

# The paleocerebellum and the integration of behavioral function

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The role of the cerebellum in motor function is well documented. Additional data clearly implicate the cerebellum in the regulation of sensory processes and autonomic functions, and more recent findings establish an influence of cerebellar systems on the regulation of emotional and motivational behaviors. The cerebellum provides extensive projections to brainstem and limbic mechanisms that have been implicated in behavioral regulation, and experimental manipulations of the cerebellum have been found to profoundly affect behavioral processes. In the present paper, we review some of these findings and offer a conceptual view of cerebellar function that reconciles these apparently disparate actions. We suggest that the cerebellum exerts functionally similar influences at all levels of sensorimotor and behavioral organization. This model provides a conceptual framework for understanding the behavioral consequences of cerebellar dysfunctions, which we suggest can be viewed as behavioral parallels to the classical cerebellar motor syndromes. Data implicating cerebellar systems in the pathogenesis of developmental disturbances in behavioral processes are also considered in the context of the present conception of cerebellar-behavioral function.

The role of the cerebellum in motor function is well documented (Dow & Moruzzi, 1958). The cerebellum asserts control over muscle tone through a relatively direct action on spinal motor neurons and reflex mechanisms (Pompeiano, 1967; Thomas, Kaufman, Sprague, & Chambers, 1956; Wilson, Uchino, Maunz, Susswein, & Fukushima, 1978). At the same time, it influences higher levels of sensorimotor organization through direct inputs to brainstem postural mechanisms (Brodal, 1957; Sherrington, 1906; Sprague & Chambers, 1953, 1959). Furthermore, the cerebellum can modulate the activity of cerebral cortical systems, contributing to the integration of the highest level sensorimotor processes (Brodal, 1981; Snider, 1967). Thus, the traditional view of cerebellar function is one of a continuity of influence throughout all major levels of organization within sensorimotor systems, ranging from simple reflex mechanisms of the spinal cord to complex processes of the cerebral cortex. In view of this global conception, it is most remarkable that there has been such a paucity of consideration of potential cerebellar influence on the neural mechanisms underlying complex motivational behaviors. Early studies documented dramatic effects of cerebellar manipulations, such as the elicitation of violent rage and escape behavior by chemical stimulation of the cerebellum in the dog [Pagano, 1902 (cited in Chambers, 1947), 1905]. However, in spite of repeated confirmation by other methods and in other species (Chambers,

1947; Clark, 1939; Lisander & Martner, 1975b; McDonald, 1953), these findings receive relatively little attention in contemporary views of cerebellar function.

Sherrington's (1906) important conception of the cerebellum as the "head-ganglion of the proprioceptive system" strongly dominated the field for the first half of this century. The cerebellum, however, receives substantial input from all major sensory systems and, in addition, has vast efferent projections to multiple levels of neuraxis (Brodal, 1981; Larsell & Jansen, 1972; Snider, 1967; Snider & Maiti, 1976). Indeed, Brodal (1981) has suggested that the cerebellum "co-ordinates and controls almost any function in which the nervous system is involved," and Dow & Moruzzi (1958) cautioned that "important facts were probably missed in previous ablation experiments and in routine clinical observations because the observers were not looking for . . . unexpected functional relationships." An important influence of cerebellar systems on vasomotor and respiratory processes was documented by Moruzzi (1940, 1950). Snider (1967) and others provided early demonstrations of cerebellar influences on sensory functions. Furthermore, more recent data have solidly implicated the cerebellum in the regulation and control of motivational and emotional behaviors (Berntson & Micco, 1976; Dow, 1974; Heath, 1976b, 1977; Snider & Maiti, 1976; Watson, 1978a). In the present paper, we will present a view of cerebellar function that reconciles these apparently disparate actions, and we will discuss the implications of such a view for the interpretation of the behavioral consequences of cerebellar dysfunctions.

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The literature on behavioral and autonomic influences of the cerebellum has consistently pointed to the involvement of what classically has been termed the paleocerebellum. The paleocerebellum, as described by Larsell (1934, 1967), includes portions of the anterior lobe and vermal cortex. In addition to interactions with the vestibular system, the paleocerebellum establishes extensive descending connections, directly and via the fastigial nucleus, to widespread areas of the brainstem reticular formation (Bharos, Kuypers, Lemon, & Muir, 1981; Larsell & Jansen, 1972; Martin, King, & Dom, 1974; Snider, Maiti, & Snider, 1976) and to the spinal cord (Batton, Jayaraman, Ruggiero, & Carpenter, 1977; Thomas, Kaufman, Sprague, & Chambers, 1956; Wilson, Uchino, Maunz, Susswein, & Fukushima, 1978). In addition, the paleocerebellum contributes direct and indirect projections to multiple areas within the limbic system (Angaut & Bowsher, 1970; Heath, 1976a; Snider, 1967; Snider & Maiti, 1976). In view of these considerations, it is the functional influences of the paleocerebellum that will be the primary focus of the present paper.

