

Adaptive Model Theory: Modelling the Modeller

Peter D. Neilson & Megan D. Neilson

The human brain is an analogical modelling device. It forms adaptive models of the environment and of the body in interaction with the environment and it uses these models in the planning and control of purposive movement. The movement system includes the entire musculoskeletal system in interaction with the environment. There are some 700 functional muscles (groups of muscle fibres with the same mechanical action that are controlled independently by the nervous system) controlling about 110 elemental movements. From the perspective of the brain, the system to be controlled consists of three multiple input–multiple output nonlinear dynamical systems connected in cascade (i) muscle control systems (muscles and their reflex systems), (ii) biomechanical system (biomechanical loads on muscles), and (iii) external systems (external world). Sensory systems continuously monitor the input and output signals of all three of these subsystems and form adaptive models of the nonlinear dynamical relations within and between the various sensory modalities involved. The brain compares model predictions with actual sensory signals (afference) and takes discrepancies very seriously. Discrepancies lead to an increase in brain activity as the brain analyses errors and attempts to update its models. It also defends against perturbations by slowing movements and stiffening.

While it can be demonstrated behaviourally that the nervous system forms these adaptive models, many technical issues stand in the way of understanding computationally how it does so. Not least of these technical issues is the large amount of redundancy in afferent signals. Tens of thousands of receptors are involved in detecting, for example, muscle tensions and elemental movements. It is not possible to form accurate models of multiple input–multiple output systems when the inputs are strongly interrelated, and it is not possible to form accurate inverse models when the number of outputs is less than the number of inputs or when the outputs are contaminated with large amounts of noise. Because of this the nervous system has to remove redundancy from afferent signals and extract well-conditioned signals suitable for adaptive modelling.

It does this in two stages involving (i) slow adaptation and (ii) fast adaptation, respectively. (i) Slow adaptation involves correlational-based mechanisms of synaptic plasticity in networks of neurons connecting sensory receptors to the cerebral cortex (sensory pathways). Over several weeks to months, correlational-based mechanisms of synaptic plasticity lead to the adaptive formation of sensory maps in the cortex. In the somatosensory cortex, for example, maps of elemental movements and of the lengths and tensions of functional muscles are formed. Similar sensory maps for all other sensory modalities are formed in other cortical areas of the brain.

(ii) According to Adaptive Model Theory, fast adaptation depends on the existence of networks of neural adaptive filters within every sensory modality. The tuneable input-output transfer characteristic of each neural adaptive filter is preset in anticipation of a planned

movement by patterns of neural activity held on-line in working memory. This activity modulates the synaptic gains of neurons in the adaptive filters. The modulating activity can be transferred from working memory into intermediate and long-term memory and, given an appropriate memory selection code, can be retrieved from intermediate or long-term memory and reinstated as a pattern of neural activity in working memory. This enables the tuning of neural adaptive filters to be switched quickly and smoothly between a library of settings acquired through previous sensory-motor experience and stored in memory.

The network of neural adaptive filters within each sensory modality extracts a small number of independently varying feature signals (determined by the movement being performed) from the large number of covarying signals within the sensory map for that modality. It does this by performing a type of Gram-Schmidt orthogonalization (or QR factorization) but, instead of algebraic regression coefficients as used in these algorithms, it employs neural adaptive filters with nonlinear dynamical transfer characteristics. For example, when turning the steering wheel of a car some 20 elemental movements at the shoulders, elbows, forearms and wrists have to be coordinated to vary together in a nonlinear dynamically coupled way in order to generate a single movement feature signal corresponding to rotation of the steering wheel. The network of neural adaptive filters “learns” this coordination by adaptively modelling the nonlinear dynamical relationships between the covarying elemental movement signals in the somatosensory cortical sensory map and by extracting a single independently varying movement feature signal, the controlled degree of freedom of the task. Higher level planning and control of the movement can then be carried out within this low-dimensional subspace thereby greatly reducing demand on central processing resources. Slave copies of the same neural adaptive filters can be employed in the inverse direction to transform low-dimensional required feature signals planned centrally back into a large number of covarying elemental movements.

Similar feature extraction takes place simultaneously in every sensory modality. The resulting feature signals in each modality are then well-conditioned for forming adaptive models of the nonlinear dynamical forward and inverse relationships between them. These between-modality models are used in the planning and control of movement. For example, in steering a car, the required visual response associated with steering the car can be transformed into the elemental movements required to turn the steering wheel, thence into the muscle tensions that must be generated to produce those movements, and finally into the descending motor commands required to generate those tensions.

In this presentation we explore circuitry in cortico-cerebellar-cortical pathways in the brain capable of functioning as neural adaptive filters with third-order nonlinear dynamical transfer characteristics. We hold that Adaptive Model Theory demonstrates a means by which such circuitry can model the relationships between the incoming sensory signals despite these typically being non-Gaussian, non-white and non-stationary. In so doing the theory delineates a neurally realistic account of how the adaptive models necessary for movement control can be achieved. In that sense Adaptive Model Theory seeks to model the supreme modeller that is the human brain.

Selected publications:

- Neilson, P. D., Neilson, M. D., & O'Dwyer, N. J. (1985). Acquisition of motor skills in tracking tasks: Learning internal models. In D. G. Russell & B. Abernethy (Eds.), *Motor Memory & Control: The Otago Symposium, Dunedin, New Zealand, 1982* (pp. 25-36). Dunedin, NZ: Human Performance Associates.
- Neilson, P. D., Neilson, M. D., & O'Dwyer, N. J. (1988). Internal models and intermittency: A theoretical account of human tracking behavior. *Biological Cybernetics*, *58*, 101-112.
- Neilson, P. D., Neilson, M. D., & O'Dwyer, N. J. (1992). Adaptive model theory: application to disorders of motor control. In J. J. Summers (Ed.), *Approaches to the Study of Motor Control and Learning* (pp. 495-548). Amsterdam: North Holland.
- Neilson, P. D. (1993). The problem of redundancy in movement control: The adaptive model theory approach. *Psychological Research*, *55*, 99-106.
- Neilson, P. D., Neilson, M. D., & O'Dwyer, N. J. (1997). Adaptive model theory: Central processing in acquisition of skill. In K. Connolly & H. Forssberg (Eds.), *Neurophysiology & Neuropsychology of Motor Development* (pp. 346-370). London: Mac Keith Press.
- Neilson, P. D., & Neilson, M. D. (2005). An overview of adaptive model theory: solving the problems of redundancy, resources, and nonlinear interactions in human movement control. *Journal of Neural Engineering*, *2*, S279-S312.
- Bye, R. T., & Neilson, P. D. (2008). The BUMP model of response planning: Variable horizon predictive control accounts for the speed-accuracy tradeoffs and velocity profiles of aimed movement. *Human Movement Science*, *27*, 771-798.
- Neilson, P. D., & Neilson, M. D. (2010). On theory of motor synergies. *Human Movement Science*, *29*, 655-683.
- Neilson, P. D., & Neilson, M. D. (2013). A Riemannian geometry model of human movement: The geodesic synergy hypothesis. *Forthcoming*.