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‘Motor cognition’ – what is it and is the cerebellum involved?

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Abstract

Motor cognition encompasses how we understand our own movement, and how movement helps us to understand the world. Here, the role of the cerebellum is discussed in two processes that could be considered aspects of motor cognition: predicting movement outcomes and understanding the meaning of movements. Recent behavioral, anatomical, and neurophysiological findings related to these processes are discussed. There are data to support a cerebellar role in predicting movement outcomes, which could be used both for motor control and for distinguishing sensory inputs due to our own movements from external influences. The data for a cerebellar role in understanding the meaning of movement are mixed, although anatomical findings suggest that it probably has some influence that bears further study.

Keywords

movement; prediction; autism; schizophrenia

Introduction

The human motor system is typically viewed as a network existing only to make movements accurate and efficient. Such a control system would carry out actions driven by a person's perception, intent, and understanding, but would not be involved in generating those mental states per se. While this scheme may be partially, or even largely correct, recent evidence suggests that the motor system does more. Here, the role of the motor system, with emphasis on the cerebellum, is reviewed as not only a movement controller, but as a structure involved in motor cognition.

The term ‘motor cognition’ is broad. ‘Cognition’ stems from the Latin term *cognoscere*, meaning ‘to know’. Thus, motor cognition could refer to anything that we know about movement – i.e., any information about movement that reaches the brain, even if this information does not reach consciousness. In this way motor cognition can be viewed as a means by which movement helps us to know something about ourselves, others, or the world. While there are other potential roles for the cerebellum in motor cognition, this review will discuss two specific cognitive phenomena that could be part of cerebellar

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function: predicting movement outcomes and understanding the meaning of movements. These processes, perhaps more so than other processes for which cerebellar involvement is hypothesized, contribute significantly to our abilities to interact with our environment, learn about the world, and develop healthy social relationships. Experimental evidence and theories about the role of the cerebellum in these processes will be highlighted.

Predicting movement outcomes

Consider the following situation: You sit in a dark theatre watching a scary movie. As you reach from one hand to the other to grab some popcorn, you inadvertently bump your own arm. Are you at all startled? Of course not. But if the person seated next to you does the same thing (perhaps intentionally during a suspenseful part of the film), it might frighten or at least surprise you.

It is thought that the brain normally predicts how our own movements will unfold based on an efference copy of motor commands and an initial estimate of the body state (e.g., position, velocity of a limb) (1). In other words, the brain does not wait for the sensory signals that result from a movement in order to know where the body is. It instead predicts where a movement will go. This ‘forward’ model of the body is important for efficient movement control because it allows a rapid comparison of the predicted and desired movement trajectories, which can drive early motor corrections and help the brain to learn optimal calibrations (2).

This computation also helps us perceptually – it allows one to distinguish whether a sensory signal is due to one's own movement versus something external that should be attended to (3). In many cases, the sensory signals from our own movement might best be attenuated, as in the example situation above, so that external stimuli are emphasized. This process of canceling re-afference, proposed by von Holst and Mittelstaedt as the ‘principle of reafference’ (4), is now thought to involve the cerebellum (5–7).

The evidence for cerebellar involvement in this process stems from work in lower animals and in humans, and spans different sensory systems. One of the best examples comes from studies of fish that use electrosensory information to ‘see’ nearby objects in the water. These animals actively generate an electric field around themselves via an electric organ, and then use electroreceptors to read out distortions that indicate the presence of nearby objects. Since electroreceptors are positioned along both sides of the body, their own swimming movements, respiration, and the pulsatile nature of the electric organ discharge itself could be interpreted as an alteration in the environment (8). To deal with this ambiguity, these fish adaptively filter out predictable features of electrosensory information – that is, they cancel reafference due to their own motor output (5,9,10). This process allows them to detect real objects of relevance (e.g., prey), and is known to depend on cerebellum-like structures called the electrosensory lobes (5).

It should be noted that the sensory cancellation in this system is not immediate; it is adaptively tuned over minutes of exposure to predictable events, resulting in the generation of a ‘negative image’ of predicted inputs. This is known to occur at the level of parallel fiber synapses with the principle output cell of the cerebellum-like structure (8). This adaptation also leads to after-effects when the predictable event is removed. It is not yet known whether similar processing occurs in the cerebellum itself, though it seems plausible.

