pp. 51–110). Hillsdale, NJ: Erlbaum.
- Crispino, L. (1983). Modification of responses from specific sensory systems in midbrain by cerebellar stimulation: Experiments on a teleost fish. *Journal of Neurophysiology*, 49(1), 3–15.
- Crossman, E. R. F. W., & Szafran, J. (1956). Changes with age in the speed of information intake and discrimination. In: *Experimental supplementum IV: symposium on experimental gerontology* (pp. 128–135). Basel, Switzerland: Birkhauser.
- Czaja, S. J., & Sharit, J. (1993). Age differences in the performance of computer-based work. *Psychology and Aging*, 8(1), 59–67.
- Daum, I., Channon, S., Polkey, C. E., & Gray, J. A. (1991). Classical conditioning after temporal lobe lesions in man: Impairment in conditional discrimination. *Behavioral Neuroscience*, 105(3), 396–408.
- Demer, J. L. (1994). Effect of aging on vertical visual tracking and visual-vestibular interaction. *Journal of Vestibular Research: Equilibrium and Orientation*, 4(5), 355–370.
- Dempster, F. N. (1992). The rise and fall of the inhibitory mechanism: Toward a unified theory of cognitive development and aging. *Developmental Review*, 12(1), 45–75.

- Diener, H. C., Dichgans, J., Guschlbauer, B., & Mau, H. (1984). The significance of proprioception on postural stabilization as assessed by ischemia. *Brain Research*, 296(1), 103–109.
- Dow, R. S. (1942). The evolution and anatomy of the cerebellum. *Biological Reviews*, 17, 179–220.
- Dow, R. S. (1949). Action potentials of cerebellar cortex in response to local electrical stimulation. *Journal of Neurophysiology*, 12, 245–256.
- Duchek, J. M., Balota, D. A., & Ferraro, R. F. (1994). Component analysis of a rhythmic finger tapping task in individuals with senile dementia of the Alzheimer type and in individuals with Parkinson's disease. *Neuropsychology*, 8(2), 218–226.
- Duncan, J. (1995). Attention, intelligence and the frontal lobes. In Gazzaniga, M. S. (Ed.), *The Cognitive Neurosciences* (pp. 721–733). Cambridge, MA: MIT Press.
- Eysenck, H. J. (1987). Intelligence and reaction time: The contribution of Arthur Jensen. In Modgil, S., & Modgil, C. (Eds.), *Arthur Jensen: Consensus and controversy*. New York: Falmer Press.
- Eysenck, H. J. (1982). *A model for intelligence*. Heidelberg: Springer.
- Escalona, P. R., McDonald, W. M., Doraiswamy, P. M., et al. (1991). In vivo stereological assessment of human cerebellar volume: Effects of gender and age. *American Journal of Neuroradiology*, 12, 927–929.
- Filley, C. M., Heaton, R. K., Nelson, L. M., Burks, J. S., et al. (1989). A comparison of dementia in Alzheimer's disease and multiple sclerosis. *Archives of Neurology*, 46(2), 157–161.
- Fisk, A. D., Cooper, B. P., Hertzog, C., & Anderson-Garlach, M. (1995). Age-related retention of skilled memory search: Examination of associative learning, interference, and task-specific skills. *Journal of Gerontology: Psychological Sciences*, 50(3), 150–161.
- Fisk, A. D., & Fisher, D. L. (1994). Brinley plots and theories of aging: The explicit muddled, and explicit debates. *Journal of Gerontology: Psychological Sciences*, 49, 81–89.
- Fisk, J. E., & Warr, P. B. (1998). Associative learning and short-term forgetting as a function of age, perceptual speed, and central executive functioning. *Journal of Gerontology B Psychological Science and Social Science*, 53(2), 112–121.
- Fiske, D. W., & Rice, L. (1955). Intra-individual response variability. *Psychological Bulletin*, 52, 217–250.
- Fozard, J. L. (1990). Vision and hearing in aging. In Birren, J. E., & Schaie, K. W. (Eds.), *Handbook of the psychology of aging*, (3rd ed.) (pp. 150–170). San Diego, CA, USA: Academic Press Inc.
- Friedman, D. (2000). Event-related brain potential investigations of memory and aging. *Biological Psychology*, 54, 175–206.
- Fujita, M. (1982a). Adaptive filter model of the cerebellum. *Biological Cybernetics*, 45(3), 195–206.
