Commentary

Passive motion and active inference

Commentary on: *Muscleless* motor synergies and actions *without movements*: From motor neuroscience to cognitive robotics.

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Mohan et al [1] offer an exhaustive and compelling survey of different paradigms for understanding an embodied exchange with the world. They describe a new way of looking at motor control that has emerged over the past years [2, 3] – a view that resolves many issues with previous (optimal motor control) formulations [4, 5]. Pleasingly, this new way of looking at things picks up on historical themes that date back to the 19th century. For example, notions of synergy formation and the equilibrium point hypothesis [6, 7] re-emerge with a new simplicity and explanatory power, when one takes a holistic and enactive view of embodied behaviour. Indeed, one might trace the ideas explored in Mohan et al (*ibid*) back to foundational notions enshrined in ideomotor theory and Helmholtz's notion of unconscious inference [8, 9]. This new way of looking at things is centred on the notion of a forward or *generative model* that plays the functional role of a "plastic configurable internal representation of the body (body schema) as a critical link enabling the seamless continuum between motor control and imagery." Mohan et al (*ibid*).

Two particular formulations of this perspective include *active inference* and the *passive motion* paradigm [2, 10]. The anti-symmetry between *active* inference and *passive* motion speaks to the complementary but convergent view of how we use our forward models to generate predictions of sensed movements. This view is another example of Dennett's 'strange inversion' [11], in which motor commands no longer cause desired movements – but desired movements cause motor commands (in the form of the predicted consequences of movement). On this view, the brain uses its forward model to predict the consequences of a desired or predicted movement and then calls on classical motor reflex arcs to fulfil its predictions. This simple account of action takes us away from a control theoretic statement of the problem towards the passive motion paradigm, in which the endpoints (i.e., attracting fixed points or trajectories) in effector space drive movement. In this sense, being able to predict the consequences of movement becomes an inference or prediction problem [12, 13] that, in principle, should yield to exactly the same principles used to explain perceptual inference – hence, active inference.

The beauty of this 'strange inversion' manifests in several guises. First, it dissolves many intractable problems that attend optimal motor control and forward-inverse model formulations [14]. For example, the degrees of freedom problem [15] disappears because: "the transformation from the position node in joint space to the position node in end effector space is well posed. In contrast, the transformation in the opposite direction is ill posed." In short, "generative (body schema) networks always operate through well posed computations/transformations." Mohan et al (*ibid*).

Note a fundamental architectural implication here: In just solving the forward problem there is no need for an inverse model. In other words, inversion of the forward model – in terms of inferring the causes of somatosensory and proprioceptive afferents – replaces the dual forward-inverse architecture and all its inherent problems [14]. Mohan et al (*ibid*) illustrate this solution nicely with the notion of a "marionette with attached strings (that represent the attractor dynamics of the force field induced by the intended goal". In other words, the generative model the authors (and our own brains) have in mind is that we are creatures whose limbs and posture are *pulled* in exactly the right sort of way to keep as upright, walking and coupled in a dextrous way to the world around us. Given simple beliefs – about the invisible 'strings' or benevolent 'forces' pulling us this way and that – it is a simple matter to predict what we would see and feel under these benevolent forces (i.e., structured flows around attracting points and trajectories). These predictions – elaborated through a hierarchical forward model – then play the role of motor commands or corollary discharge that (in active inference) are realised by motor reflexes.

The nice thing about this millennial approach to motor control is that it also supplies the goals of action that are left unspecified in control theoretic accounts. The benevolent forces above can, in the forward model, be construed as forces to attracting points in effector space that, effectively, pull our bodies through space in that we expect them to be pulled if we were engaged in a particular goal directed activities. In this construction, things like 'central pattern generators' become internal prescriptions of our goals, in terms of the trajectories we predict our limbs and bodies to assume. An important aspect of this formulation is that exactly the same generative model can be used to test predictions beyond the proprioceptive domain. For example, if I ignore proprioceptive sensations from my own body, I can use exactly the same generative or predictive machinery to infer the visual consequences of movements made by others [10, 16, 17]. This means that I can re-purpose *my generative model* for my own behaviour to explain *your behaviour* – leading to a deep connection between the passive motion paradigm and action observation – and understanding [2]. An example of using generative models to recognise another's behaviour – in the context of handwriting or drawing – can be found in [10].

This commentary has emphasised the 'strange inversion' implicit in the passive motion paradigm and active inference. On this view, everything is in the game of providing descending predictions of the consequences of movement (that are nuanced by ascending prediction errors, which drive belief updating and implicit model inversion). This interpretation of recurrent message passing in the somatomotor hierarchy has led to a remarkably detailed set of proposals for sensorimotor circuits at the cortical and spinal level [18, 19]. We conclude with an example of how far this can be taken by summarising recent characterisations of the oculomotor system in terms of active inference [20]; see Figure 1.

