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THE FUNCTION OF THE CEREBELLUM IN COGNITION, AFFECT AND CONSCIOUSNESS: EMPIRICAL SUPPORT FOR THE EMBODIED MIND

Introduction

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A growing movement in cognitive science views consciousness and cognition as self-organizing systems involving emotion and sensory-motor agency (e.g. Damasio 1994, 1999; Clark 1996; Glenberg, 1997; Hurley 1998). The view that cognition is best understood as embodied is replacing models involving amodal symbol systems like the arbitrary, intrinsically meaningless symbols of computer programs, which notoriously fail to explain common-sense reasoning and consciousness. The embodied-cognition approach sees such behavior as extensions of the animal=s value-laden interaction with its environment.

How can abstract reasoning (e.g. logic and mathematics) make use of bodily action abilities? Briefly: sensorimotor imagery, conscious or semiconscious activated memory traces of the experiences of performing basic actions, functions not only in action contemplation and planning but also in the mental manipulation of objects in abstract reasoning. Abstract thought builds on basic action schemas: bodies interacting with objects in space (e.g. Huttenlocher 1968). To those claiming to lack such imagery, it can be argued that such images are not necessarily fully conscious, and brain imaging studies are now available that can decide such matters.

Actions require motivation. Even covert attention shifts depend on emotional interests of the organism; subcortical structures such as the amygdala, hippocampus and the hypothalamus influence voluntary attention mechanisms in the anterior cingulate. Actions imagined but not performed are both activated and inhibited in the frontal lobes and motor cortex; inhibition, controlled in large part by the hypothalamus, allows action images to be consciously experienced (Jeannerod 1998) along with the emotional values associated with the actions.

The combination of the above approach with recent work on emotion is powerful, allowing the formation of a global theory of brain function in which dynamic interactions among brain areas and brain events can be mapped at many levels of organization. An important prediction of the approach is that brain mechanisms once thought devoted to motor activity are also active in emotional and cognitive activities. Our example is the cerebellum. As we shall see, it appears that the cerebellum is not only a coordinator of motor actions, but also of reasoning and, most recently discovered, of emotional with cognitive states. If reasoning and other cognitive activities make use of motor schemas, this is exactly what one would expect. The cerebellum appears to be not just an organ for the coordination of actual motor activities, but also for coordinating the output of both cortical and subcortical structures involved in affect-laden cognitive activity at all levels.

The Role of the Cerebellum in Cognition and Affect

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Many studies suggest that the cerebellum is essential to the neural circuitry subserving cognition and emotion. It connects with the reticular system (arousal), hypothalamus (autonomic function and emotional expression), limbic system (experience and expression of emotion), and paralimbic and neocortical association areas critical for higher order function (cognitive dimensions of affect). Behavioral changes in adults and children with focal cerebellar lesions provide clinical support for the relationship between the cerebellum and cognition. A cerebellar cognitive affective syndrome in adults and children is defined by impairments in executive, visual spatial, and linguistic function and dysregulation of affect. A cerebellar role in the modulation of aggression and mood appears in children with the posterior fossa syndrome following surgery involving the vermis, and during clinical and experimental neurosurgical manipulation. Functional imaging studies reveal cerebellar involvement in nociception, autonomic behaviors, affective experiences, and multiple cognitive paradigms. These suggest topographic organization in the human cerebellum with the somatosensory homunculus in the anterior lobe, cognitive operations in the neocerebellum in lobules VI and VII, and emotion particularly influenced by the vermis. We have extended the hypothesis that the phylogenetically older fastigial nucleus, vermis and flocculonodular lobe constitute the "limbic cerebellum" to include these structures in the Papez circuit.
The cerebrocerebellar system appears to consist of discretely organized parallel anatomic subsystems that serve as substrates for differentially organized functional subsystems. We have proposed that there is a universal cerebellar transform (UCT), possibly error detection, prevention, and correction utilizing an internal model that facilitates the production of harmonious motor, cognitive, and affective/autonomic behaviors: the cerebellum detects, prevents, and corrects mismatches between intended and perceived outcome of interactions with the environment. Disruption of circuitry linking the cerebellum with the cerebral hemispheres prevents cerebellar modulation of functions subserved by the affected subsystems, and produces dysmetria, the universal cerebellar impairment (UCI). Dysmetria of movement, or ataxia, is matched by "dysmetria of thought", the proposed fundamental mechanism underlying disorders of intellect and emotion resulting from cerebellar dysfunction, including the cerebellar cognitive affective syndrome, abnormalities of affect, and psychotic thinking.