#### **Fastigiobulbar Pathways and the Integration of Autonomic and Somatic Responses**

**Autonomic influences.** In addition to its contribution to somatomotor control, a significant role of the paleocerebellum in autonomic function is now well documented. The cerebellum receives input from visceral afferents carried by the splanchnic and vagal nerves, and it has been shown to exert influence on mechanisms controlling cardiovascular tone, respiration, gastrointestinal functions, and bowel and bladder activity, as well as other autonomic processes (Dow & Moruzzi, 1958; Martner, 1975). These autonomic influences are exerted primarily by the anterior paleocerebellum and appear to reflect, at least in part, a direct action on autonomic mechanisms of the brainstem and spinal cord (Martner, 1975).

One of the more thoroughly studied autonomic influences of the paleocerebellum is revealed by what is termed the fastigial pressor response (FPR). The FPR consists of a marked cardiovascular pressor effect that can be induced by stimulation of a restricted area within the rostral pole of the fastigial nucleus (Achari & Downman, 1969; Lisander & Martner, 1975a; Miura & Reis, 1969). This pressor response is mediated by direct fastigiobulbar projections carried by the juxtarestiform body to a pressor zone in the paramedian reticular formation (Wang, 1981). These projections are indicated by the fact that the FPR can be abolished by lesions of the paramedian reticular nucleus or by sections of the juxtarestiform body (Miura & Reis, 1970, 1971) but is not affected by pre-collicular decerebration (Achari & Downman, 1970) or by transections of the middle or superior cerebel-

lar peduncles (Miura & Reis, 1970, 1971). Inputs from the fastigial nucleus and carotid baroreceptors exert antagonistic influences on individual neurons within the reticular formation pressor zone and thereby modulate cardiovascular tone (Miura & Reis, 1970).

**Behavioral influences.** While somatomotor and autonomic functions of the cerebellum are clearly documented and have commanded a great deal of experimental attention, developments in recent years have mandated a major expansion in conceptions of the range of cerebellar influence. Electrical stimulation within certain regions of the paleocerebellum in animals not only can induce relatively simple motor adjustments, but also can elicit behaviors showing a high degree of complexity and serial organization, including eating, drinking, grooming, gnawing, rage and threat behavior, and attack (Berntson & Micco, 1976; Martner, 1975; Watson, 1978a). The behaviors induced by cerebellar stimulation are not mere motor automatisms, but evidence goal directedness and are highly responsive to stimulus features of the goal objects. Thus, attack induced by cerebellar stimulation in the cat includes specific approach to a rat, followed by vigorous biting that is primarily directed to the head and neck (Reis, Doba, & Nathan, 1973). In addition, grooming induced by paleocerebellar stimulation is directed specifically toward furry-textured objects, and the presence of surface irregularities in the fur greatly increases the proportion of grooming directed to that area (Berntson & Hughes, 1976; Berntson, Potolicchio, & Miller, 1973). Furthermore, grooming induced by cerebellar stimulation in the cat includes two components of natural grooming, fur-licking and groom-biting, and the relative frequencies of these components and the fine features of their form have been shown to be highly determined by the stimulus properties of the goal object (Berntson & Hughes, 1976; Berntson et al., 1973). The spatiotemporal integration of the individual elements of complex behaviors induced by cerebellar stimulation stands in striking contrast to the simple motor adjustments classically reported upon stimulation of the cerebellum. These findings indicate that, in addition to a relatively direct action on lower motor neurons and reflex mechanisms, the cerebellum provides modulatory influences over higher levels of sensorimotor organization—levels of organization that are responsible for the elaboration of complex patterns of behavior (Berntson & Micco, 1976; Huang & Mogenson, 1972).

As illustrated in Figure 1, the most effective area in the cerebellum for the elicitation of complex behaviors is the rostral pole of the fastigial nucleus and its input pathways from the anterior vermis and output pathways through the superior cerebellar peduncle (Ball, Micco, & Berntson, 1974; Berntson &