The active inference formulation of oculomotor control depends upon finding the appropriate generative model to explain proprioceptive data from the oculomotor muscles [21-23]. The natural explanatory variables for these data are the positions of the eyes in vertical and horizontal dimensions. This is consistent with the functional anatomy of the brainstem, as the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF) represents vertical position, and the paramedian pontine reticular formation (PPRF) represents horizontal position [24-26]. Under active inference, the expected angular position of the eyes, jointly represented by these structures, must be updated by prediction errors derived from the proprioceptive input to the cranial nerve nuclei, and by errors in descending predictions about the rate of change of this position. This implies the existence of a structure that signals the initiation of a saccade (the error that must be resolved to go from stationary to moving), receives descending predictions, and is connected to the riMLF and PPRF. These criteria are met by the raphe interpositus nucleus (RIP), which interrupts its tonic inhibition of these structures at the start of an eye movement [27] and receives a descending signal from the superior colliculus [28].

Pursuing equilibrium point hypotheses, the superior colliculus is well placed to signal an oculomotor set-point. By anticipating the final position of the eyes following a saccade, it can form a prediction about the velocity of the eyes based upon their displacement from this position. This amounts to a belief that the eyes are being pulled towards the target location by some invisible force. By inducing a prediction error in the RIP, it drives updates in beliefs about position. This has consequences for proprioceptive predictions, which are then fulfilled by cranial nerve reflexes as a saccade to the anticipated location. We can take this approach further by considering how the anticipated fixation location may itself be derived [29] from a hierarchical generative model that draw inferences about ‘how I will behave’. These inferences comprise beliefs about the likely consequences of alternative eye movements, and beliefs about which of these movements is most probable. This view provides a useful perspective on the dual corticonigral [30, 31] input to the superior colliculus, and has implications for the computational roles of the cortex and basal ganglia in eye-movement control. This example illustrates how far we can get by thinking about the structure of the generative model the brain would have to employ to explain proprioceptive data from the oculomotor muscles, given some prior belief about a target fixation location.

The purpose of this example is to illustrate how having the right kind of theoretical construct helps makes sense of the neuronal processes and infrastructure that underlie the active sampling of the world: namely, *active* inference, under the prior belief that we are pulled *passively* by the right sort of forces – *beliefs* realised by our reflexes and *forces* that we might infer to constitute our ‘intentions’.

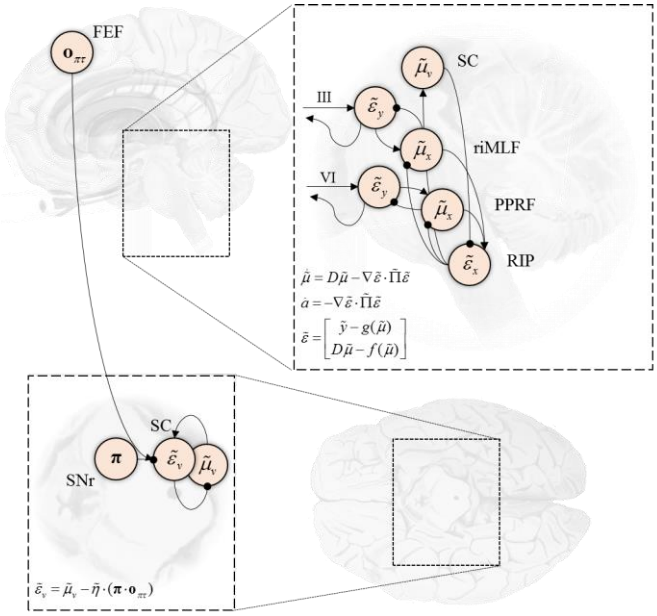

Figure 1 – Active inference and oculomotion. This schematic illustrates how the reciprocal message passing associated with a plausible generative model of proprioceptive input from the oculomotor muscles recapitulates the structure of the oculomotor system. These are expressed in terms of expectations (μ) and prediction errors (ε). The upper right box shows the superior collicular (SC) inhibition (circular arrow head) of the raphe interpositus nucleus (RIP) as a descending prediction based upon an anticipated fixation location. The prediction error

computed in the RIP is used to update beliefs about the horizontal and vertical eye-position in the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF) and paramedian pontine reticular formation (PPRF). These are reciprocally connected to the nuclei of cranial nerves III and VI that mediate vertical and horizontal eye movements respectively. These represent prediction errors in proprioceptive data that may be resolved through changing the eye position (brainstem reflexes) or by adjusting expectations about eye position. The lower left box expresses the notion that we may represent several plausible alternative outcomes ($\mathbf{o}$) of a saccade, each corresponding to a different location in space (or a different attracting point). These alternatives are modulated by the probability of performing that saccade ($\boldsymbol{\pi}$). While cortical projections from the frontal eye-fields (FEF) may identify the appropriate attracting points for each possible saccade, these must be contextualised by the evaluation of competing plans in the basal ganglia, consistent with the collicular projecting neurons of the substantia nigra pars reticulata (SNr) in the midbrain.

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