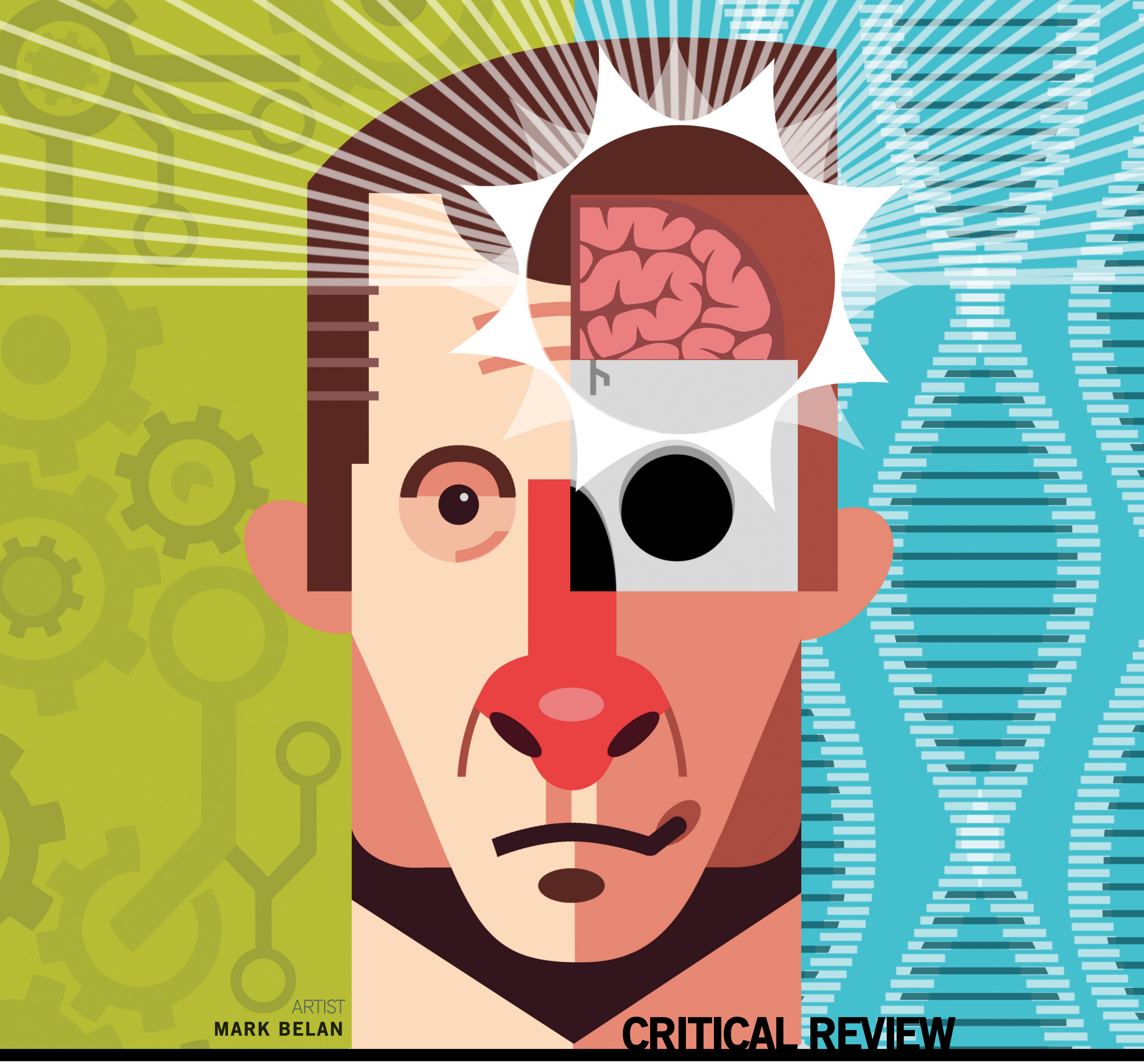

Internal Models of Motor Control

REACH ADAPTATION TASK AND AUTISM

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ABSTRACT The internal models theory is one of many hypotheses that aim to explain the mechanism of motor control in humans. The theory proposes that the central nervous system (CNS) forms neural representations of the external world, which are used to predict and adjust movements.[1,2] Internal models have been well-studied, and this paper provides a general insight into the internal models theory before examining how subjects adapt during a reaching task.[3] This reaching task, as explained via the internal models theory, will be compared between normal and disease states, specifically autism, a disorder of neural development. Through this comparison, it will be possible to determine how autistic patients differ in their motor abilities.