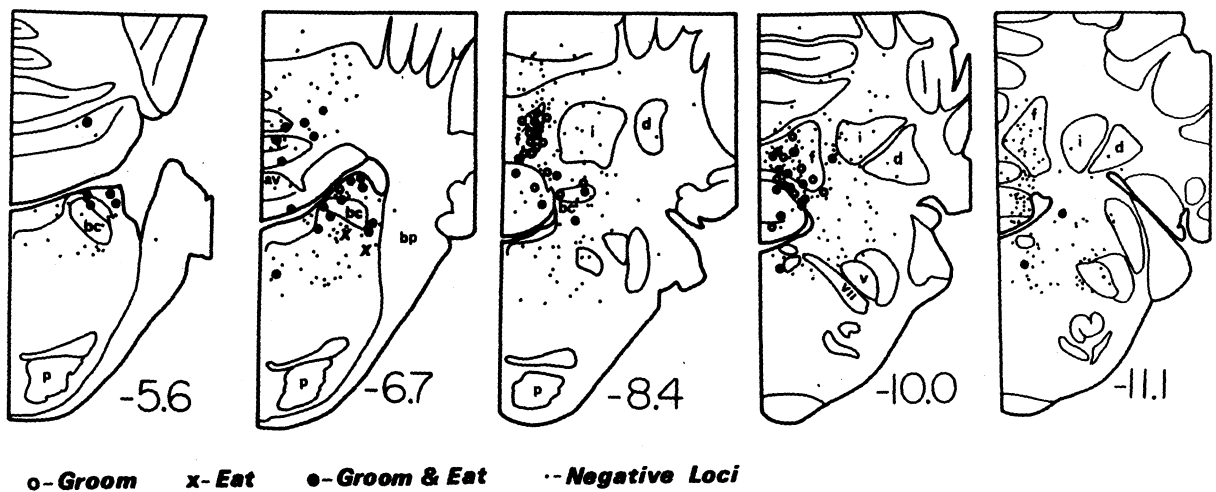


Figure 1. Anatomical distribution of electrode sites that elicit stimulation-bound grooming (open circles), eating (x), or both grooming and eating (closed circles). Negative loci are indicated by small dots. Plates are drawn from the atlas of Berntson, Paulucci, and Torello (*Brain Research Bulletin*, 1978, 3, 465-492). Numbers to the lower right of each plate show the stereotaxic frontal plane. Abbreviations: av, anterior vermis; bc, brachium pontis; d, dentate nucleus; f, fastigial nucleus; i, nucleus interpositus; p, pontine nuclei; v, fifth cranial nucleus; vII, facial nerve.

Paulucci, 1979; Berntson et al., 1973; Lisander & Martner, 1975a; Reis et al., 1973). The fastigial nucleus has two principal trajectories of projection: (1) descending projections, via the juxtarestiform body and the hook bundle of Russell, to widespread areas of the brainstem and the spinal cord (Bharos et al., 1981; Larsell & Jansen, 1972; Martin et al., 1974; Snider, 1967; Snider & Snider, 1976); and (2) ascending projections, via the superior cerebellar peduncle, to the diencephalon, limbic system, and basal forebrain (Angaut & Bowsher, 1970; Heath, Dempsey, Fontana, & Meyers, 1978; Heath & Harper, 1974; Snider & Maiti, 1975). Precollicular decerebration in animals, which eliminates the influence of diencephalic and telencephalic mechanism, does not preclude the spontaneous expression of integrated behavioral activities, including righting, locomotion, eating, grooming, behavioral thermoregulation, and escape and defensive behaviors (Berntson & Micco, 1976). These findings reveal that a great deal of behavioral organization is accomplished at brainstem levels (Berntson & Micco, 1976; Huang & Mogenson, 1972; Siegel, 1979). Recent findings indicate that complex behaviors elicited by paleocerebellar stimulation are mediated at least in part by descending projections to brainstem response mechanisms. Lesions of the superior cerebellar peduncle, which destroy ascending fastigial projections, do not alter either the threshold or the form of eating and grooming behaviors elicited by fastigial stimulation in the cat (Berntson & Paulucci, 1979). These findings suggest that complex behaviors induced by paleocerebellar stimulation are not dependent upon direct ascending projections to limbic or forebrain systems. These results further in-

dicate that such behaviors do not result from antidromic activation of the catecholaminergic projections from the locus coeruleus that could indirectly influence limbic activity, since these projections would also be disrupted by the lesions. In addition, stimulation of specific brainstem sites that receive anatomical projections from the fastigial nucleus can induce eating and grooming behaviors that are highly comparable to those obtained by stimulation of the fastigial nucleus (Berntson, 1973; Berntson & Hughes, 1974, 1976; Buchholz, 1976; Martin, 1976; Micco, 1974; Waldbillig, 1975). Moreover, these stimulation-induced eating and grooming responses persist after decerebration (Buchholz, 1976). Similarly, rage and threat reactions that can be elicited by stimulation of the fastigial nucleus are not prevented by complete precollicular transections (Lisander & Martner, 1975b).