The Integrative Role of the Cerebellar Vermis in Cognition and Emotion

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The cerebellar vermis and the fastigial nucleus are treated here as the "the cerebellar vermis-fastigial nucleus" (VFN) complex. The fastigial nucleus, phylogenetically the oldest of the four cerebellar nuclei, influences eye movements, posture, equilibrium and autonomic activity (Beitz, 1982). The role of VFN complex in cognitive/emotional synergy is supported by imaging studies and by observations of its focal and myriad interconnections among key brainstem nuclei and bi-hemispheric networks of motor and limbic system structures. The neocerebellar hemispheres, lateral extensions of the VFN, are activated during mental imagery, tactile learning and language and sensory-processing. Although motoric aspects of articulation, balance and bimanual coordination may involve more medial areas of the cerebellum or VFN, this region is also nonspecifically activated during many of the same functional imaging studies of neocerebellar activation. This apparent lack of specificity hints at the role of the VFN in consciousness.

As it bridges the hemispheres, pathology of the VFN appears to connect many apparently unconnected psychiatric disorders. Although the cerebellum occupies only 10% of the human brain, it contains more than half of its neurons (except in the psychiatric disorders detailed below where the VFN is significantly smaller). Among mammals, Homo Erectus relies most heavily on the VFN for integrating visual, vestibular and proprioceptive cues. Bipedal standing robustly activates anterior and posterior vermal regions (Ouchi et al., 1999). Destruction of the vermal cortex (Sullivan et al., 2000), a result of chronic alcoholism, produces out-of-balance staggering gait ataxia through inflexible coordination of visual, vestibular and proprioceptive feedback. Childhood trauma appears to result in pervasive cerebellar damage. This may be due to the protracted postnatal ontogeny of the cerebellum rendering it sensitive to early corticosteroid exposure (Lauder, 1983). In this case VFN pathology is associated with the development of limbic seizures (Heath, 1976; Strain et al., 1979; Cooper et al., 1974, 1985; Riklan et al., 1976). An association between the VFN and limbic seizures was first observed in electrical recordings from the hippocampus and fastigial nucleus of violent adult Harlow monkeys (Heath ,1972). Aggressive behavior in these animals resulted from the stress of total maternal deprivation (Harlow, 1971). Bremer (1997) found that lesions of the vermis, but not the cerebellar hemispheres, tamed their aggression, suggesting that deprivation disordered the developing vermal cortex. Heath accordingly used electrical stimulation of the vermis (which inhibits cortex and disinhibits the fastigial nucleus) to relieve psychotic symptoms in humans (Heath, 1980). Interestingly, research by Mason and Harlow (1975) has shown that rocking during early life, which stimulates the VFN, mitigates the adverse effects of maternal deprivation. Child abuse is also associated with dissociation, increased prevalence of abnormal EEG=s (Ito, 1998), and symptoms suggestive of limbic seizures (Teicher et al., 1993). It seems to cause a limbic "kindling" that produces epilepsy in experimental animals. Repeated electrical stimulation of the limbic system in experimental animals can lead to seizures. Repeated abuse in humans may also result in limbic electrical abnormalities associated with epileptic-like behavioral experiences. Electrical stimulation of the VFN in humans suppresses the spread of epileptic seizures (Cooper et al., 1974; Cooper and Upton, 1985). We used fMRI to assess the relationship between behavioral measures of limbic kindling and blood volume in the VFN of young adults with a history of childhood abuse and found a strong correlation between VFN blood flow and kindling (Anderson et al., 1999; Teicher et al., 1993); early abuse seems associated with a functional deficit in limbic-VFN networks. Converging data suggest involvement of VFN abnormalities in various disorders including depression (Fischler et al., 1996; Lauterbach, 1996; Beauregard et al., 1998), schizophrenia (Loeber et al.,1999; Jacobsen et al., 1997),
autism (Courchesne et al., 1991) and ADHD (Berquin et al., 1998). The VFN innervates the locus coeruleus (LC), ventral tegmental area (VTA), substantia nigra (SN), and midline raphe, cell body regions of the dopaminergic, noradrenergic and serotonergic pathways (Reis & Golanov, 1997; Snider & Maiti, 1976; Snider et al., 1976). We also found a strong dose-dependent effect of methylphenidate on blood flow in the VFN of ADHD children (Anderson et al., 2000). Pettigrew (1998) shows that binocular rivalry occurs between, not within, cerebral hemispheres, and that the rate of perceptual rivalry is slow in bipolar disorder. Pettigrew's interhemispheric "sticky switch" in manic depression could be due to VFN pathology observed in bipolars (Lauterbach, 1996). The VFN complex projects to pons and reticular formation sites where network cascades are easily activated. Fastigial electrical stimulation desynchronizes EEG, characteristic of the behavioral states of REM sleep and attention orienting. Snider (1976) demonstrated direct and indirect projections from the VFN to the LC (Ruggiero et al., 1997) and paragigantocellularis (Astier et al., 1990) and parabrachial nuclei (Supple & Kapp, 1994). All regions that could contribute to desynchronized EEG and facilitate cortical binding. Ushur (1999) proposes that electrotonic coupling within the LC plays a role in attentional modulation and regulation of goal-directed versus exploratory behaviors. This electrotonic syncytium structure may represent the fingerprint of dynamical internal models in the cerebellum (Imamizu et al., 2000). Makarenk (1998) demonstrates that synchrony of inferior olive neurons arises from chaotic subthreshold oscillations. These neurons, while having maximum functional permissiveness, can also transform rapidly into robustly determined functional patterns of multicellular coherence. Along with a hypothesis of how pontine organization may be controlled by the cerebellum for binding assemblies of cortical- striatal-thalamic loops into coherent motor strategies (Schwarz & Their, 1999), these findings suggest that consciousness (in terms of motor patterns) may develop in the spatial-temporal chaos of phase synchronized pontine olive ensembles.