THE THEORY OF INTERNAL MODELS

An early theory of how humans control their movements is the feedback learning theory. The feedback learning theory suggests that when a motor instruction is given, the brain receives sensory feedback outlining the effects of that movement, to which it bases future decisions (Figure 1a).[1] However, the sole reliance on post-movement feedback to make future motor decisions is too slow and cannot predict outcomes. For these reasons, it fails to explain how humans make fast and coordinated movements.[1,4] The internal models theory accounts for these limitations, making it the front-runner in the explanation of complex motor movements.

Internal models of motor control are neural representations of the external world used to predict and adjust movements.[1,2] Internal models are formed in the cerebellum through learning and are adjusted as movement is repeated.[1,2,5] The internal models theory includes two components: a forward and an inverse model. The forward model is a feed-forward system whose goal is to predict the consequences of a motor command (Figure 1b).[1,2,5] Forward models are stored in the cerebellum and predict the likely sensory feedback that would result from a movement.[1,6] They make these predictions using the body's current state, a model of the system, and an efference copy of the motor command.[7,8] An efference copy is a duplicate of the motor command, containing a motor command's predicted movement and resulting sensations.[5] For example, if the motor command was to move one's arm, the efference copy would contain the predicted sensations resulting from the movement (e.g., position of one's Golgi tendon organs). The output, or prediction, from the forward model is then compared with the actual position of the body following movement. The actual and predicted body positions may differ due to noise introduced into the system by either internal sources (e.g., from sensory systems) or external sources (i.e., forces acting on the body).[1,5] Efference copies enable the forward model to distinguish between these external and internal signals by comparing the outgoing predictive signals to post-movement feedback.[5]

FOR EXAMPLE, WHEN TICKLING ONESELF, AN EFFERENCE COPY OF THE TICKLING MOTOR COMMAND IS SENT TO THE FORWARD MODEL TO PREDICT THE LIKELY SENSORY OUTCOME ONE WOULD EXPECT.[10] IF THIS SENSORY PREDICTION MATCHES THE ACTUAL SENSORY FEEDBACK (WHICH IT USUALLY DOES WHEN TICKLING ONESELF), THE FEEDBACK IS ATTENUATED AND THE TICKLING IS LESS INTENSE. IF ANOTHER PERSON IS TICKLING YOU, THERE IS NO ACCURATE PREDICTION OF THE SENSORY OUTCOME AND NO MATCH TO BE MADE, RESULTING IN GREATER TICKLING SENSATION.[26]

The inverse model determines the motor commands needed to achieve a desired movement trajectory (Figure 1c).[1,2,5] It uses the desired and actual body positions as inputs to estimate the necessary motor commands that would transform the current position into the desired one.[2,5] For example, in an arm reaching task, the desired position of the arm is inputted into the inverse model, which generates the motor commands necessary to control the arm and bring it to the desired position. Motor command signals generated by the controller can reflect feedback errors, as any discrepancies between the limb motor output and instruction signals indicate a malfunctioning internal model.[1]

It is suggested that proprioception helps build an internal representation of one's arm and its dynamical properties.[9] In the internal model, error comparison between the proposed and actual sensory feedback usually involves multiple sensory modalities (e.g., visual, proprioceptive, somatosensory).[5] The relative importance of proprioceptive versus visual feedback in forming an internal model is still being explored, though one thesis dissertation found that the process primarily depends on proprioceptive cues from the limb (although visual information did provide additional benefits to learning).[10] Other research also suggests a distinction between kinematic and dynamic internal models, which are mediated by vision and proprioception respectively.[2]