Behavioral and neuroimaging studies demonstrate some similarities in the sensory attenuation phenomena that occur in humans, and that the cerebellum is likely involved. One relevant observation is that an individual's feeling of ‘ticklishness’ is markedly attenuated if the same tactile stimulation is self generated versus externally generated (11). In other words, it is harder to tickle yourself. This was further studied by Blakemore et al. to determine whether attenuation relates to a prediction about a specific motor command (i.e., only that which could produce the sensation) or something more general about concurrent movement. They found that the attenuation of ticklishness requires spatial and temporal congruency between the motor command and sensory outcome – evidence that the predictive motor mechanisms were indeed important (12).

In a related neuroimaging study, cerebellar cortical activity was found to be reduced during self-generated versus external tactile stimulation. The authors interpreted this as evidence of cerebellar involvement in sensory prediction, which then leads to reduction of activity the somatosensory cortex (6). The anatomical connection by which this could occur remains to be shown, as it is not known if the primate cerebellum projects (via thalamus) directly to the secondary somatosensory cortex.

Recent human work confirms and extends these observations to the visual system (7). During smooth pursuit eye movements, retinal signals reflect the movement of the eye as well as movement of the environment. In order to optimize perception of the environment, it is important to cancel the self-generated image motion. The brain is able to predict this self-generated motion using an efference copy of motor commands to the eye as well as information about visual context. In an interesting paradigm, Lindner et al. have shown that activity within area Crus I of the lateral cerebellum is related to the predicted self-motion signal. Cerebral cortical areas, such as the supplementary eye fields and parieto-insular cortex, were coupled to the cerebellar activity, and the authors suggest that they might be sites where the actual sensory cancellation occurs (7).

In sum, there is convergent evidence from animal and human studies suggesting that the cerebellum predicts movement outcomes. This information is critical for movement control (as recently reviewed by Bastian (13)), but as discussed here, is probably also important for interpreting sensory signals and even for sensory perception. Though the results described here have similarities, there are some clear differences. Sensory cancellation in the electric fish is adaptive – it is learned over minutes. This is also true of the visual cancellation study by Linder et al. (7), but does not seem to be true of the tactile attenuation studies of Blakemore et al. (6,12). The tactile attenuation appears to be more obligatory. Sensory cancellation in the electric fish also can occur for any repeating or predictable stimulus – it does not have to be self-generated. It is not known whether this is true of the human system, as the studies cited here all involve cancellation relating to a person's own movement.

While the specifics remain to be determined, the cerebellum certainly appears to play a role in predicting movement outcomes. One could ask, then, whether cerebellar predictive mechanisms (i.e., a forward model), are important for predicting not only our own motions, but also the actions or even intentions of other people? The idea that a forward model would be useful for this process has been proposed (3), but not tested. Related issues are discussed in the following section.

Understanding the meaning of movements

Recently, a great deal of attention has been focused on whether the parts of the brain involved in generating our own movements also help us to interpret the meaning of other individuals' movements. This idea largely originates from neurophysiological studies in monkeys showing a class of neurons that respond when the animal makes a particular movement and also when it observes other individuals performing the same movement. In fact, some of these neurons respond even when the animal does not actually observe the movement – activity can be driven if the animal thinks that the movement has been performed (14). These ‘mirror neurons’ can be found in the frontal and parietal lobes, most prominently in the ventral premotor cortex (PMv) and area 7b in the anterior portion of the inferior parietal lobule (IPL) (15).

Neuroimaging results suggest that humans also have a ‘mirror system,’ comprising brain areas that are active during one's own movement, when observing the movement of others, and during imitation (16). Human cortical areas that display these properties have been found in human ventral premotor cortex, Brodmann's area 44 (i.e., Broca's area), and in the rostral inferior parietal cortex (17). The mirror neuron system in humans might be important for learning through imitation and also for understanding the actions of others, as recently reviewed by Iacaboni and Dapretto (18).

Could the cerebellum also be involved in this type of processing? Anatomical studies in monkeys have shown that different regions of the dentate nucleus of the cerebellum projects to PMv (19) and area 7b of the inferior parietal lobule in monkeys (20). This raises the possibility that the cerebellum could influence mirror neurons in these regions. Yet, there are no reports of mirror neuron properties in the cerebellar cortex or dentate nucleus. It is not clear, though, that mirror neuron properties have ever specifically been tested for in the cerebellum.

A recent human neuroimaging study argues that the cerebellum could be considered a part of the mirror network. Calvo-Merino and colleagues asked a general question about the human mirror system: Does it really use a representation of motor commands in order to understand action, or do processes of visual inference and knowledge underlie this ability? To answer this, they studied male and female ballet dancers as they watched videos of different ballet moves (21). Many moves are gender-specific – only men or women perform them even though both genders have good visual knowledge of them. This study reports that the mirror system became more active when dancers watched the moves from their own gender's repertoire, versus those of the opposite gender, with which they were equally visually familiar. The active network comprised premotor, parietal, and cerebellar regions. Thus, motor command representations do indeed drive the mirror system, which appears to involve cerebellar contributions.