- Fujita, M. (1982b). Simulation of adaptive modification of the vestibulo-ocular reflex with an adaptive filter model of the cerebellum. *Biological Cybernetics*, 45(3), 207–214.
- Gao, J. H., Parsons, L. M., Bower, J. M., Xiong, J., et al. (1996). Cerebellum implicated in sensory acquisition and discrimination rather than motor control. *Science*, 272(5261), 545–547.
- Ghelfi, P. (1975). *Zusammenhang zwischen dem quasistatischen Gleichgewichtsverhalten und Leistungen in verschiedenen Faechergruppen*. Unpublished diploma thesis. Zurich: Swiss Institute for Technology, Department of Biomechanics.
- Gluck, M. A., Reifnider, E. S., & Thompson, R. F. (1990). Adaptive signal processing and the cerebellum: Models of classical conditioning and VOR adaptation. In Gluck, M. A., & Rumelhart, D. E. (Eds.), *Neuroscience and connectionist theory* (pp. 131–185). Hillsdale, NJ: Lawrence Erlbaum Assoc.
- Goldman-Rakic, P. S. (1992). Working memory and the mind. *Scientific American*, 267, 111–117.
- Grady, C. L. (2000). Functional brain imaging and age-related changes in cognition. *Biological Psychology*, 54, 259–281.
- Grafman, J., Weingartner, H. J., Newhouse, P. A., Thompson, K., et al. (1990). Implicit learning in patients with Alzheimer's disease. *Pharmacopsychiatry*, 23(2), 94–101.
- Grasby, P. M., Frith, C. D., Friston, K. J., Simpson, J., et al. (1994). A graded task approach to the functional mapping of brain areas implicated in auditory & verbal memory. *Brain*, 117(6), 1271–1282.
- Green, L. S., & Williams, H. G. (1993). Age related differences in timing control of reparative movement: Application of the Wing-Kristofferson model. *Research Quarterly in Exercise and Sport*, 64(1), 32–38.
- Greenwood, P. M. (2000). The frontal aging hypothesis evaluated. *Journal of the International Neuropsychological Society*, 6(6), 705–726.

- Gunning-Dixon, F. M., & Raz, N. (2000). The cognitive correlates of white matter abnormalities in normal aging: A quantitative review. *Neuropsychology*, *14*(2), 224–232.
- Gur, R. C., Gur, R. E., Obrist, W. D., Skolnick, B. E., et al. (1987). Age and regional cerebral blood flow at rest and during cognitive activity. *Archives of General Psychiatry*, *44*(7), 617–621.
- Hallet, M., Shahani, B. T., et al. (1975). EMG analysis of patients with cerebellar deficits. *Journal of Neurology, Neurosurgery and Psychiatry*, *38*(12), 1163–1169.
- Hasher, L., & Zacks, R. T. (1988). Working memory, comprehension, and aging: A review and a new view. In Bower, G. (Ed.), *The psychology of learning and motivation*, Vol. 22 (pp. 193–225). New York: Academic Press.
- Haug, H., & Eggers, R. (1991). Morphometry of the human cortex cerebri and corpus striatum during aging. *Neurobiology of Aging*, *12*(4), 336–338.
- Heilman, K. M., et al. (1985). Directional hypokinesia: Prolonged reaction times for leftward movements in patients with right hemisphere lesions and neglect. *Neurology*, *35*(6), 855–859.
- Hertzog, C., Dixon, R. A., & Hultsch, D. F. (1992). Intraindividual change in text recall of the elderly. *Brain and Language*, *42*(3), 248–269.
- Hogan, M. J. (2004). Average speed or variable speed—what do older adults really need? *Irish Journal of Psychology*, *24*, in press.
- Hogan, M. J., Gregory, R. J., Swanwick, G. R. J., Kaiser, J., Rowan, M., & Lawlor, B. (2003). Memory-related EEG power and coherence reductions in mild Alzheimer's Disease. *International Journal of Psychophysiology*, *49*, 147–163.
- Holmes, G. (1939). The cerebellum of man. *Brain*, *62*, 1–30.
- Ismail, A. H., Kane, J., et al. (1969). Relationships among intellectual and nonintellectual variables. *Research Quarterly*, *40*(1), 83–92.
- Ito, M. (1986). Neural systems controlling movement. *Trends in Neurosciences*, *9*(10), 515–518.
- Ito, M. (1993). How does the cerebellum facilitate thought? In Ono, T., & Squire, L. R. (Eds.), *Brain mechanisms of perception and memory: From Neuron to Behavior* (pp. 651–658). New York, NY, USA: Oxford University Press.