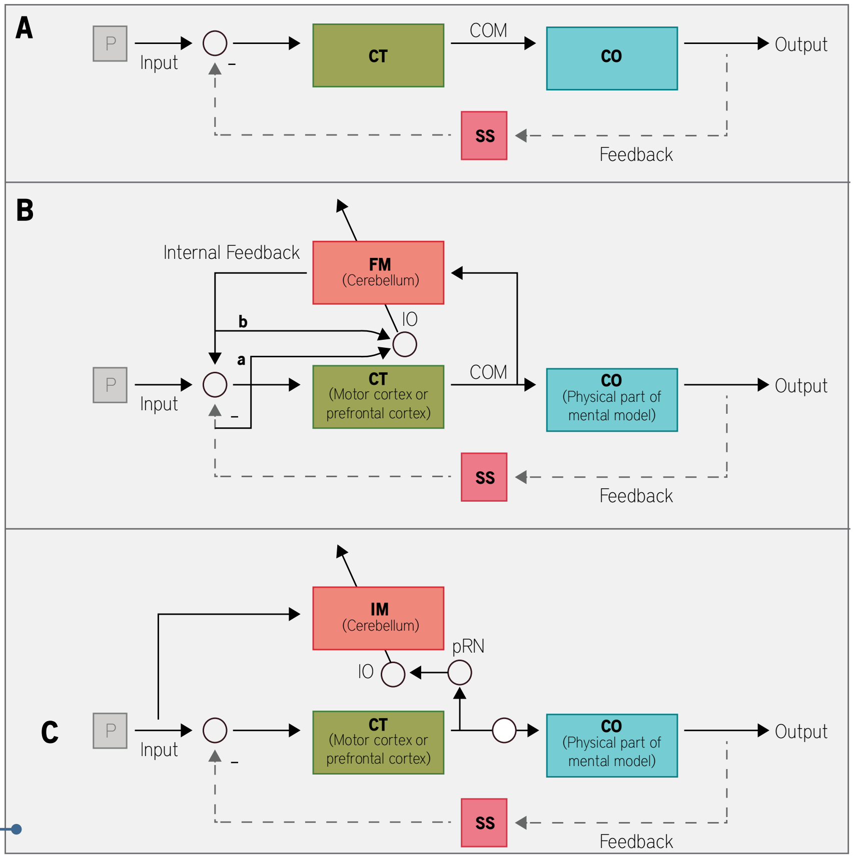

FIGURE 1: The Feedback, Forward, and Inverse Models.[1]
A) *The feedback control system.* An instructor (P) gives an instruction to the controller (CT) that provides a command (COM) to manipulate a controlled object (CO). The sensory system (SS) provides feedback to the controller (dashed line).
B) *The forward model control system.* The outputs of the CT and CO (via SS) are compared with the forward model's predictions to derive an error signal. This real-time comparison happens in the inferior olive (IO) and is sent to the forward model to modify it.
C) *The inverse model control system.* Feedback errors are derived from the CT-generated COM signal and tune the dynamics of the IM. The paraventricular red nucleus (pRN) acts as a relay.

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Localized U-fiber connections between adjacent brain regions contain proprioceptive inputs to the internal models, whereas distant cortical and subcortical connectivity contains visual feedback inputs.[11]

LEARNING TO CONTROL A NOVEL TOOL: REACH ADAPTATION

The goal of reaching is to transport the hand to a specific environmental location for meaningful object manipulation.[12] Reaching begins early in post-natal development – as early as at the age of 3 to 12 weeks (although movement may be poorly coordinated and jerky).[12] Through error learning, infants develop smoother hand paths, greater hand speed, less inter-trial variability, and improved accuracy. [12] Kinematic improvements during the development of reaching reflect an increasing ability of the child to rely on their internal model of the limb when organizing the movement.[12,13] Research supports the involvement of internal models in reaching. Clifton *et al.*[14] found that infants develop reaching at similar ages in both light and dark conditions.[14] Since the dark provides no visual feedback, an internal representation of the limb must be available at the onset of reaching behaviours.[14] Further, as a child ages, errors decrease and fewer experimental trials are needed to attain complete adaptation during motor tasks—indicative of a more developed internal model.[15]

The evidence for internal models in a reaching task relies on the concept of error-based learning. After one establishes a goal and begins to reach (e.g., to pick up a cup), the sensorimotor system compares the movement outcome to the desired outcome, producing a sensory prediction error.[3,12,13] This error tells the system if, and in what way, the hand missed the target—allowing the forward internal model to make real-time movement corrections to ensure the target is reached.[3]

The body's adaptation of reaching movements has been studied by exposing subjects to novel force fields or visual perturbations. To do this, subjects move their arms towards a target that they see on a computer screen, while grasping a handle hooked up to a robotic arm. The robotic arm can apply different forces, and visual perturbations are introduced by changing the target image the subject sees on the computer screen.[16] Initial movements under the perturbed conditions are error-ridden, but gradually straighten with adaptation. The CNS adapts quickly, and it can learn from error on a single trial.[16] For example, Gidley Larson *et al.*[17] examined children's learning ability in manipulating a robotic arm (exerting a novel force) to aim for targets projected on a screen.[17] The catch trials (random, unperturbed trials within a series of perturbed trials, or field trials) illustrated mirror-image aftereffects. These aftereffects indicate that subjects learned and formed a predictive internal model to anticipate the effects of the force field on the reaching task.[17]

