Primer

Motor prediction

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The concept of motor prediction was first considered by Helmholtz when trying to understand how we localise visual objects. To calculate the location of an object relative to the head, the central nervous system (CNS) must take account of both the retinal location of the object and also the gaze position of the eye within the orbit. Helmholtz's ingenious suggestion was that the brain, rather than sensing the gaze position of the eye, predicted the gaze position based on a copy of the motor command acting on the eye muscles, termed efference copy. He used a simple experiment on himself to demonstrate this. When the eye is moved without using the eye muscles (cover one eye and gently press with your finger on your open eye through the eyelid), the retinal locations of visual objects change, but the predicted eye position is not updated, leading to the false perception that the world is moving. The concept of efference copy was firmly established by experimental work of Von Holst and Sperry in the 1950s. Since then the idea that we predict the consequences of our motor commands has emerged as an important theoretical concept in all aspects of sensorimotor control.

In general, prediction refers to estimating future states of a system. The extent to which our CNS can influence these future states covers a continuous range. For example, most people have little influence on the behaviour of the stock market, but a great deal of influence over the behaviour of their own body. We consider motor prediction as representing predictions of systems which are directly and usually immediately influenced by our motor commands. Therefore, motor prediction could predict how our arm moves in response to a motor command, as well as how a car we are driving responds to our foot movement on the pedals. The relationship between a motor command sent to the eye and the consequences for eye position are relatively simple. However, when we consider limb motion the relationship between our motor commands and behaviour is far more complex due to the dynamics of multi-joint motion. This complexity is even greater when we consider the plethora of interactions that our bodies can engage in with the environment, such as tool use. To predict the consequences of a motor command in such complex situations requires a system that can simulate the dynamic behaviour of our body and environment. Such a system is termed an internal forward model as it is internal to the CNS, models the behaviour of the body and captures the forward or causal relationship between actions and their consequences.

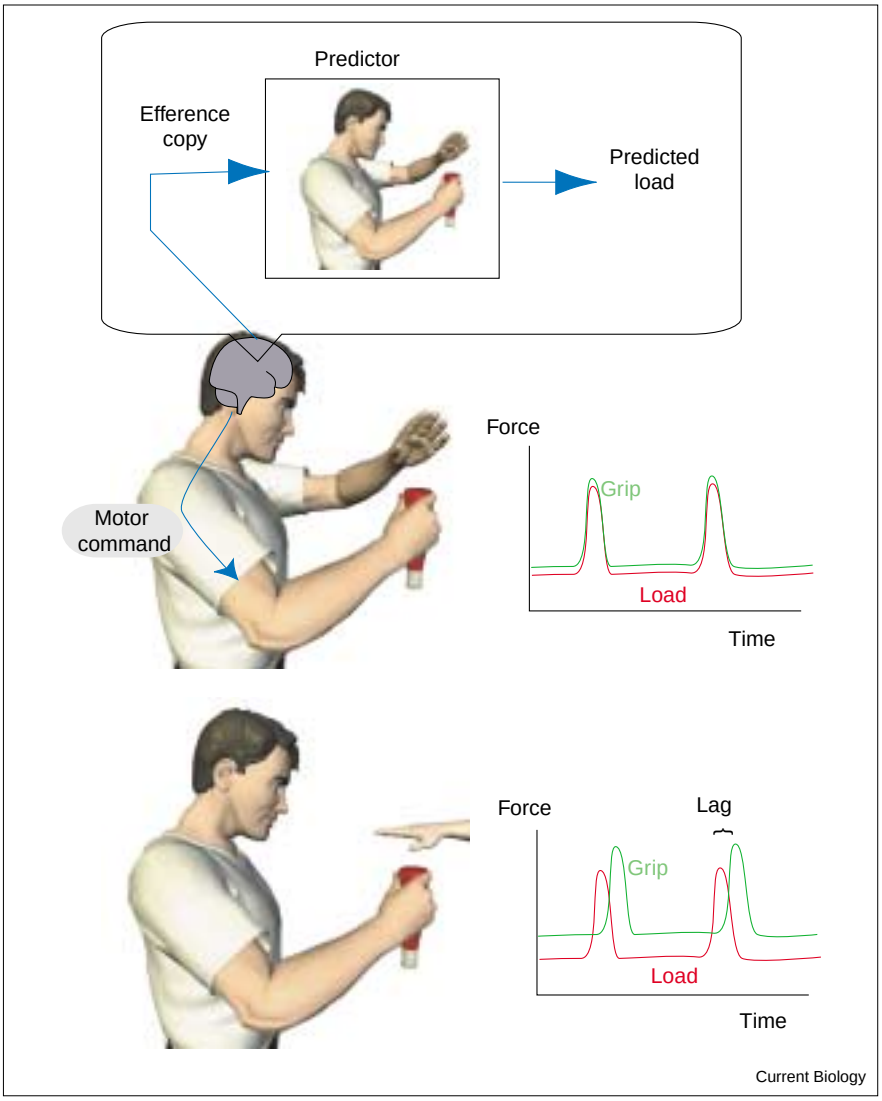
Skilled motor behaviour relies on accurate predictive models of both our own body and tools we interact with. As the dynamics of our body change during development and as we experience tools which have their own intrinsic dynamics, we need to acquire new models and update existing models. Thus forward models are not fixed entities but must be learned and updated through experience. Forward models can be trained and updated using prediction errors, that is by comparing the predicted and actual outcome of a motor command. Well established computational learning rules can be used to translate these errors in prediction into changes in synaptic weights which will improve future predictions of the forward model. Here we review the uses of motor prediction in sensorimotor control.