- Ivry, R. B., & Baldo, J. V. (1992). *Is the cerebellum involved in learning and cognition?* *Current Opinion in Neurobiology*, *2*(2), 212–216.
- Ivry, R. B., & Keele, S. W. (1989). Timing functions of the cerebellum. *Journal of Cognitive Neuroscience*, *1*(2), 136–152.
- Ivry, R. B., Keele, S. W., & Diener, H. C. (1988). Dissociation of the lateral and medial cerebellum in movement timing and movement execution. *Experimental Brain Research*, *73*(1), 167–180.
- Jenkins, I. H., Brooks, D. J., Nixon, P. D., Frackowiak, R. S. J., et al. (1994). Motor sequence learning: A study with positron emission tomography. *Journal of Neuroscience*, *14*(6), 3775–3790.
- Jenkins, L., & Hoyer, W. J. (2000). Instance-based automaticity and aging: Acquisition, reacquisition, and long-term retention. *Psychology and Aging*, *15*(3), 551–565.
- Jenkins, L., Myerson, J., Joerding, J. A., & Hale, S. (2000). Converging evidence that visuospatial cognition is more age-sensitive than verbal cognition. *Psychology and Aging*, *15*(1), 157–175.
- Jensen, A. R. (1992). The importance of intraindividual variation in reaction time. *Personality and Individual Differences*, *13*(8), 869–881.
- Jones, J. G., Calder, M., & Hughes, J. V. (1975). *An examination of the relationship between academic skills and motor abilities in children*. Research Report. Nedlands, Western Australia: University of Western Australia, Department of Physical Education and Recreation.
- Junque, C., Pujol, J., Vendrell, P., Bruna, O., et al. (1990). Leuko-araiosis on magnetic resonance imaging and speed of mental processing. *Archives of Neurology*, *47*(2), 151–156.
- Kausler, D. H. (1994). *Learning and memory in normal aging*. San Diego, CA: Academic Press.
- Keele, S. W., & Ivry, R. (1990). Does the cerebellum provide a common computation for diverse task? A timing hypothesis. *Annals of the New York Academy of Sciences*, *608*, 179–207.
- Kim, S. G., Ugurbil, K., & Strick, P. L. (1994). Activation of a cerebellar output nucleus during cognitive processing. *Science*, *265*(5174), 949–951.
- Kimble, G. A., & Pennypacker, H. S. (1963). Eyelid conditioning in young and aged subjects. *Journal of Genetic Psychology*, *103*(2), 283–289.

- Kitano, K., Ishida, Y., et al. (1976). Responses of extralemniscal thalamic neurones to stimulation of the fastigial nucleus and influences of the cerebral cortex in the cat. *Brain Research*, 106(1), 172–175.
- Klingberg, T., Roland, P. E., & Kawashima, R. (1995). The neural correlates of the central executive function during working memory—A PET study. *Human Brain Mapping [Suppl]*, 1, 414.
- Kohen-Raz, R. (1988). *Learning disabilities and postural control*. London: Freund.
- Kok, A. (2000). Age-related changes in involuntary and voluntary attention as reflected in components of the event-related potential (ERP). *Biological Psychology*, 54(1-3), 107–143.
- Kraemer, H. C., Gullion, C. M., et al. (1994). Can state and trait variables be disentangled? A methodological framework for psychiatric disorders. *Psychiatry Research*, 52(1), 55–69.
- Kramer, A. F., Hahn, S., & Gopher, D. (1999). Task coordination and aging: explorations of executive control processes in the task-switching paradigm. *Acta Psychologica*, 101, 339–378.
- Krampe, R. T., Engbert, R., & Kliegl, R. (2001). Cognitive behavior in hereditodegenerative ataxias. *European Neurology*, 33, 351–357.
- Lehrl, S., & Fischer, B. (1988). The basic parameters of human information processing: Their role in the determination of intelligence. *Personality and Individual Differences*, 9(5), 883–896.
- Lehrl, S., & Fischer, B. (1990). A basic information psychological parameter (BIP) for the reconstruction of concepts of intelligence. *European Journal of Personality*, 4(4), 259–286.
- Leiner, H. C., Leiner, A. L., & Dow, R. S. (1986). Does the cerebellum contribute to mental skills? *Behavioural Neuroscience*, 100(4), 443–454.
