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The cognitive neuropsychology of the cerebellum

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Summary

We review evidence from neuropsychological studies of patients with damage to the cerebellum that suggests cerebellar involvement in four general categories of cognition: (1) speech and language; (2) temporal processing; (3) implicit learning and memory; (4) visuospatial processing and attention. A relatively strong case can be made for cerebellar contributions to language (including speech perception, lexical retrieval, and working memory) and to temporal processing. However, the evidence concerning cerebellar involvement in non-motor implicit learning and visuospatial processing is more equivocal. We argue that cerebellar contributions to cognition are computationally plausible, given its reciprocal connectivity with the cerebral cortex, and suggest that this function of the cerebellum may be an example of an evolutionary process by which mechanisms originally evolved for one function (in this case, motor control) are adapted to other functions (cognition).

Introduction

Traditional views of cerebellar function have emphasised how this subcortical structure contributes to the control of coordinated movement. However, in recent years many investigators have argued for a role of the cerebellum in higher cognitive functions such as language and attention. For those sceptical about the possibility of cerebellar involvement in cognition, it is useful to consider the often-cited evolutionary history of the mammalian malleus and incus, two of the small bones of the middle ear (Gould, 1997). In modern reptiles and our common ancestors, these two bones form part of the jawbone, but during the course of mammalian evolution, they developed new functions within the auditory system. Although this example may engender disagreement concerning selection mechanisms, rates of change, and terminology, it serves to illustrate the evolutionary process by which that which came before is adapted to new functional demands.

A similar story has been told about the cerebellum. Leiner *et al.* (1993) have argued that the cerebellum underwent functionally significant changes during the course of hominid evolution, increasing both in size and in the number of reciprocal connections with various regions of the cerebral cortex (see Schmahmann, this issue). Circuitry within the cerebellum that had been shaped by natural selection as part of the motor system may have been well suited to perform cognitive tasks requiring similar neural architecture. Cognitive operations of the cerebellum may have been the result of the large expansion in size and connectivity to the cerebral hemispheres. In fact the advantages conferred by this new set of abilities may themselves have been part of the selection pressures driving the neuroanatomical expansion. Such a scenario differs from that of the malleus and incus in that cognitive operations are added to prior motor functions rather than replacing them. Still, both examples involve modern structure and function constrained and shaped by ancestral structure and function.

One of the ways in which cerebellar contributions to cognition have been examined is though neuropsychological experimentation with patients who, from either progressive degeneration or focal stroke or tumours, have suffered a loss of cerebellar cortex. In this article, we review evidence obtained by such experiments related to four general categories of function: those involving language, temporal processing, implicit learning and memory, and visuospatial processing and attention. Given the links between the cerebellum and motor control, it is not surprising that many of the hypothesised cognitive roles are, at least metaphorically, related to movement.

Speech and language

Speech production and perception

Falling within the more traditional motor domain of the cerebellum is its role in speech production. Numerous case studies have supported the connection between cerebellar damage and ataxic dysarthria (e.g.

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Marien *et al.*, 2000). These deficits are similar to those of Broca's aphasia and may reflect a cooperative role between frontal and cerebellar cortices in managing certain aspects of speech production. Impairment can include slower performance on syllable repetitions, unusual prosodic patterns, and a loss of distinct phonological contrasts (Ackermann & Hertrich, 2000; Ivry & Gopal, 1992). For example, when one group of cerebellar patients was recorded saying examples of pairs differing only in voice onset time (VOT), as in the German words *Daten* (data) and *Taten* (deeds), several of them could not consistently produce the shorter VOT required for /*da*/ and the longer VOT required for /*ta*/ (Ackermann *et al.*, 1997). Similarly, another group of patients had difficulty producing the vowel-length distinction between *Gram* (grief) and *Gramm* (gram). The impairment in this case, however, was contingent upon the degree of articulatory complexity; an equivalent vowel-length distinction between two words that are simpler to articulate, *Rate* (instalment) and *Ratte* (rat), was produced normally by the cerebellar patients (Ackermann *et al.*, 1999).

These impairments have parallels in speech perception, suggesting a cerebellar role in speech that extends beyond production. Initial evidence argued against the hypothesis of a deficit in categorical speech perception in cerebellar patients. Ivry & Gopal (1992) found normal classification of a set of stimuli that varied along a VOT continuum between /*ba*/ and /*pa*/. However, these phonemes also differ in the presence of aspiration noise. When the phoneme distinction is purely temporal, a perceptual impairment is observed in patients with cerebellar degeneration. Ackermann *et al.* (1997) demonstrated that some of their patients were unable to distinguish between the words *Boten* (messengers) and *Boden* (ground). These sounds differ in the duration of the silent period associated with the production of the medial stop consonant. Such 'cognitive' processing may require motoric representations either by virtue of the articulatory nature (see Liberman & Mattingly, 1985) or the temporal requirements (see Ivry *et al.*, 2001) of speech perception.