Drug addiction is also associated with early child abuse, ADHD and bipolar disorder. A potent anti-addiction drug, ibogaine, causes hallucinations, cerebellar tremor, transient ataxia, and vermal lesions in rats. Ibogaine strongly activates climbing fiber activity in VFN Purkinje cells (O’Hearn & Molliver, 1997). Hallucinations associated with ibogaine treatment indicate impairment of the cerebellar efferent copy mechanism. Subjects may then sleep for 24 hrs and awaken free from addiction (Kovera et al, 1999), suggesting a connection between ibogaine action and changes in the fractal organization of REM sleep (Anderson, 1998). The cerebellar vermis is most active during REM, especially in human infants (Chugani, 1998). Schlesinger et al. (1998) found that REM deprivation implicated VFN function in postural control and attention. Interpreted in the context of vertically convergent fractal time processes, early stress appears to disrupt organization of fractal REM patterns, leading to alteration of patterns of nuchal atonia occurring during REM sleep in fetuses and neonates (Anderson, 1995; Anderson et al., 1998); suggesting a connection between REM sleep, the VFM and cognitive/emotional synergy. Our hypothesis is that early stress results in pathological fastigial regulation of chaotic spatial-temporal patterns of pontine olive ensembles. As the VFM appears to influence the architecture of REM sleep, abnormal spatial-temporal patterns lock into a negative feedback loop, with further disorganization of pontine olive ensembles. Ibogaine, by overdriving VFM climbing fiber activity, breaks these cycles, resulting in REM rebound and the flooding of abuse memories as efferent copy mechanisms are reset during the treatment. Thus the VFN may represent a key node in the interface of limbic-brainstem network oscillations and self-organized attentional/orienting mechanisms with dynamic internal motor schemas during our ongoing emotion-laden experience of consciousness.