- Leiner, H. C., Leiner, A. L., & Dow, R. S. (1989). *Reappraising the cerebellum: What does the hindbrain contribute to the forebrain?* *Behavioral Neuroscience*, 103(5), 998–1008.
- Leiner, H. C., Leiner, A. L., & Dow, R. S. (1991). The human cerebro-cerebellar system: its computing, cognitive, and language skills. *Behavioural Brain Research*, 44(2), 113–128.
- Leiner, H. C., Leiner, A. L., & Dow, R. S. (1993). The role of the cerebellum in the human brain. *Trends in Neurosciences*, 16(11), 453–454.
- Levey, A. B., & Martin, I. (1968). Shape of the conditioned eyelid response. *Psychological Review*, 75(5), 398–408.
- Li, & Lindenberger, U. (1998). Cross level Unification: A computational exploration of the link between deterioration of neurotransmitter systems and dedifferentiation of cognitive abilities in old age. In Nilsson, L. G., & Markowitsch, H. (Eds.), *Neuroscience of memory*. New York, NY, USA: Oxford University Press.
- Li, S., Lindenberger, U., & Frensch, P. A. (2000). Unifying cognitive aging: From neuromodulation to representation to cognition. *Neurocomputing: An International Journal*, 32, 879–890.
- Liemohn, W. P., & Knapczyk, D. R. (1974). Factor analysis of gross and fine motor ability in developmentally disabled children. *Research Quarterly*, 45(4), 424–432.
- Light, L. L. (1991). Memory and aging: Four hypotheses in search of data. In Rosenzweig, M. R., & Porter, L. W. (Eds.), *Annual Review of Psychology* (pp. 333–376). Palo Alto, CA, USA: Annual Reviews Inc.
- Lima, S. D., Hale, S., & Myerson, J. (1991). How general is general slowing? Evidence from the lexical domain. *Psychology and Aging*, 6(3), 416–425.
- Lindenberger, U., & Baltes, P. B. (1994). Sensory functioning and intelligence in old age: A strong connection. *Psychology and Aging*, 9(3), 339–355.
- Logan, G. D. (1988). Towards an instance theory of automation. *Psychological Review*, 95(4), 92–127.
- Logan, G. D. (1990). Repetition priming and automaticity: Common underlying mechanisms. *Cognitive Psychology*, 22, 1–35.
- Logan, G. D. (1992). Shapes of reaction time distributions and shapes of learning curves: A test of the instance theory of automaticity. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 18, 883–914.
- Lord, S. R., Clark, R. D., & Webster, I. W. (1991). Physiological factors associated with falls in an elderly population. *Journal of the American Geriatrics Society*, 39(12), 1194–1200.
- Madden, D. J., Turkington, T. G., et al. (1999). Adult age differences in the functional neuroanatomy of verbal recognition memory. *Human Brain Mapping*, 7(2), 115–135.

- Magnusson, M., Padoan, S., & Oernhagen, H. (1989). Evaluation of smooth pursuit and voluntary saccades in nitrous oxide-induced narcosis. *Aviation, Space, and Environmental Medicine*, *60*(10, Sect. 1), 977–982.
- Manchester, D., Woollacott, M., Zederbauer-Hylton, N., & Marin, O. (1989). Visual, vestibular and somatosensory contributions to balance control in the older adult. *Journals of Gerontology*, *44*(4), m118–m127.
- Marr, J. N., Bayer, D. J., & Borchelt, P. L. (1969). Conditioning of eye movements with auditory stimulation. *Journal of Experimental Psychology*, *81*(2), 370–375.
- Mauk, M. D., & Ruiz, B. P. (1992). Learning-dependent timing of Pavlovian eyelid responses: Differential conditioning using multiple interstimulus intervals. *Behavioral Neuroscience*, *106*(4), 666–681.
- Mayberg, H. S., & Solomon, D. H. (1995). Depression in Parkinson's disease: A biochemical and organic viewpoint. In Weiner, W. J., & Lang, A. E. (Eds.), *Behavioral neurology of movement disorders* (pp. 49–60). New York, NY, USA: Raven Press.
- McClelland, J. L., & Rummelhart, D. E. (1981). An interactive model of context effects in letter perception: Part I. An account of basic findings. *Psychological Review*, *88*, 375–407.
- McCormick, D. A., & Thompson, R. F. (1984). Cerebellum: Essential involvement in the classically conditioned eyelid response. *Science*, *223*(4633), 296–299.