State estimation

Knowing our body's state, for example the positions and velocities of our body segments, is fundamental for accurate motor control. However, sensory signals that convey information about state are subject to significant delays due to receptor transduction, neural conduction and central processing. Moreover, sensors are not perfect and provide information which is corrupted by random processes, known as noise. Using sensory information to estimate the state can lead to large errors especially for fast movements, and when this erroneous state is used to control movement it can lead to instability. An alternative is to estimate state using prediction based on motor commands. Here the estimate is made ahead of the movement and therefore is better in terms of time delays, but the estimate will drift over time if the forward model is not perfectly accurate. The drawbacks of both these mechanisms can be ameliorated by combining sensory feedback and motor prediction to estimate the current state. Such an approach is used in engineering and the system which produces the estimate is known as an observer, an example of which is the Kalman filter. The major objectives of the observer are to compensate for the delays in the sensorimotor system and to reduce the uncertainty in the state estimate which arises through noise inherent in both the sensory and motor signals. Such a model has been supported by empirical studies examining estimation of hand position, posture and head orientation.

Skilled motor behaviour involves different modes of control which rely on prediction and sensory feedback to different extents. These models of control are nicely illustrated within the context of object manipulation. When holding an object in a precision grip with the fingertips on either side, sufficient

Figure 1



To prevent a ketchup bottle from slipping, sufficient grip force must be exerted to counteract the load. When the load is increased in a self-generated manner (left hand strikes the ketchup bottle, top), a predictor can use an efference copy of the motor command to anticipate the upcoming load force and thereby generate grip which parallels load force with no delay. However, when the load is externally generated (another person strikes the bottle, bottom), then it cannot be accurately predicted. As a consequence, the grip force lags behind the load force and the baseline grip force is increased to compensate and prevent slippage.

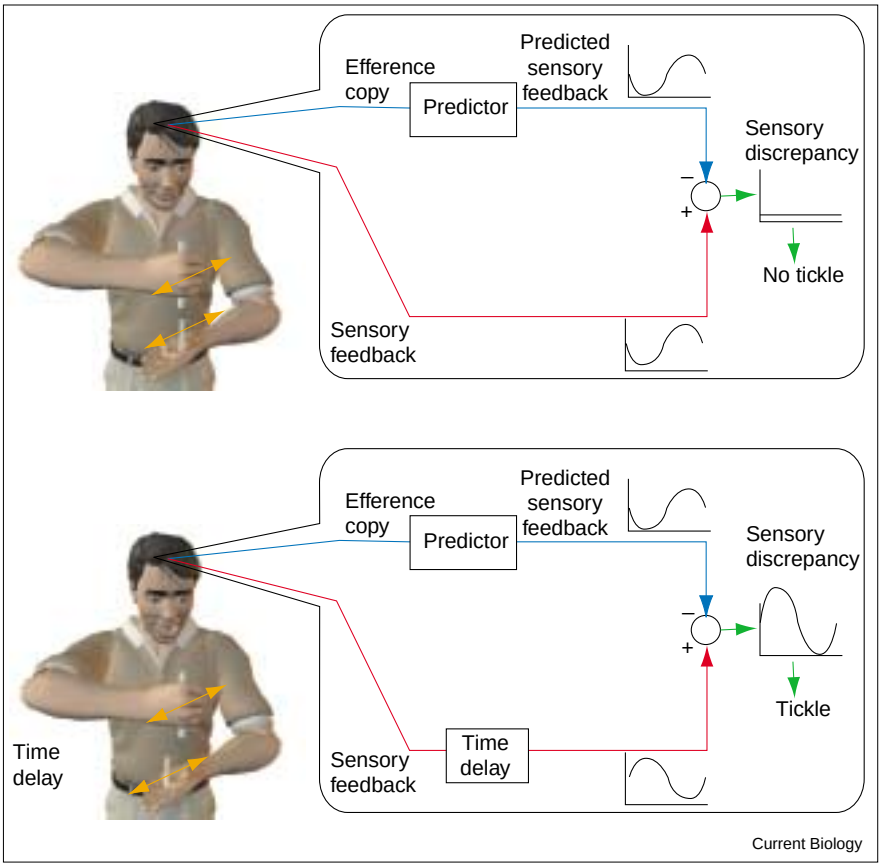
grip force must be generated to prevent slip due to load force exerted by the object. When the object's behaviour is unpredictable, sensory feedback provides the most useful signal for estimating load. For example, when flying a kite or holding the hand of a rambunctious child, we need to adjust our grip in response to the unpredictable actions of the kite or child. When dealing with such unpredictable objects our grip force is modified reactively in response to sensory feedback from the fingertips, with the consequence that grip tends to lag behind load. However, when we direct behaviour towards objects in the environment that exhibit stable properties, predictive control mechanisms can be effectively exploited (Figure 1). For example, when the load is increased by a self generated action, such as moving the arm, the grip force increases in parallel with load force with no delay. Sensory detection of the load is too slow to account for this increased grip force which relies on predictive processes. Such predictive control is essential for the rapid movements commonly observed in dexterous behaviour.

