Neural mechanisms for prediction

Neural mechanisms for prediction: do insects have forward models?

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Abstract

`Forward models' are increasingly recognised as a critical explanatory concept in vertebrate motor control. The essential idea is that an important function implemented by nervous systems is prediction of the sensory consequences of action. This is often associated with higher cognitive capabilities; yet many of the purposes forward models are thought to serve have analogues in insect behaviour; and the concept is closely connected to those of 'efference copy' and 'corollary discharge'. This article considers recent evidence from invertebrates that demonstrates the predictive modulation of sensory processes by motor output, and discusses to what extent this supports the conclusion that insect nervous systems also implement forward models. Several promising directions for further research are outlined.

Introduction

A forward model is a mechanism that predicts the future state of a system given the current state and the control signals (Box 1). This concept is playing an increasing role in neuroscientific explanations of motor control, context dependent action, and cognition [1][2], as it is argued that biological systems need to be able to predict the sensory consequences of their actions to be capable of rapid, robust, and adaptive behaviour. In vertebrate neuroscience there is substantial interest in interpreting the function of various brain areas in these terms (e.g. the cerebellum [3][4]). Several authors have suggested forward modelling could be a unifying framework for understanding the brain circuitry that underlies cognition [5][6][7][8].

It is of interest to note, therefore, that many of the problems that have motivated investigation of forward models in vertebrate neuroscience have close parallels in invertebrate neuroscience. For example, a cockroach executing a rapid escape response needs to know the current position of its legs to send the right motor command. It has been suggested that proprioceptive feedback may be too slow to serve this function, and that instead they maintain a prediction of their current position based on previous motor output [9] (although the sensory feedback loop in invertebrates is often much faster than in vertebrates and some cases extremely rapid e.g. on the order of a millisecond in

[10]). Flying insects need to be able to distinguish self-induced stimulation (such as rotation of the visual field caused by tracking a target) from externally imposed stimulation (such as visual rotation due to air disturbances) if they are to use the latter for flight stabilisation [11]. This could be done by using motor outputs to predict expected visual input, and taking the difference from the actual input as a measure of the external disturbance. Locusts [12] and fruit flies [13] appear to adaptively adjust the gain parameters in their motor system to deal with alterations of the expected feedback when tested in flight simulators. These examples have often been addressed by reference to `efference copy' or `corollary discharge': terms that are closely related to forward models (Box 2).

The purpose of this article is to analyse what evidence might support the ascription of forward models to insects and other invertebrates, and to assess whether such evidence is available. If insects do have forward models they may be convenient experimental systems for understanding the underlying neural mechanisms of prediction. On the other hand, if they do not, then we should be able to draw clear distinctions between aspects of vertebrate behaviour and neurophysiology that require such an interpretation, and those better explained by simpler alternatives.

Is there central modulation of sensory processes?

An important feature of forward modelling is that what the system is doing should modulate its sensory processing. That is, the perceptual system is not simply a feed-forward one, driven by the sensory input alone. There is ample evidence that the behavioural state of an insect can influence sensory and subsequent processing through neuromodulation. More interesting is that this can occur in a targeted fashion, i.e. specific sensory processes are enhanced or inhibited in a way that seems closely tied to the reafferent input that would be expected from the efferent output.

Poulet and Hedwig [14] have shown reduced responsiveness in auditory interneurons during singing in the male cricket (figure 1, discussed further below). Gebhart & Honnegger [15] report, again in crickets, that interneurons sensitive to movement of the antennae are less sensitive during active movement by the cricket itself. It is well established that proprioceptive sensory neurons, in a number of invertebrate systems including crayfish [16], stick insects [17] and locusts [18][19], have responses that are modulated in phase with central pattern generator rhythms. The alteration is not always suppression of the response, for example, Evans et al [20] report on enhanced sensory neuron responses linked to motor rhythms in the *Aplysia* feeding network.