Lexical retrieval and verbal fluency

In addition to these more purely phonological aspects of speech perception, the ability to access the mental lexicon may be compromised after cerebellar damage. Fiez *et al.* (1992) examined a patient (RC1) who had suffered a cerebellar infarct in the right hemisphere. This patient generated incorrect and atypical responses across four word generation tasks (category, attribute, synonym, and verb generation). For example, he generated the word *eat* as the category for *cookie*, *insect* as an attribute for *butterfly*, *old* as a synonym for *garbage*, and *small* as an associated verb for *pill*. In contrast, he correctly generated words beginning with the same initial phoneme as the presented word. A similar pattern was found in four multilingual Italian patients studied by Fabbro *et al.* (2000). Not all investigators have reported this impairment, however; Helmuth *et al.* (1997) did not find any lexical retrieval problems in a group of 12 cerebellar patients, including six with focal lesions in the right cerebellar hemisphere.

Another verbal impairment that has been associated with damage to the cerebellum is verbal fluency. For example, patients are asked to generate as many words as they can in 1 minute, with the words either beginning with a particular letter (phonological fluency) or belonging to a particular category (semantic fluency). Impairments in both kinds of fluency have been associated with cerebellar damage (Appollonio *et al.*, 1993). In contrast to the results during single word lexical retrieval tasks, some authors have reported that the impairment is greater for phonological fluency than for semantic fluency (Bürk *et al.*, 1999, Leggio *et al.*, 2000; Silveri & Misciagna, 2000). Verbal fluency was also among the largest impairments in a group of children with excised cerebellar tumours, particularly for those with damage to the right cerebellar hemisphere (Riva & Giorgi, 2000). The fluency impairment does not appear to be related to problems in speech production. Appollonio *et al.* (1993) reported that performance between the patient and control groups in their study did not differ in the first 15 seconds of the task, and the lowered performance of the patients was due to perseveration on these initial items. Cerebellar patients are less likely than controls to benefit from category structure in tests of word list memory, which may also be a reflection of a decrease in category fluency (Daum *et al.*, 1993; Dimitrov *et al.*, 1996; Bürk *et al.*, 1999). If the cerebellum does play a role in lexical retrieval, this again could stem from the hypothesised need to engage articulatory representations in many forms of linguistic processing.

Evidence against cerebellar involvement in lexical retrieval, at least in terms of the aspect of the task that requires response selection, comes from studies that have manipulated the number of response alternatives during retrieval. For example, there are many equally strong verb associates for the noun *cat*, while there is only one strong verb associate for the noun *scissors*. Activation in the left inferior frontal gyrus is correlated with selection demands, and is higher for words with many associates (Thompson-Schill *et al.*, 1997). Moreover, patients with lesions encompassing this region produce more errors than controls on the generate task, but only for words that have a large number of associates (Thompson-Schill *et al.*, 1998). In contrast, patients with cerebellar lesions perform as well as controls for both high- and low-selection words (discussed in Ivry *et al.*, 2001).

Verbal working memory, reading, and dyslexia

Considerable attention has been focused on the possibility that the cerebellum might be part of a network involved in verbal working memory. The evidence here has come from both neuroimaging (see Cabeza & Nyberg, 2000; Desmond, this issue) and neuropsychology. For example, Silveri *et al.* (1998) studied a patient who suffered a temporary impairment in verbal working memory following the removal of the right cerebellar hemisphere. This patient not only had a reduced digit span but also showed unusual effects of two working memory manipulations common in the cognitive psychological literature. First, the patient showed no word-length effect, which is the recall advantage for shorter words over longer words, thought to reflect the use of articulatory rehearsal. Second, he showed no phonological similarity effect, which is the recall advantage for sets of phonologically dissimilar words over phonologically similar words, thought to reflect the use of phonological representation. Importantly, the loss of the latter effect was for the visual modality only. This pattern is consistent with a role for the cerebellum in the articulatory rehearsal component of working memory as conceptualized by Baddeley (1986), in which phonological representation and articulatory rehearsal are separate processes, and the phonological representation of written language is dependent upon articulatory re-coding.