- Meiran, N., Gotler, A., & Perlman, A. (2001). Old age is associated with a pattern of relatively intact and relatively impaired task-set switching abilities. *Journal of Gerontology: Psychological Sciences*, *56B*(2), 88–102.
- Mellet, E., Tzourio, N., Denis, M., & Mazoyer, B. (1995). A positron emission tomography study of visual and mental spatial exploration. *Journal of Cognitive Neuroscience*, *7*(4), 433–445.
- Mesulam, M. M. (1990). Large-scale neurocognitive networks and distributed processing for attention, language, and memory. *Annals of Neurology*, *28*(5), 597–613.
- Mittenberg, W., Seidenberg, M., O'Leary, D. S., & DiGiulio, D. V. (1989). Changes in cerebral functioning associated with normal aging. *Journal of Clinical and Experimental Neuropsychology*, *11*(6), 918–932.
- Morse, C. K. (1993). Does variability increase with age? An archival study of cognitive measures. *Psychology and Aging*, *8*(2), 156–164.
- Myerson, J., & Hale, S. (1993). General slowing and age invariance in cognitive processing: the other side of the coin. In Cerella, J., & Rybash, J. M. (Eds.), *Adult information processing: limits on Loss* (pp. 115–141). San Diego, CA, USA: Academic Press Inc.
- Nesselroade, J.-R., & Featherman, D.-L. (1994). Intraindividual variability in older adults' depression scores: some implications for developmental theory and longitudinal research. In Magnusson, D., & Bergman, L. R. (Eds.), *Problems and methods in longitudinal research: stability and change* (pp. 47–66). Cambridge, England, UK: Cambridge University Press.
- Oguro, H., Okada, K., Yamaguchi, S., & Kobayashi, S. (1998). Sex differences in morphology of the brain stem and cerebellum with normal ageing. *Neuroradiology*, *40*, 788–792.
- Papka, M., Ivry, R. B., & Woodruff-Pak, D. S. (1995). Selective disruption of eyeblink classical conditioning by concurrent tapping. *Neuroreport*, *6*(11), 1493–1497.
- Parsons, L. M., Fox, P. T., Downs, J. H., Glass, T., et al. (1995). Use of implicit motor imagery for visual shape discrimination as revealed by PET. *Nature*, *375*(6526), 54–58.
- Paulin, M. G. (1993a). A model of the role of the cerebellum in tracking and controlling movements. *Human Movement Science*, *12*(1–2), 5–16.
- Paulin, M. G. (1993b). The role of the cerebellum in motor control and perception. *Brain, Behavior and Evolution*, *41*(1), 39–50.
- Perrett, S. P., Ruiz, B. P., & Mauk, M. D. (1993). Cerebellar cortex lesions disrupt learning-dependent timing of conditioned eyelid responses. *Journal of Neuroscience*, *13*(4), 1708–1718.
- Peterka, R. J., Black, F. O., & Schoenhoff, M. B. (1990). Age-related changes in human vestibulo-ocular and optokinetic reflexes: pseudorandom rotation tests. *Journal of Vestibular Research: Equilibrium and Orientation*, *1*(1), 61–71.
- Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M., et al. (1989). Positron emission tomographic studies of the processing of single words. *Journal of Cognitive Neuroscience*, *1*(2), 153–170.

- Piaget, J. (1952). *The origins of intelligence in children* (trans M. Cook). Oxford, England: International Universities Press.
- Polich (1996). Meta-analysis of P300 normative aging studies. *Psychophysiology*, *33*, 334–353.
- Polich, J., & Kok, A. (1995). Cognitive and biological determinants of P300: An integrative review. *Biological Psychology*, *41*, 103–146.
- Posner, M. I., & Peterson, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42.
- Pyykko, I., Jantti, P., et al. (1988). Postural control in the oldest olds. *Advances in Otorhinolaryngology*, *41*, 146–151.
- Rabbitt, P., & Lowe, C. (2000). Patterns of cognitive ageing. *Psychological Research*, *63*(3–4), 308–316.
- Rabbitt, P.-M., & Patrick, D. (2000). Measurement indices, functional characteristics and psychometric constructs in cognitive aging. In Perfect, T. J., & Maylor, E. A. (Eds.), *Models for cognitive aging*. Oxford, UK: Oxford University Press.
- Rao, S. M., Mittenberg, W., Bernardin, L., Haughton, V., et al. (1989). Neuropsychological test findings in subjects with leukoaraiosis. *Archives of Neurology*, *46*(1), 40–44.