The studies outlined above document an influence of paleocerebellar networks on somatic and autonomic mechanisms of brainstem origin. Additional evidence suggests a high degree of somatovisceral integration within these systems. Cerebellar loci yielding complex behaviors and those resulting in pressor responses are both focused in the rostral fastigial nucleus and both exert their actions through brainstem mechanisms. Fastigial stimulation that results in grooming and eating also induces cardiovascular adjustments that normally accompany spontaneous grooming and eating behaviors (Lisander & Martner, 1975a; Reis et al., 1973). At the same time, this stimulation suppresses inhibitory gastrointestinal reflexes, consistent with natural somatovisceral patterns underlying feeding (Lisander & Martner,

1975a). Additional documentation of the integrated somatic and autonomic influences of the paleocerebellum comes from the observation that fastigial stimulation, at a single locus, can elicit both somatic components and autonomic correlates of feline rage behavior (Lisander & Martner, 1975b; Zanchetti & Zoccolini, 1954). Indeed, while somatic and autonomic systems may have segregated lower motor neurons and peripheral pathways, it has become clear since Hess's pioneering studies on the diencephalon (Hess, 1957, 1964) that central regulatory systems draw no such distinction. For example, the integrated hypothalamic organization of hormonal, autonomic, and behavioral adjustments to homeostatic challenges is now so fully established that it requires no documentation. The combined somatic and autonomic influences of the cerebellum are highly consistent with this integrated pattern of central nervous system organization.

#### **Fastigiolimbic Projections and the Integration of Motivational and Emotional Behaviors**

**Anatomical connectivity.** In addition to its descending brainstem and spinal projections, the paleocerebellum provides widespread ascending projections to diencephalic and telencephalic areas that have been heavily implicated in the control of emotional and motivational behaviors. Electrophysiological and neuroanatomical studies have shown that the fastigial nucleus establishes ascending connections with a wide variety of limbic areas, including the basolateral amygdala, hippocampal field CA III, hypothalamus, medial and dorsal-anterior septal nuclei, and nucleus accumbens (Anand, Malhotra, Singh, & Dua, 1959; Angaut & Bowsher, 1970; Harper & Heath, 1973; Heath & Harper, 1974; Snider & Maiti, 1976). In addition, the paleocerebellum provides indirect input to the limbic system via projections onto the limbic-midbrain structures of Nauta (1958), including the ventral tegmental area, periaqueductal gray, interpeduncular nucleus, and substantia nigra (Snider, 1975; Snider & Maiti, 1976; Snider et al., 1976). These midbrain structures, in addition to receiving paleocerebellar and limbic system inputs, provide reciprocal projections back onto limbic structures, including the medial septal nucleus, preoptic area, and multiple loci within the hypothalamus (Nauta, 1958).

An additional and potentially important route of ascending cerebellar influence on limbic function is via the paleocerebellar projections to ascending catecholamine neurons of the locus coeruleus (Snider, 1975) and the ventral tegmental area (Snider et al., 1976). These ascending catecholamine neurons, constituting major portions of the dorsal noradrenergic pathway and the mesolimbic dopaminergic pathway, project to widespread areas of the limbic sys-

tem and basal forebrain (Crutcher & Humbertson, 1978; Jacobowitz & MacLean, 1978; Lindvall & Björklund, 1974; Ungerstedt, 1971b) and have been heavily implicated in the regulation of many aspects of motivated behavior, including aggression (Reis, 1974; Welch & Welch, 1971), feeding and drinking (Ahlskog & Hoebel, 1973; Leibowitz, 1976; Ungerstedt, 1970, 1971a), and reinforcement processes (German & Bowden, 1974; Wise, 1978). Norepinephrine-containing neurons of the locus coeruleus also project back onto paleocerebellar structures, establishing a reciprocal feedback interaction with the anterior vermis and fastigial nucleus (Chu & Bloom, 1974; Snider, 1975).

The functional significance of ascending cerebellar projections is indicated by the fact that stimulation of the paleocerebellum can strongly inhibit epileptiform discharges in limbic system structures, as well as in cerebral cortical areas (Cooke & Snider, 1955; Dow, 1974; Mutani, Bergamini, & Doriguzzi, 1969; Snider & Maiti, 1975). Furthermore, ablation of the cerebellum results in an appreciable enhancement of epileptiform activity in these rostral systems (Dow, 1974; Dow, Fernandez-Guardiola, & Manni, 1962). These findings indicate that cerebellar networks can exert modulating influences over the excitability not only of cerebral cortical motor systems, but also of limbic structures that are not historically associated with motor function.