However, other patients have shown reduced word-length and phonological similarity effects for both visual and auditory modalities (Justus *et al.*, 2001). This result is inconsistent with the idea that the cerebellum is specifically part of Baddeley's articulatory rehearsal mechanism, which does not play a role in the immediate phonological representation of spoken language in his model. A different hypothesis centres on the idea that the cerebellum may serve as a discrepancy detector between the 'output' of rehearsal and the 'input' in the phonological short-term store (Desmond *et al.*, 1997; Desmond, this issue). While some neuropsychological studies suggest a reduction in the overall capacity of working memory, as measured by digit span (e.g. Bürk *et al.*, 1999), others have reported that the digit spans of patients with cerebellar lesions fall in the normal range (e.g. Bracke-Tolkmitt *et al.*, 1989; Fiez *et al.*, 1992).

The relationship between verbal working memory and the cerebellum also underlies the provocative link hypothesised to exist between cerebellar abnormalities and developmental dyslexia (Nicholson & Fawcett, 1999; Nicholson *et al.*, 2001; see Rapoport, this issue). Dyslexic children are impaired on various tasks thought to assess cerebellar function, including tests of balance and coordination (Fawcett *et al.*, 1996; Fawcett & Nicholson, 1999) and perceptual tests involving temporal processing (Nicholson *et al.*, 1994). Although poor phonological representation is typically described as the core deficit of dyslexia (see Snowling, 2000 for a review), these studies have reported that the magnitude of dyslexics' impairment on cerebellar tasks is greater than their impairment on measures of reading and phonological processing (Fawcett & Nicholson, 1999). Interestingly, the 21-year-old patient with posterior fossa tumour reported by Fabbro *et al.* (2000) had suffered from clumsiness, coordination difficulties, and dyslexia since the age of seven. These results are consistent with the connection between dyslexia and verbal rehearsal, which together suggest that the integrity of cerebellar function may be essential for the development of normal phonological representations because of its contributions to articulatory rehearsal (see Baddeley *et al.*, 1998; Ivry *et al.*, 2001; Nicholson *et al.*, 2001). Thus, although it is correct to characterise the underlying cognitive deficit of dyslexia as phonological, such processing may have its roots in motor-based processing done by the cerebellum.

Temporal processing

Ivry & Keele (1989) have argued that the cerebellum serves as a general timing device in perception and action. Again, such a role is consistent with the idea that certain cognitive processes may be rooted in motor-like representations. The cerebellar cortex may be specialised in part for precise temporal representation (see O'Hearn & Molliver, this issue), allowing us to coordinate the timing of muscle groups with each other and with environmental events. Selection for this kind of computation may also have granted the cerebellum with the appropriate circuitry for handling temporal perception even when no movement is required.

One source of evidence regarding temporal processing in the cerebellum is from experiments measuring isochronous tapping (Ivry & Keele, 1989). Patients with damage to the cerebellum showed an increase in variability for their tapping intervals in these tasks. This is not surprising given the motor demands required. However, when this variability was parcelled into two components, one associated with central timing mechanisms and the other with motor implementation (Wing & Kristofferson, 1973), the increase in variability for patients with lateral cerebellar lesions was attributed to the central timing component (Ivry *et al.*, 1988). Furthermore, patients with cerebellar lesions are impaired on *perceptual* timing tasks (Ivry & Keele, 1989; Mangels *et al.*, 1998).

These impairments are distinct from the temporal processing deficits observed in patients with frontal lobe lesions. While cerebellar patients are impaired at discriminating intervals both in the 400 milliseconds and 4 seconds ranges, frontal patients are only impaired at the latter (Mangels *et al.*, 1998), suggesting that the frontal impairment may be related to the increased working memory demands that arise for the longer intervals. That the frontal contribution is related to working memory is supported by a study in which the patients concurrently compared the duration and pitch of two stimuli (Casini & Ivry, 1999). Cerebellar patients only showed a dual-task cost on the duration judgements. Patients with prefrontal lesions showed a dual-task cost on both the duration and pitch judgements, suggesting a general role in coordinating the two tasks.

Implicit learning and memory

The cerebellum is essential for eyeblink classical conditioning, a model task for studying sensorimotor learning, and the relevant circuitry in rabbits has been detailed at the systems, cellular, and molecular level (see Thompson *et al.*, 1997). In humans, the link between the cerebellum and this form of implicit (unconscious) learning is supported by the fact that cerebellar patients show an impairment in eyeblink conditioning for the eye ipsilateral to their cerebellar lesion (Woodruff-Pak *et al.*, 1996), and their rate of conditioning acquisition is also correlated with their consistency on isochronous tapping tasks (Ivry *et al.*, 1988). Additionally, the slower acquisition rate of elderly participants is correlated with a reduction in Purkinje cell volume (Woodruff-Pak *et al.*, 1990). Finally, neurologically normal individuals show a reduced acquisition rate when engaged in a simultaneous tapping task, but not when performing other difficult tasks (Papka *et al.*, 1995, 1997).