Consciousness and the Cerebellum
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If the cerebellum plays a coordinating and synchronizing role in the brain, this role must be an important determinant of the structure of conscious processing, because conscious processing is a whole brain activity of a self-organizing system. That consciousness does not result from passive stimulation is clear since occipital activity alone does not yield perceptual consciousness (Aurell 1989; Posner & Rothbart 1995; perceptual studies by Mack & Rock 1998 also entail this). Moreover, cerebellar activity is similar for abstract thought, physical movement, or imagination of physical movement (Ito 1993); this suggests that the cerebellum
subserves intellectual operations, and that intellectual understanding is an extension of manipulation of action affordances (Newton 1996).

Wakefulness results from synchronization of wave patterns in diverse regions, especially between the thalamus and the cortex (Asimov 1965). Since the cerebellum controls widely distributed synchronizations, it is crucial for the difference between sleep and wakefulness; hence again, for consciousness. Equally important, coordination between hippocampus and other subcortical regions, and the effect of this coordination on the extended reticular thalamic activating system (ERTAS), which tunes the thalamus to select for incoming stimuli with emotionally important action affordances, is also needed for perceptual consciousness. Occipital processing alone is not conscious; other areas, including anterior areas such as anterior cingulate and frontal and parietal lobes; must be activated in response to input from emotional brain areas; since this activity involves widespread synchronization, the cerebellum also plays a part. If consciousness begins with action affordances, or Damasio’s (1999) as if body loop, then the cerebellum is pivotal for consciousness.

The hippocampus shows an event related potential within 20 ms. of a perceptual stimulus (Coles 1990), indicating subcortical activation with wave synchronization phenomena, this implies cerebellar involvement as well: the first occipital ERP does not begin until around 100 ms. Rather than anterior and subcortical activation’s being a response to an occipital stimulus, this activity must already have taken place prior to consciousness. ERTAS, guided by emotional subcortical purposes, determines registration of perceptual input in consciousness.

When a visual stimulus is unexpected, there is a 1/4 second delay from occipital processing to the other brain processes needed for perceptual consciousness (Srebro 1985) C too long to be explained by the speed of spreading activation. The delay allows emotional areas to activate thalamus, frontal and parietal areas in response to hippocampal and cerebellar tuning toward relevant action affordances; this “looking for” activity has already begun prior to occipital effects on perceptual consciousness (since the occipital P200 has not yet occurred). Even in involuntary attention and in cases of frontal lobectomy, the limbic system selectively gates incoming stimuli according to general motivational purposes via subcortical control of neurotransmitters, tuning the thalamus (Damasio 1999; Faw forthcoming) and allowing consciousness rather than blindsight. Persons with no anterior cingulate are in vegetative states (Damasio 1999), so even involuntary attention is impossible without it.

This reverses traditional thought about the causal ordering of brain events: perception was thought to drive emotion, which in turn drove action. Instead, the organism must first be geared up to seek important data, the most fundamental of which involve action and thus cerebellar functions. Subcortical tuning activates frontal and limbic regions to form preconscious image schemas associated with important perceptual categories, prior to processing of the stimulus. If the stimulus resonates with this self-generated activity, a more vivid image is formed, and one that is felt as the image of a present perceptual object rather than as an image (Aurell, 1989).

In tracking a soccer ball, expectation is at each moment motivated by categories of utility and retention of the ball’s previous location. When the ball suddenly turns up where we are not looking, we do not see it, but have a vivid image of where it should have been. It then takes a fourth of a second to find the ball. It catches attention by presenting affordances to the motivated organism. Self-organization must be holistically coordinated, requiring cerebellar synchronizations. Since perception is motivated by utility (Newton 1996) and frontal and parietal areas are tuned by emotional areas (hypothalamus, hippocampus, cerebellum, amygdala), we see the sinister smile without noticing its sinister details; we note a room=s disorder but not the crooked picture frame that makes it disorderly (Merleau-Ponty, 1942, p. 173).

Emotion is not sufficient for consciousness. Plants and low animal species have organismic purposes, but little consciousness. Consciousness occurs only when emotion combines with representation, occurring not passively but as an activity of the organism. Emotional agnosics cannot represent what emotions are “about.” We are conscious of emotions through representation. Even unconscious emotions still drive the representational processes in which we do engage, and even pure curiosity is an emotion that motivates us to explore our environment and represent what is there (Panksepp 1998).

References