What could those contributions be? The cerebellum is known to be necessary for practice-dependent motor learning across many movement types (22–26). Perhaps it is also important for learning movement through observation of other individuals' actions. Rats can learn the spatial pattern associated with a Morris water maze simply by watching another rat perform it many times. It has been reported that cerebellar lesions abolish this ability (27). Specifically, cerebellar damage impaired how the animals searched for the platform in the water, rather than altering the gross motor pattern of swimming. Leggio and colleagues suggest that the role of the cerebellum may be to help sustain the rehearsal of cortical processes of action in the absence of any overt movements.

Or, is the cerebellum part of a network that makes predictions about the outcomes of another individual's movements? Such predictions allow for a more rapid assignment of meaning to movements and in turn more efficient responses. Anticipating the actions of others can rely on plans related to one's own actions (28), and therefore might involve overlapping brain networks. The PMv has been shown to be active when predicting the actions of others during a visually cued motor task, but cerebellar activity was not observed (29). Thus, it would seem that the cerebellum is not important for that process. In that study, the visual cues were abstract computer generated symbols, and no actual human motion was observed. There are studies, however, where cerebellar activity occurs in response to biological motion (30), or when motor rehearsal is required (31). Because cerebellar activity it not always seen during motor observations (32), further studies are clearly necessary to uncover what role, if any, the cerebellum plays in understanding the actions of others.

Disorders of motor cognition

With evidence suggesting that the cerebellum is involved in predicting the outcomes and understanding the meanings of movements, questions can be posed as to what role the cerebellum may play in certain disorders that affect motor cognition.

Schizophrenia, for example, is a disease that can cause delusions and misattribution of one's own movement to an external source. A recent study showed individuals with schizophrenia to have reduced attenuation of self-produced versus external tactile stimulation (33). It is possible that this could be due to poor prediction of movement outcomes, which involves the cerebellum. Yet, people with focal cerebellar damage do not show such misattributions, suggesting the schizophrenia deficit may have more to do with *use* of the prediction for cancellation, a function possibly done by cerebral areas.

Motor cognition appears to also be dysfunctional in autism spectrum disorders. Many individuals with autism experience abnormal sensitivity of the senses, notably hypersensitivity to touch (34,35). This tactile hypersensitivity may be caused by an inability to correctly attenuate sensory signals due to faulty movement predictions, suggesting either impaired cerebellar contributions or misuse of intact contributions. Interestingly, in a recent study Asperger patients rated all types of tactile stimulation as more tickly and intense than controls, but both groups rated self-produced touch as less tickly than external touch (35). This suggests, then, that at least some predictive mechanisms may be intact in autism spectrum disorders.

Other evidence suggesting motor cognition impairments in autism includes deficits in visual processing of biological motion and deficits in imitation. It has been shown that autistic patients are impaired at perceiving biological motion in point-light animations (36). For imitation, impairments in autism are a robust finding that cannot be accounted for by unpracticed motor skills or by generalized difficulty with motor planning (37). What could account for imitative deficits, as well as deficits in the perception of biological motion, is an impaired ability to understand the meaning of movements. Thus, a potential role of the mirror neuron system has been proposed in autism (38). In support of this, a recent fMRI study found that autistic children showed less activity in mirror neuron areas during the observation and imitation of facial expressions compared with controls (39).

It should be noted, however, that there is no direct evidence that the cerebellum is involved in the impairments of motor cognition that are observed in autism, though it is theoretically possible. Cerebellar damage, specifically Purkinje cell loss, is a consistent postmortem finding in individuals with autism (40). As in the case of schizophrenia, a better understanding of the role the cerebellum plays in motor cognition could lead to a better understanding of how that role may be irregular in autism.

Conclusion

The purpose of this review was to discuss cerebellar function as it relates to motor cognition. Since motor cognition could represent countless things, the focus here was on two phenomena – predicting movement outcomes and understanding the meaning of movement. There is clear evidence for the role of the cerebellum in predicting one's own movement outcome. This is important not only for motor control, but also for understanding whether sensory signals are due to an external source. The evidence for cerebellar involvement in interpreting the meaning of movement is less robust. Yet, the cerebellum projects to cerebral cortical areas thought to be important for understanding movement meaning (PMv and IPL), making it a likely participant in some aspect of this process. Future work should explore when and how the cerebellum contributes to these aspects of motor cognition, as well as how symptoms observed in disorders involving motor cognition may be linked to cerebellar abnormalities.

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