**Behavioral influences.** Several lines of evidence indicate that ascending projections from the paleocerebellum serve to modulate functional activity in limbic mechanisms for emotional and motivational behaviors. Direct ascending projections of the fastigial nucleus and anterior vermis can mediate short-latency evoked responses in limbic areas, including the hippocampus, hypothalamus, septal area, and amygdala (Anand et al., 1959; Heath, 1973; Heath & Harper, 1974; Snider & Maiti, 1976). Related to these findings, there is a remarkable similarity in many of the behavioral effects of paleocerebellar and limbic manipulations. Destruction of the amygdala has classically been reported to have a dramatic "taming" effect (King & Meyer, 1958; Kluver & Bucy, 1937; Schreiner & Kling, 1956), and lesions of the anterior vermis result in equally dramatic decreases in aggressiveness (Berman, Berman, & Prescott, 1974; Peters & Monjan, 1971). Likewise, both amygdaloid lesions and lesions of the fastigial nucleus greatly attenuate the otherwise exaggerated "irritability" of rats with septal lesions (Berntson & Torello, 1980; King & Meyer, 1958). Conversely, aggressive behaviors can be induced by stimulation of the fastigial nucleus or by stimulation of the amygdala or the hypothalamus in the cat (Hess, 1957; Lisander & Martner, 1975b; Reis et al., 1973; Ursin & Kaada, 1960; Zanchetti & Zoccolini, 1954). In addition, electrical stimulation

of the amygdala or the hypothalamus can induce eating and grooming behaviors that are similar to those induced by stimulation of the fastigial nucleus (Berntson & Micco, 1976; Hess, 1957; Kaada, 1951).

Additional findings further suggest an influence of the paleocerebellum on yet other classes of motivated behavior and provide further notable parallels between the effects of paleocerebellar and limbic manipulations. Destruction of the cerebellar fastigial nuclei, but not other deep cerebellar nuclei, results in a substantial and relatively specific disruption of conspecific social interactions in the rat (Berntson & Schumacher, 1980). This effect, which was not related to the motoric effects of the lesions, persisted with no sign of recovery for the duration of the 4-week period of postlesion testing. Essentially identical reductions in social interactions have been reported after lesions of the amygdala (Corman, Meyer, & Meyer, 1967; Jonason, Enloe, Contrucci, & Meyer, 1973).

In addition to the findings outlined above, stimulation of sites in the anterior vermis, fastigial nucleus, and superior cerebellar peduncle has been shown to be highly reinforcing and can maintain high rates of self-stimulation in the rat and monkey (Ball et al., 1974; Plotnik, Mir, & Delgado, 1972; Routtenberg & Malsbury, 1969; Watson, 1978b). Similarly, stimulation of the vermal cortex has been reported to induce purring and "pleasure" reactions in the cat (Clark, 1939; McDonald, 1953). The specific cerebellar pathways mediating the rewarding effects of paleocerebellar stimulation are not clear, although the fastigial nucleus has been shown to project to limbic structures such as the septal area and hypothalamus from which self-stimulation can also be maintained in both humans and animals (Bishop, Elder, & Heath, 1963; Olds, 1977). In addition to direct projections to the limbic system, however, other potential routes of cerebellar input to reward mechanisms exist, including the fastigial projections to ascending noradrenergic and dopaminergic systems that appear to be significantly involved in reward processes (German & Bowden, 1973; Wise, 1978). Regardless of the particular routes of influence, the reinforcing effects of paleocerebellar stimulation support the view that cerebellar systems can exert powerful influences over motivational processes.

It is recognized that the mere existence of direct and indirect anatomical projections from the fastigial nucleus to the limbic system is not sufficient to establish the existence of a functional interaction with regard to behavioral processes. Nevertheless, the pattern of anatomical connectivity in conjunction with the demonstration of electrophysiological influences of the fastigial nucleus on limbic system activity (Anand et al., 1959; Heath et al., 1978; Snider, 1975; Snider & Maiti, 1975) indicates that fastigial projections can exert modulatory control over limbic system func-

tion. These findings, together with the outlined parallels between the behavior consequences of paleocerebellar and limbic manipulations, are highly suggestive that such a functional relationship may obtain.

### **The Modulatory Role of the Cerebellum and the Consequences of Cerebellar Dysfunction**

As discussed in the previous section, paleocerebellar systems exert direct descending influences on brainstem mechanisms for eating, grooming, and aggressive behaviors. The anatomical and behavioral data outlined above suggest additional ascending paleocerebellar projections to limbic areas, such as the amygdala, hypothalamus, and septal region, which may further serve to regulate and control the expression of motivated behaviors. This paleocerebellar influence on behavioral substrates at both brainstem and limbic levels is highly reminiscent of the multiple cerebellar projections to different levels of organization within classical motor systems. In light of these results, we suggest that the cerebellum may well provide comparable modulatory control over all major levels of functional organization within sensorimotor mechanisms, including neuronal networks subserving complex behavioral processes. The merit of such a view is that it offers a parsimonious reconciliation of the classically recognized influences of the cerebellum on somatic-motor systems, with data indicating a cerebellar influence on systems related to autonomic processes and emotional and motivational behaviors.