AUTISM AND THE REACH ADAPTATION TASK

Autism is a pervasive developmental disorder with a strong genetic basis.[18] Symptoms must be noticed before 3 years of age and typically include: impaired social interaction, behavioural stereotypes (e.g., repetitive behavior such as hand flapping), delays in motor milestones, and a large range of cognitive deficits.[18,19] Motor impairments are not part of the formal diagnosis of autism, though they are among the earliest symptoms.[20] Motor signs commonly include poor muscle tone, incoordination, poor balance and dexterity, the presence of motor stereotypes, imitation impairments, and a lack of anticipatory postural adjustments.[20,21,22] Although the specific cortical abnormalities in autism are still being elucidated, it has been shown that the cerebellum is a constant site of neuroanatomic abnormality—more than 95% of cases show cerebellar pathology.[20,21] This is commonly caused by a decrease in Purkinje neurons (the inhibitory output cell), although reductions in Purkinje cell size and molecular and receptor abnormalities have also been reported.[20,21] The cortex of autistic patients also has altered nerve cell synapse connections and organization.[20,11] This usually presents as overgrowth in localized cortical connections.[11,23]

The reach adaptation task in autistic children can be compared to controls. Gidley Larson *et al.*[17] assessed learning ability in manipulating a robotic arm in typically developing and autistic children.[17] Despite the usual cerebellar abnormalities in autistic patients, both autistic and normal children adapted and formed internal models. This was demonstrated through reduced errors in field trials (the regular, perturbed trials) and increased errors in catch trials over time.[17] Thus, autistic subjects are able to form internal models, and the anomalous pattern of motor learning must result from an error in the process, such as the balance in the use of proprioceptive or visual feedback.

Haswell *et al.*[23] used a similar task to investigate this phenomenon and concluded that children with autism spectrum disorder (ASD) have a stronger-than-normal reliance on proprioceptive feedback when generating motor commands.[23] This reliance on proprioception may result from the typical overgrowth in localized cortical connections seen in autistic brains.[11,23] Alternatively, autistic patients may be forced to rely on proprioceptive information due to deficits in visually-guided action—causing a localized cortical overgrowth. Regardless, Haswell *et al.*[23] further demonstrated that a greater use of proprioceptive feedback correlated with greater impairments in social interactions and observational learning, which rely on visual cues.[23] Interestingly, one study found that autistic patients, and not controls, transferred adaptation to perturbed conditions to a non-adapted hand.[24] This further demonstrates a focus on proprioceptive information instead of real-time visual feedback to execute movements during the adaptation phase.[24] Increased proprioceptive feedback relative to other sensory modalities could result in an abnormal error comparison.[17] This would likely change how the internal model is fine-tuned (though changes were not observed in Gidley Larson *et al.*'s[17] study, possibly due to an unrepresentative sample due to the sole participation of high functioning autistics).

Autistic patients' reliance on proprioceptive signals also provides some explanation for the observation that autistic children are 'blind while seeing and deaf while hearing'.[24] Increased proprioception may suppress other sensory information, limiting visual and auditory processing.[24] This likely affects an autistic child's observational learning and their success in social situations. Other research also suggests a distinction between kinematic and dynamic internal models, which are mediated by vision and proprioception respectively.[2] Besides the large range in autistic symptoms, this could also explain why some studies show differences between autistic participants and controls in internal model formation and other studies do not. Studies where visual feedback is preferred would likely show worse performance in autistic children, since they rely on proprioceptive information. The opposite would be true when proprioceptive information is preferred. Future research should examine the autistic patient's error comparison and the role of proprioception in both kinematic and dynamic internal models.

CONCLUSION

According to the internal models theory, the CNS develops an internal representation of the body in reference to a task. Forward and inverse models are used to predict sensations and correct movements without delay. These models can be combined to facilitate more complex movements. Internal model formation is typically demonstrated through the adaptation that occurs during an arm-reaching task. Conflicting results have emerged with regards to autistic patients' performance when reaching, likely due to the great variability of symptoms in patients. However, strong evidence suggests that autistic patients rely more heavily on proprioceptive feedback when generating movements. This is supported by neuroanatomical abnormalities (increased localized connections), and can ultimately influence their error comparison and internal model function. A greater understanding of the autistic brain and internal models is necessary to determine where exactly deficits arise. Continued study will likely provide improved diagnostic and clinical treatments for autism.

REVIEWED BY SEAN RASMUSSEN

Sean Rasmussen is a M.D./Ph.D. candidate in the MINDS program at McMaster University working in the lab of Dr. Michael Mazurek. His research makes use of rat models to study the monoaminergic effects of various drugs used for the treatment of schizophrenia, depression, and bipolar disorder.

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