Sensory confirmation and cancellation

In addition to state estimation, prediction allows us to filter sensory information, attenuating unwanted information or highlighting information critical for control. Sensory prediction can be derived from the state prediction and used to cancel the sensory effects of movement (reafference). By using such prediction, it is possible to cancel out the effects of sensory changes induced by self-motion, thereby enhancing more relevant sensory information. For example, predictive mechanisms underlie the observation that the same tactile stimulus, such as a tickle, is felt less intensely when it is self-applied. This mechanism has been supported by studies in which a time delay is introduced between the motor command and the resulting tickle (Figure 2). The greater the time delay the more ticklish the percept, presumably due to a reduction in the ability to cancel the sensory feedback based on the motor command.

Similarly, sensory predictions provide a mechanism to determine whether motion of our bodies has been generated by us or by an external agent. For example, when I move my arm, my predicted sensory feedback and the actual feedback match and I therefore attribute the motion as being generated by me.

Figure 2



An experiment in which subjects tickle themselves through a robotic interface (not shown). In the top Figure the motion of the right hand is directly transmitted to the left. Using a predictor the sensory consequences of this motion are estimated and subtracted from the actual sensory feedback leaving little discrepancy. In the lower Figure a time delay was introduced between the motion of the right hand and the effect on the left. The motion of the right hand and stimulus on the left hand is the same as in the upper figure. However, the temporal rearrangement between cause and effect means that the prediction is out of synchronisation with the actual feedback, leading to a large sensory discrepancy which is felt as tickle.

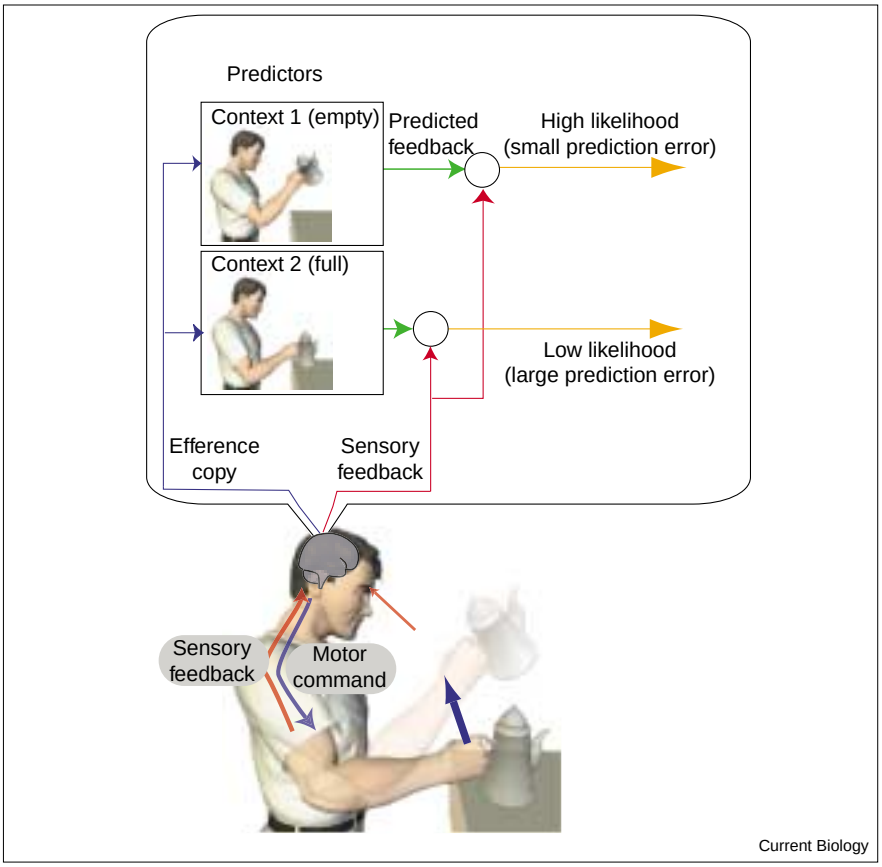
However, if someone else moves my arm, my sensory predictions are discordant with the actual feedback and I attribute the movement as not being generated by me. Therefore, in general, movements predicted based on my motor command are labelled as self-generated and those that are unpredictable are labelled as not produced by me. Frith has proposed that a failure in this mechanism may underly delusions of control in schizophrenia, in which it appears to the patient that their body is being moved by forces other than their own. Interestingly, Sirigu and colleagues have shown that damage to the left parietal cortex can lead to a relative inability to determine whether viewed movements are ones own or not.