- Rauch, S. L., Baer, L., Cosgrove, G. R., & Jenike, M. A. (1995). Neurosurgical treatment of Tourette's syndrome: A critical review. *Comprehensive Psychiatry*, *36*(2), 141–156.
- Raven, J. C. (1958) *Guide to using the coloured progressive matrices*. London, England.
- Raz, N., Dupuis, J. H., Briggs, S. D., McGavran, C., & Acker, J. D. (1998). Differential effects of age and sex on the cerebellar hemispheres and the vermis: A prospective MR study. *American Journal of Neuroradiology*, *19*, 65–71.
- Raz, N., Gunning-Dixon, F., Head, D., Williamson, A., & Acker, J. D. (2001). Age and sex differences in the cerebellum and the ventral pons: A prospective MR study of healthy adults. *American Journal of Neuroradiology*, *19*, 65–71.
- Robinson, G. H., Koth, B. W., & Ringenbach, J. P. (1976). Dynamics of the eye and head during an element of visual search. *Ergonomics*, *19*(6), 691–709.
- Rogers, W. A., Fisk, A. D., & Hertzog, C. (1994). Do ability-performance relationships differentiate age and practice effects in visual search? *Journal of Experimental Psychology: Learning, Memory and Cognition*, *20*(3), 710–738.
- Rogers, W. A., Hertzog, C., & Fisk, A. D. (2000). An individual differences analysis of ability and strategy influences: Age-related differences in associative learning. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *26*(2), 359–394.
- Ryding, E., Decety, J., Sjoeholm, H., Stenberg, G., et al. (1993). Motor imagery activates the cerebellum regionally: A SPECT rCBF study with super (99m) Tc-HMPAO. *Cognitive Brain Research*, *1*(2), 94–99.
- Salthouse, T. A. (1991). *Theoretical perspectives on cognitive aging*. Hillsdale, NJ, USA: Lawrence Erlbaum Associates, Inc.
- Salthouse, T. A. (1993a). Attentional blocks are not responsible for age-related slowing. *Journals of Gerontology*, *48*(6), 263.
- Salthouse, T. A. (1993b). Influence of working memory on adult age differences in matrix reasoning. *British Journal of Psychology*, *84*(2), 171–199.
- Salthouse, T. A. (1994). How many causes are there of aging-related decrements in cognitive functioning? *Developmental Review*, *14*(4), 413–437.
- Salthouse, T. A. (1996a). General and specific speed mediation of adult age differences in memory. *Journals of Gerontology: Series B: Psychological Sciences and Social Sciences*, *1*, 30.
- Salthouse, T. A. (1996b). The processing-speed theory of adult age differences in cognition. *Psychological Review*, *103*(3), 403–428.
- Sanes, J. N. (1990). Motor representations in deafferented humans: a mechanism for disordered movement performance. In Jeannerod, M. (Ed.), *Attention and performance 13: motor representation and control* (pp. 714–735). Hillsdale, NJ, USA: Lawrence Erlbaum Associates Inc.
- Sasaki, K., & Gemba, H. (1982). Cortical field potentials preceding visually initiated hand movements and cerebellar actions in the monkey. *Experimental Brain Research*, *46*, 29–36.

- Sasaki, K., Gemba, H., & Tsujimoto, T. (1990). Cortical field potential associated with hand movement on warning-imperative visual stimulus and cerebellum in the monkey. *Brain Research*, *519*, 343–346.
- Schaie, K. W. (1996). Intellectual development in adulthood. In Birren, J. E., & Schaie, K. W. (Eds.), *Handbook of the psychology of aging*, (4th ed.) (pp. 266–286). San Diego, CA, USA: Academic Press Inc.
- Schmahmann, J. D. (1996a). From movement to thought: Anatomic substrates of the cerebellar contribution to cognitive processing. *Human Brain Mapping*, *4*, 174–198.
- Schmahmann, J. D. (1996b). Dysmetria of thought: Correlations and conundrums in the relationship between the cerebellum, learning, and cognitive processing. *Behavioral and Brain Sciences*, *19*(3), 472–473.
- Schmahmann, J. D. (2000). The role of the cerebellum in affect and psychosis. *Journal of Neurolinguistics*, *13*, 189–214.