These results have been interpreted in terms of a temporal deficit, as classically conditioned responses often must be timed precisely on the order of milliseconds to anticipate the unconditioned stimulus correctly (e.g. Ivry & Keele, 1989). Other forms of implicit learning may be mediated by the cerebellum not by virtue of their temporal properties but by virtue of the fact that many forms of unconscious knowledge are procedural and are rooted in motor representations. The role of the cerebellum in procedural learning is well established (see Thach, 1996 for a review), and it may be the case that the cerebellum is recruited in other forms of implicit learning. The spared skill learning, priming, and other forms of implicit learning in amnesic patients with medial temporal lobe damage are consistent with the idea that other brain areas, including perhaps the cerebellum, may mediate the consolidation of these kinds of implicit knowledge (Fiez *et al.*, 1992).

To consider one example of procedural knowledge, patients with cerebellar lesions consistently fail to exhibit learning on the serial reaction time task (Pascual-Leone *et al.*, 1993; Molinari *et al.*, 1997). In this task, participants' responses are based on the spatial position of series of stimuli that either follow a sequence or occur randomly. Normal individuals respond with increasing speed to stimuli presented in a consistent sequence, even though they may not be able to identify, when asked, that the stimuli are presented non-randomly. The failure of cerebellar patients on this task appears to extend beyond implicit learning; the patients also fail to become aware of the repeating pattern under conditions in which control participants do develop awareness. Moreover, even when informed of the sequence prior to testing, they fail to show benefits of such explicit knowledge during testing.

Another cognitive task speaking to the issue of procedural learning is paired-associate learning, which, although involving an explicit goal, often is performed without subjects developing awareness that improvement is being made. Studies testing the associative learning abilities of cerebellar patients in cognitive tasks have yielded mixed results. Bracke-Tolkmitt *et al.* (1989) reported a deficit in a group of cerebellar patients on two tests of associative learning: learning verbal paired associates and word-colour paired associates. This result was replicated in a study by Drepper *et al.* (1999) in which the colours chosen were all shades of green and blue, and thus not easy to encode verbally. However, Daum *et al.* (1993; Daum *et al.*, this issue) argue that while the cerebellum may play a role in motor skill learning, the more cognitive skill learning deficits are associated with patients who have extracerebellar damage (degeneration that extends beyond the cerebellum). Further, they argue that caution must be taken in matching control participants with cerebellar patients in terms of mood and IQ. When patients were selected with pure cerebellar damage, Daum *et al.* (1993) failed to find impairments on many tests of cognitive ability, including paired associate learning. Appollonio *et al.* (1993) also did not find an impairment on paired associative learning in patients with cerebellar lesions.

Tasks showing improvement in cognitive skills with repeated exposure are more clearly implicit forms of non-motor learning. The evidence for cerebellar involvement here is also mixed. Fiez *et al.*'s (1992) patient RC1 not only gave unusual responses in the word generation tasks described earlier, but also failed to show an effect of learning for these same tasks with repeated practise (but see Helmuth *et al.*, 1997 for a failure to replicate in a group study). On a simplified version of the Tower of Hanoi puzzle, RC1 showed some practise-related improvements but the effect was less than that found for controls. However, Daum *et al.* (1993) did not find any difference in skill acquisition in their patients over repeated trials of a mirror reading task and the Tower of Hanoi puzzle. Patient RC1 also failed to learn to respond to the arbitrarily correct item in pairs of words and pictures. A similar result was found by Helmuth *et al.* (1997). However, age could account for this result in the latter study.

Given the amount of conflicting evidence, we cannot say at present whether or not the cerebellum plays a role in non-motor implicit learning. Although the link between procedural learning and more cognitive forms of implicit learning may be compelling, the current empirical evidence is unclear.

Vision, space, and attention

A final area of cognition that has been suggested to engage the cerebellum is visuospatial processing and visuospatial attention. However, standard neuropsychological tests of visuospatial ability do not provide strong support for such an activity of the cerebellum. Consider the Rey-Osterrieth Complex Figure, a test in which the figure must first be copied and later drawn from memory, with the memory score calculated based on the differences in detail between initial and delayed copy. The patients studied by Bürk *et al.* (1999) and one of the five patients studied by Bracke-Tolkmitt *et al.* (1989) were impaired on the initial copy, which may have stemmed from motor difficulty. Nonetheless, in both studies, the patients performed normally when re-tested after a delay period, suggesting that they could successfully encode and retrieve visuospatial information. Moreover, Daum *et al.* (1993) found that the initial impairment was restricted to patients with atrophy extending into the brainstem.