The discrepancy between actual and predicted sensory feedback is essential in motor control. For example, when we pick up an object we anticipate the timing of discrete events such as object lift off. The CNS is particularly sensitive to the occurrence of unexpected events or the absence of an expected event. Thus if the object is lighter or heavier than expected, and therefore lifts off too early or fails to lift off, reactive responses are envoked. The CNS seems to specifically monitor these critical moments to confirm the progress of the task and to engage subsequent phases in the cascade of actions underlying natural tasks.

Context estimation

Humans demonstrate a remarkable ability to generate accurate and appropriate motor behaviour under many different and often uncertain environmental conditions. It has been proposed that the CNS uses a modular approach in which multiple controllers co-exist and are selected based on the movement context. Therefore when we pick up an object with unknown dynamics we need to identify the context and select the appropriate controller. One possible solution to this identification and selection problem has been proposed in the form of the MOdular Selection and Identification for Control (MOSAIC) model. The idea is that, when lifting an object, the brain simultaneously runs multiple forward models that predict the behaviour of the motor systems when interacting with different previously learned objects (Figure 3). Each forward model generates a prediction of the sensory feedback that should be obtained for its context. Moreover, each forward model is paired with a corresponding controller forming a predictor-controller pair. If the prediction of one of the forward models closely matches the actual sensory feedback, then its paired controller will be selected and used to determine subsequent motor commands. In computational terms, the sensory prediction error from a given forward model is represented as a probability; if the error is small then the probability that the forward model is appropriate is high. The set of probabilities from an array of forward models is used to weight the

Figure 3



A schematic of context estimation with just two contexts, that a teapot is empty or full. When a motor command is generated, an efference copy of the motor command is used to simulate the sensory consequences under the two possible contexts. The predictions based on an empty teapot suggest that lift-off will take place early compared to the full teapot context and that the lift will be higher. These predictions are compared with actual feedback. As the teapot is in fact empty, the sensory feedback matches the predictions of the empty teapot context. This leads to a high likelihood for the empty teapot and a low likelihood for the full teapot.

outputs of the corresponding controllers.

Mental practice, imitation and social cognition

Not only is prediction essential for motor control, it may also be fundamental for high level cognitive functions including action observation and understanding, mental practice, imitation and social cognition. The forward model may provide a general framework for prediction in all of these domains. In these situations a forward model is used to predict the sensory outcome of an action, without actually performing the action. For example, it is conceivable that mental practice can improve performance by tuning controllers or selecting between possible mentally rehearsed actions. Imaging studies have shown that brain areas active during mental rehearsal of an action are strikingly similar to those used in performing the action. Moreover, the durations of mentally simulated movements are tightly correlated with the durations of actual movements, a correlation that is lost with damage to parietal cortex.

In motor control, a forward model can be used to predict the sensory consequences of our actions. In perception of action we could use multiple forward models to make multiple predictions and, based on the correspondence between these predictions and the observed behaviour, we could infer which of our controllers would be used to generate the observed action. Finally, in social interaction, a forward social model could be used to predict the reactions of others to our actions. It may be that the same computational mechanisms which developed for sensorimotor prediction have adapted for other cognitive functions.

Further reading

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