**Behavioral consequences of cerebellar dysfunction.** To the extent that cerebellar influences on autonomic function and behavioral processes are viewed as being similar to influences on somatic reflexes and postural mechanisms, comparable classes of functional deficits would be expected to eventuate from cerebellar disturbances. Thus, Fulton (1936) considered the possibility of "ataxia and asynergia in autonomic regulation similar to that now held for cerebellar disturbances in the somatic sphere," and we have documented above considerable alterations in emotional and motivational behaviors following cerebellar manipulations. In his classic treatment of cerebellar syndromes, Holmes (1917, 1939) described several motoric consequences of cerebellar damage. These include: asynergia, which denotes a loss of coordination within or between the elements of a movement; decomposition of movement, in which particular elements of a movement pattern fail to occur; and dysdiadochokinesia, which involves a disturbance in the ability to alternate sequentially between antagonistic movements. The effects of cerebellar damage on operant performance provide several notable behavioral parallels to these motoric syndromes.

**Dysdiadochokinesia.** Cerebellar damage can result

in motoric disturbances in the sequential alternation of antagonistic movements, such as pronation and supination of the forearm (Holmes, 1917, 1939). Behavioral parallels to this syndrome have been reported in rats with varying degrees of cerebellar agenesis resulting from focal x-radiation during development. Spontaneous alternation between opposing responses (such as turning left vs. turning right) is highly characteristic of the normal exploratory behavior of animals (Dember & Fowler, 1958). Pellegrino and Altman (1979), however, report that animals with cerebellar agenesis fail to show this normal pattern of response alternation. Moreover, while these animals can acquire numerous complex maze habits as readily as normal animals, they are greatly impaired when the maze is configured so as to require the serial alternation between right and left turns. In the maze task used by Pellegrino and Altman, sequential turns were of sufficient temporal separation, due to the distance between choice points, so as to rule out an interpretation of the alternation deficit based on simple disturbances in rapid transitions between individual antagonistic muscle movements. Rather, this maze deficit reflects a disturbance of sequential alternation in the behavioral sphere, over a relatively long time frame and involving organized responses of a variety of muscle groups.

#### **Asynergia, Decomposition of Movement, and the Failure of Associated Movements**

These conditions entail, at various levels within the organization of motor acts, a deficit in the rate, range, or uniformity of response elements or in the spatiotemporal organization between these elements. These disorders have been considered disturbances in the coordination of movements. Since motivational behaviors consist of organized motor responses, cerebellar lesions would be expected to result in ataxia and asynergia of the individual motor elements of such behaviors. The view of cerebellar function presented in the present paper, however, would also predict disturbances in motivated behaviors at a much more global level of organization, deficits in the behavioral sphere that parallel the decomposition of movements and the failure of associated movements resulting from cerebellar lesions (Holmes, 1917, 1939). The decomposition of movements involves a disintegration between the elements of a movement, which in the extreme case of the failure of associated movements become completely dissociated. (As an example of the latter, Holmes gives the absence of arm swinging during locomotion after cerebellar lesions in the human.)

A behavioral parallel to these latter deficits involving the disintegration between patterns of behavior is suggested by results on DRL performance in

rats with cerebellar lesions (Kirk, Berntson, & Hothersall, 1982). DRL (differential reinforcement of low rates of responding) performance requires the animal to emit a response and then to withhold that response for a specified period of time. Animals on DRL schedules have been reported to develop various alternative collateral or mediating responses during interresponse periods (responses such as grooming or stereotyped circling) which contribute to improved performance (Slonaker & Hothersall, 1972). Normal and efficient performance on this task thus requires the sequential integration between discrete behavioral elements. Rats with anterior vermal lesions show normal acquisition of a barpressing response for food under a continuous reinforcement schedule and thus are not impaired in learning or barpressing performance. When shifted to the DRL task, however, rats with paleocerebellar lesions fail to integrate effective collateral behaviors into the operant sequence. Rather, barpressing continues at a high and uninterrupted rate, resulting in poor performance efficiency and a small number of reinforcements. No improvement was seen in daily performance over a period of 1 month. Further studies indicated that this DRL deficit could be attenuated by altering the stimulus environment so as to facilitate the development of collateral behaviors. In this study, the introduction of a wood block resulted in the development of gnawing or other collateral behaviors, and DRL efficiency consequently increased to normal levels, as did the number of reinforcements. These findings indicate that the DRL deficit was not related to a fundamental disruption of operant performance or timing capacities. Rather, the performance deficit appeared to be related to a deficiency in the initiation of spontaneous collateral responses and the integration of these responses into a pattern of ongoing behavior in the DRL task. These are precisely the class of deficits that characterize decompositions and failures of associated movements. The present results suggest that, in addition to the motor coordination aspects of cerebellar function, one must also consider what Pellegrino and Altman (1979) have termed its "action coordination functions"—functions that relate to the integration of patterns of behavior.