- Schmahmann, J. D., & Pandya, D. N. (1997). The cerebrocerebellar system. In Schmahmann, J. D. (Ed.), *The cerebellum and cognition. International Review of Neurobiology*, Vol. 41 (pp. 31–60). San Diego: Academic Press.
- Schroots, J. J. F. (1995). Gerodynamics: toward a branching theory of aging. *Canadian Journal on Aging*, *14*(1), 74–81.
- Seitz, J. A. (2000). The bodily basis of thought. *New Ideas in Psychology*, *18*, 23–40.
- Sekuler, R., Hutman, L. P., & Owsley, C. J. (1980). Human aging and spatial vision. *Science*, *209*(4462), 1255–1256.
- Shallice, T. (2002). Fractionation of the supervisory system. In Stuss, D. T., & Knight, R. T. (Eds.), *Principles of frontal lobe function* (pp. 261–277). London: Oxford University Press xxi, 616pp.
- Sharpe, J. A., & Sylvester, T. O. (1978). Effect of aging on horizontal smooth pursuit. *Investigative Ophthalmology and Visual Science*, *17*(5), 465–468.
- Sheldon, J. H. (1963). The effects of age on the control of sway. *Gerontology Clinics*, *5*, 129–136.
- Shilling, V. M., Chetwynd, A., & Rabbitt, P. M. A. (2002). Individual inconsistency across measures of inhibition: An investigation of the construct validity of inhibition in older adults. *Neuropsychologia*, *40*(6), 605–619 Elsevier Science, US.
- Shimamura, A. P. (1995). Memory and frontal lobe function. In Gazzaniga, M. (Ed.), *The Cognitive Neurosciences* (pp. 803–813). Cambridge, MA: MIT Press.
- Silveri, M. C., Leggio, M. G., & Molinari, M. (1994). The cerebellum contributes to linguistic production: A case of agrammatic speech following a right cerebellar lesion. *Neurology*, *44*(11), 2047–2050.
- Simon, H. A., & Kaplan, C. A. (1989). Foundations of cognitive science. In Posner, M. I. (Ed.), *Foundations of cognitive science*. Cambridge, MA: MIT Press.
- Singer, R. N. (1968). Interrelationship of physical perceptual-motor, and academic achievement variables in elementary school children. *Perceptual and Motor Skills*, *27*(3, Pt. 2), 1323–1332.
- Smith, A. D. (1996). Memory. In Birren, J. E., & Schaie, K. W. (Eds.), *Handbook of the psychology of aging*, (4th ed.) (pp. 236–250). San Diego, CA, USA: Academic Press Inc.
- Smith, M. C., Coleman, S. R., & Gormezano, I. (1969). Classical conditioning of the rabbit's nictitating membrane response at backward, simultaneous, and forward CS-US intervals. *Journal of Comparative and Physiological Psychology*, *69*(2), 226–231.
- Snider, R. S. (1950). Recent contributions to the anatomy and physiology of the cerebellum. *Archives of Neurology and Psychiatry, Chicago*, *64*, 196–219.
- Snider, R. S., & Eldred, E. (1951). Electroanatomical studies on cerebro-cerebellar connections in the cat. *Journal of Comparative Neurology and Psychology*, *95*, 1–16.
- Soechting, J. F., Ranish, N. A., Palminteri, R., & Terzuolo, C. A. (1976). Changes in a motor pattern following cerebellar and olivary lesions in the squirrel monkey. *Brain Research*, *105*(1), 21–44.
- Solomon, P. R., Pomerleau, D., Bennett, L., James, J., et al. (1989a). Acquisition of the classically conditioned eyeblink response in humans over the life span. *Psychology and Aging*, *4*(1), 34–41.
- Solomon, P. R., Stowe, G. T., & Pendlbeury, W. W. (1989b). Disrupted eyelid conditioning in a patient with damage to cerebellar afferents. *Behavioral Neuroscience*, *103*(4), 898–902.
- Spooner, J. W., Sakala, S. M., & Bahol, R. W. (1980). Effects of aging on eye tracking. *Archives of Neurology*, *35*, 575–576.
- Stelmach, G. E., Teasdale, N., DiFabio, R. P., & Phillips, J. (1989). Age related decline in postural control mechanisms. *International Journal of Aging and Human Development*, *29*(3), 205–223.

- Stone, L. S., & Lisberger, S. G. (1990). Visual responses of Purkinje cells in the cerebellar flocculus during smooth-pursuit eye movements in monkeys. Simple spikes: I. *Journal of Neurophysiology*, 63(5), 1241–1261.
- Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, 18, 643–662.
- Stuss, D. T., Floden, D., Alexander, M. P., Levine, B., & Katz, D. (2001). Stroop performance in focal lesion patients: Dissociation of processes and frontal lobe lesion location. *Neuropsychologia*, 39(8), 771–786.
- Tachibana, H., Aragane, K., & Sugita, M. (1995). Event-related potentials in patients with cerebellar degeneration: Electrophysiological evidence for cognitive impairment. *Cognitive Brain Research*, 2(3), 173–180.
- Teasdale, N., Stelmach, G. E., & Breunig, A. (1991). Postural sway characteristics of the elderly under normal and altered visual and support surface conditions. *Journals of Gerontology*, 46(6), B238–B244.
- Thompson, R. F., Donegan, N. H., & Lavond, D. G. (1988). The psychobiology of learning and memory. In: R. C. Atkinson, & R. J. Herrnstein (Eds.), *Stevens' Handbook of Experimental Psychology. Learning and Cognition, Vol. 2* (2nd ed.) (pp. 245–347). New York, NY, USA: Wiley.
- Verhaeghen, P., & Cerella, J. (2002). Aging, executive control, and attention: A review of meta-analyses. *Neuroscience & Biobehavioral Reviews*, 26(7), 849–857.
- Wilis, T., & Hore, J. (1980). Central neural mechanisms contributing to cerebellar tremor produced by limb perturbations. *Journal of Neurophysiology*, 43(2), 279–291.
- Wang, J. J., Kim, J.-H., & Ebner, T. J. (1987). Climbing fiber afferent modulation during a visually guided, multi-joint arm movement in the monkey. *Brain Research*, 410(2), 323–329.
- Warren, L. R., Butler, R. W., Katholi, C. P., & Halsey, J. H., Jr. (1985). Age differences in cerebral blood flow during rest and during mental activation: Measurements and without monetary incentive. *Journal of Gerontology*, 40, 53–59.
- Weiner, M. J., Hallett, M., & Funkenstein, H. H. (1983). Adaptation to lateral displacement of vision in patients with lesions of the central nervous system. *Neurology*, 33(6), 766–772.
- Welford, A. T. (1962). Changes of performance time with age: A correction and methodological note. *Ergonomics*, 5(4), 581–582.
- West, R. L. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin*, 120(2), 272–292.
- Wing, A., & Kristofferson, A. (1973). Response delays and the timing of discrete motor responses. *Perceptions and Psychophysics*, 14, 5–12.
- Woodruff-Pak, D. S., & Jaeger, M. E. (1998). Predictors of eyeblink classical conditioning over the adult age span. *Psychology and Aging*, 13(2), 193–205.
- Woodruff-Pak, D. S., & Thompson, R. F. (1988). Classical conditioning of the eyeblink response in the delay paradigm in adults aged 18–83 years. *Psychology and Aging*, 3(3), 219–229.
- Woodruff-Pak, D. S., Coffin, J. M., & Sasse, D. K. (1991). Learning, memory and aging: Neural changes and drug actions. In Schaie, K. W. (Ed.), *Annual review of gerontology and geriatrics*, Vol. 11 (pp. 23–54). New York: Springer.
- Woolacott, M. H., & Jensen, J. L. (1996). Posture and locomotion. In Heuer, H., & Keele, S. W. (Eds.), *Handbook of perception and action* (pp. 333–403). London, England, UK: Academic Press Inc.
- Yeo, C. H. (1991). Cerebellum and classical conditioning of motor responses. In Wolpaw, J. R., & Schmidt, J. T. (Eds.), *Activity-driven CNS changes in learning and development* (pp. 292–304). New York, NY, USA: New York Academy of Sciences.
- Yeo, C. H., Hardiman, M. J., & Glickstein, M. (1984a). Discrete lesions of the cerebellar cortex abolish the classically conditioned nictitating membrane response of the rabbit. *Behavioural Brain Research*, 13(3), 261–266.
- Yeo, C. H., Hardiman, M. J., Moore, J. W., & Russell, I. S. (1984b). Trace conditioning of the nictitating membrane response in decorticate rabbits. *Behavioural Brain Research*, 11(1), 85–88.
- Ylikoski, R., Ylikoski, A., Erkinjuntti, T., Sulkava, R., et al. (1993). White matter changes in healthy elderly persons correlate with attention and speed of mental processing. *Archives of Neurology*, 50(8), 818–824.