Ivry & Diener (1993) suggested that cerebellar patients would be impaired on any visual task requiring precise timing. In support of this hypothesis, they reported an impairment on a velocity judgement task but not a control task involving a position judgement. However, Thier *et al.* (1999) argue that the visual perception deficits are more general: patients with degenerative cerebellar disorders were impaired on discrimination judgements for displays differing in position, movement direction, velocity (when presentation was simultaneous but not sequential), coherent motion, and velocity gradient. These impairments, particularly on the first two tasks, are not explainable in terms of a timing deficit. Furthermore, these results are consistent neither with Thier *et al.*'s (1999) magnocellular deficit hypothesis, as a position discrimination impairment would not have been expected, nor with a spatial working memory hypothesis, as sequential velocity discrimination impairment in particular would have been expected. A second study in Thier *et al.*'s (1999) study demonstrated relatively normal performance by the cerebellar patients on tasks involving visual search (see Treisman & Gelade, 1980), suggesting that this aspect of spatial attention was not impaired.

However, cerebellar patients have shown abnormalities in reorienting spatial attention in response to a cue. Townsend *et al.* (1999; but see Dimitrov *et al.*, 1996; Helmuth *et al.*, 1997) used the Posner spatial cueing task (e.g. Posner, 1980) in which a peripheral cue indicates the more probable of two locations of a forthcoming stimulus. For the majority of trials this cue is valid, with the stimulus appearing at the cued location. For the remaining trials this cue is invalid, with the stimulus appearing at the opposing location. The difference in response time between valid and invalid trials constitutes a measure of the effect of spatial attention. In the study by Townsend and colleagues, the patients with cerebellar lesions and autistic patients with abnormally developed cerebellar cortex showed an optimal effect of an attention cue after 800–1200 milliseconds, rather than the typical 50–100 milliseconds. Furthermore, this deficit was correlated with the size of cerebellar lobules VI–VII, which are part of an oculomotor network.

A further impairment in attention reorienting has been reported in a cross-modal attention-shifting paradigm. Courchesne *et al.* (1994) found that both cerebellar patients and autistic patients were impaired on a task involving rapid shifting between auditory and visual modalities. In focused attention tasks, participants were asked to respond each time a specified colour or frequency was presented. In the shift attention task, participants had to disengage attention to the visual modality and attend to the auditory modality after each visual response, and vice versa. Both autistic and cerebellar patients were impaired relative to controls at detecting targets in the shift condition when they occurred within 2.5 seconds of the attention shift. However, the impairment on this task, at least for patients with acquired cerebellar lesions, appears to be related to the demands on having to make two responses in rapid succession. When the motor requirements are reduced, the patients' performance improves even though the attention demands remain constant (Ravizza & Ivry, 2001).

The similar pattern of results between cerebellar patients and autistic patients suggests that there may be a common attention problem in the two groups, or perhaps a cerebellar abnormality underlying autism (see Courchesne, 1997). This fits with the theme that the cognitive functions associated with the cerebellum may build on the role this structure plays in motor control. First, just as the cerebellum is involved in overt shifts of attention involving eye movement, it may have the appropriate architecture for facilitating covert shifts of attention as well (Townsend *et al.*, 1999). Second, just as the cerebellum is involved in coordinating physical movement, it may have the appropriate architecture for 'mental coordination' (Courchesne *et al.*, 1994).

Conclusions

Neuropsychological studies have suggested that cognitive deficits can result from damage to the cerebellum in four broad categories: language (including speech perception, lexical retrieval, and working memory), temporal processing, implicit learning and memory, and visuospatial attention. The evidence concerning its relationship to the latter two categories, however, is sometimes conflicting. In all of these cases, the proposed cerebellar involvement may stem from representational abilities and processing mechanisms that evolved primarily in the context of motor control.

If the cerebellum contributes to these aspects of cognition, it likely does so as part of a cortical network, interacting with numerous other brain areas. Such an acknowledgement should not be taken as a diminishment of the value or legitimacy of the cerebellum as an organ of cognition. Even though various regions of the cerebral cortex may perform specific cognitive tasks, the regions nonetheless interact heavily with one another and with subcortical structures, including the cerebellum, for all complex cognitive domains. The changes in the hominid brain over the course of evolution may have taken advantage of the powerful processing capacity and extensive cortical connectivity of the cerebellum to modify our cognitive capacities in subtle yet significant ways.

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