Among the basic deficits underlying the cerebellar syndromes of asynergia and decomposition is an impairment in mechanisms involved in the initiation and termination of elementary movements (Dow, 1974; Holmes, 1917, 1939). A dramatic behavioral parallel to disturbances in the ability to check or inhibit movements has been observed after cerebellar lesions in animals. Numerous studies have reported an abnormal and maladaptive perseveration of ongoing responding after cerebellar lesions, as evidenced by: (1) the delayed extinction of a condi-

tioned response (Fanardjian, 1961); (2) impairments in tasks requiring the intermittent inhibition of responding (Butchel, 1970; Davis, Watkins, Angermeier, & Rubia, 1970; Rubia, Angermeier, Davis, & Watkins, 1969); and (3) deficiencies in the ability to withhold prepotent response tendencies (Buchtel, 1970). In each of these cases, the behaviors consisted of a series of distinct responses that were separated in time. Consequently, these deficits cannot be viewed to result simply from impairments in the termination of discrete motor responses, as is the case in classical motor ataxia and asynergia. Rather, these disturbances involve an impaired ability to inhibit an organized sequence of behavioral responding. This condition can be considered to reflect a behavioral asynergia that entails a disturbance in the ability to terminate or check not a simple movement, but a pattern of movements. Consequently, one sees a disturbance in the temporal features of a behavior and in its temporal integration with other classes of behaviors.

These examples illustrate appreciable parallels between characteristics of the classic cerebellar motor syndromes and the behavioral consequences of cerebellar lesions. These similarities support the concept that the cerebellum may exert comparable functional influences at different levels of organization within motor systems and behavioral mechanisms. Furthermore, when viewed from the standpoint of the cerebellar syndromes, otherwise disparate behavioral findings can be parsimoniously reconciled. Cerebellar lesions have been reported in some cases to impair performance in learning tasks, while in other cases no effects have been observed (Buchtel, 1970; Davis et al., 1970; Lashley & McCarthy, 1926; Meyer & Woolsey, 1952; Rubia et al., 1969). The studies reporting deficits, however, employed tasks that specifically require the inhibition of responding. Since, as discussed above, the ability to terminate responding is impaired by cerebellar lesions (see also Buchtel, 1970, and Watson, 1978a), primary disturbances in cerebellar mechanisms of response termination could account for these apparent inconsistencies. In addition, however, McCormick, Lavond, Clark, Kettner, Rising, and Thompson (1981) have recently reported that multiple unit activity in the cerebellum shows changes in firing patterns that correspond temporally to a simple conditioned response (CR). Moreover, large unilateral lesions of the cerebellum abolish this eyeblink CR ipsilaterally, while the unconditioned response remained unaffected. Furthermore, the CR could not be reconditioned ipsilaterally but could be readily established in the contralateral eye. These findings indicate that, for certain tasks, the elaboration or initiation of learned responses is also dependent on cerebellar influences.

**Developmental disturbances and behavioral disorders.** The cerebellum is relatively undeveloped at birth (Altman, 1969; Scheibel & Scheibel, 1964)

and is consequently quite sensitive to disruption or alteration from perinatal conditions such as anoxia (Faro & Windle, 1969), hormonal influences (Howard, 1968; Litteria & Thorner, 1974), malnutrition (Barnes & Altman, 1973; Hillman & Chen, 1981a, 1981b), and early rearing conditions (Floeter & Greenough, 1979; Pysh & Weiss, 1979). In view of these considerations and of the data outlined above indicating significant behavioral and autonomic functions of the cerebellum, attention to potential behavioral consequences of cerebellar developmental dysfunctions seems warranted. Prescott (1971) has suggested that cerebellar dysfunction, resulting from early somatosensory and vestibulosensory deprivation, may underlie the behavioral deficits of the social isolation syndrome in the primate. This syndrome is characterized by profound disturbances in social interactions, hyperactivity, and exaggerated aggressive behaviors directed toward self or others (Harlow, Harlow, & Suomi, 1971). Prescott points to associated movement disorders and motor stereotypies, such as repetitive rocking, head banging, and stereotyped pacing, which are also seen in isolation-reared monkeys. These features, he suggests, are indicative of vestibulocerebellar dysfunction, a view that he argues is further supported by the finding that a rocking, but not a stationary, surrogate mother greatly attenuates the deficits associated with isolation (Mason, 1968). In this regard, the paleocerebellum has been shown to have extensive interactions with vestibular systems (Brodal, 1974), and the isolation-induced alterations in activity and in social and aggressive behaviors are highly representative of the classes of behavioral function that, as discussed above, have been found to be altered by paleocerebellar manipulations. Further evidence for the potential involvement of cerebellar systems in the behavioral effects of social isolation is provided by the finding that isolation-reared monkeys show a characteristic pattern of abnormal electrical activity and spiking in the fastigial nucleus (Heath, 1972). Moreover, lesions of the anterior vermis have been shown to eliminate or greatly attenuate the exaggerated aggressiveness of isolation-reared monkeys (Berman et al., 1974). Additional studies provide more direct evidence for a role of vestibulocerebellar interactions in the development of emotional and motivational behaviors. Douglas, Clark, Erway, Hubbard, and Wright (1979) report that genetic disturbances in peripheral vestibular end organs result in a syndrome of hyperactivity, hyperemotionality, and deficiencies in alternation behavior in adult mice. This syndrome is highly similar to that seen after focal cerebellar x-radiation in neonatal rats (Pellegrino & Altman, 1979), indicating similar behavioral consequences of vestibular or cerebellar maldevelopment.

The behavioral effects of early vestibulocerebellar disruption and the behavioral consequences of social isolation have many features in common with certain

classes of developmental dysfunction in the human, such as autism and hyperkinesis. These features include hyperactivity, hyperemotionality, and motor stereotypies (Prescott, 1971). In addition, hyperkinetic children show notable deficits in DRL performance (Gordon, 1979), as do rats with paleocerebellar lesions (Kirk et al., 1982). In both cases, the pattern of deficit is similar and is characterized by high response rates and the failure to inhibit responding during the delay interval. Related to these parallels are reports that autistic and hyperkinetic children show a high frequency of abnormal vestibulo-ocular reflexes and an atypical vestibular nystagmus (Bhatara, Clark, & Arnold, 1978; Frank & Levinson, 1975; Ornitz, 1970)—functions that are in part under the control of cerebellar circuits (Ito, 1972; Robinson, 1968). These findings suggest the existence of vestibulocerebellar dysfunction in individuals with certain classes of developmental disturbances. Highly related to these results are the recent provocative findings of Bhatara et al. (1978 and personal communications). These authors report substantial clinical improvements in hyperkinetic children following a regimen of vestibular stimulation. As an additional development, recent studies have shown a high incidence of cerebellar atrophy in chronic schizophrenics (Heath, Franklin, & Shraberg, 1979; Weinberger, Kleinman, Luchins, Bigelow, & Wyatt, 1980; Weinberger, Torrey, & Wyatt, 1979), although the causal linkage between cerebellar atrophy and the symptomatology of schizophrenia has yet to be clarified (Snide, 1982). Taken together, however, the overall pattern of findings discussed in the present paper is supportive of the view that cerebellar networks may exert important modulatory influences on behavioral processes and that cerebellar dysfunction may underlie certain classes or features of developmental-behavioral disturbances. Experimental efforts to further evaluate the role of cerebellar systems in normal and abnormal behaviors now appear imperative.

### Overview

In the present paper, we present a conception of cerebellar function in which cerebellar systems are viewed as providing comparable modulatory influences at all major neuraxial and functional levels of sensorimotor and behavioral organization. The paleocerebellum, by virtue of its extensive projections to brainstem and limbic mechanisms, exerts important modulatory control over neural systems underlying motivational and emotional behaviors. The paleocerebellum provides two major routes of projection, descending projections to brainstem and spinal systems and ascending projections to limbic and telencephalic mechanisms. Descending influences exert control over basic brainstem autonomic and

behavioral substrates and mediate the complex somatovisceral behaviors, such as eating, grooming, and rage, which can be induced by paleocerebellar stimulation. Ascending influences on the limbic system are seen to modulate tonic activity within neural mechanisms controlling motivational and emotional behaviors and to provide for integration and coordination within and between general classes of behaviors.

This conception of cerebellar function permits a parsimonious reconciliation of the motoric, autonomic, and behavioral consequences of paleocerebellar manipulations. Furthermore, since cerebellar influences at different levels of sensorimotor organization are viewed as functionally similar, this conception makes specific predictions as to the nature of behavioral alterations resulting from paleocerebellar damage. Such behavioral deficits, including disturbances in emotional and motivational behaviors, can be viewed in the context of the classical cerebellar syndromes.

The data implicating cerebellar systems in behavioral function are now overwhelming. The potential clinical and scientific implications of these findings are of sufficient magnitude to warrant considerable experimental attention. Moreover, specific attention to the possible differentiation of function between cerebellar influences on brainstem and on limbic processes may provide important insights into the nature of cerebellobehavioral functions.

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