It could be argued that the specialised layout and peripheral processing characteristics of invertebrate sensors (characterised by Wehner [21] as “neural models of the external world”) are already a 'modulation' of the sensory system to optimise it for the expected feedback from certain actions. An example is the receptive fields of horizontal cells in the fly visual system, which closely resemble optical flow fields resulting from specific movements [22]. Or the animal might adopt a specific position or pattern of movement so as to enhance sensory data relevant to the specific task, such as the movements of the praying mantis used to extract depth information from parallax [23]. However this kind of tuned sensing and active perception, though interesting, can be distinguished from the forward model concept by the criteria discussed in the next section.

Is there evidence of internal connections from the motor system to the sensory areas?

Motor output might affect sensory input via the environment or via proprioceptive feedback. But the implication of forward modelling is that there should be a specific output stream from motor areas that is routed not to muscles but to sensory areas. A useful example that illustrates the distinction is the modulation of wind-sensitive interneurons in the cockroach during flight [24]. Two pairs of identified ‘giant’ interneurons (GIs) in the terminal abdominal ganglion show different modulation. The ventral GIs have a strongly suppressed sensitivity, which appears in part to be caused by mechanical pinching of the nerve due to the different position of the cerci during

flight. The dorsal GIs show a strong rhythmic response linked to the wingbeat frequency, and this appears to have three different sources. One is proprioceptive feedback from the flight-linked oscillation of the cerci, one is external feedback caused by detection of the wind produced by each wingbeat, and the last is a centrally generated motor signal, correlated with the motor output, which passes from the thoracic ganglion down to the terminal abdominal ganglion [24]. Similarly, a combination of central and peripheral modulation of the GIs is found during walking [25].

Heterosynaptic modulation is also found in the much explored feeding mechanism in Aplysia. One sensory neuron in this circuit (B21) has been shown for example to have a variety of inhibitory and excitatory synaptic inputs including interconnections from motor neurons that modulate its sensitivity [26]. However it is, perhaps surprisingly, difficult to find many other examples where the specific connectivity from motor outputs to sensory inputs has been clearly confirmed. What is more common is the indirect evidence provided by demonstrating that the modulatory effect is still seen in the sensory systems when the motor output, and any potential proprioceptive feedback, has been prevented from occurring, e.g. through de-afferentation. This, for example, was the form of the evidence reported by Zaretsky and Rowell [27] as evidence of a corollary discharge for saccadic suppression in the locust. More recent studies have focused particularly on primary afferent depolarisation (PAD) as an indicator of presynaptic inhibition of sensory inputs by motor outputs. For example, the biophysical mechanisms of PADs found in crayfish proprioception have been the subject of extensive study [28]. An interesting possibility here is that the prediction is actually implemented by rather low-level properties such as the precise synaptic positions of inhibitory inputs on the dendritic tree of the sensory neuron.

One question this discussion raises, however, is how to define 'motor output' and 'sensory area'. The simple box and arrow diagram of figure 1, though conceptually convenient, is potentially misleading. In most biological systems, the generation of a motor command is a multistage process, and the 'efference copy' signal could branch off at any level, or indeed at several different levels. Similarly, sensory processing passes through a number of stages, and the predictive modulation might occur at any of these stages. Some areas of the nervous system combine sensory and motor functions. The forward model ‘loop’ could be from the final motor neurons to the primary sensory afferents, or it could occur wholly within the brain of the animal. In fact it is possible to describe even a simple feedback mechanism as containing a predictor [29] as the goal state can be taken to be both a ‘high-level’ motor command, and a prediction of the state that should result from executing the command: the difference of this from the actual feedback drives the behaviour. Yet this simple ‘copying’ of the goal does not seem to require any forward model process to derive out the prediction, which brings us to the next criterion.

Does the modulation of sensory input by motor output involve non-trivial predictive processes?

In the standard control theory paradigm, the forward model is constructed by representing the motor, environment and sensory mechanisms in sufficient detail to be able to predict the exact sensory consequences of a given motor command. In principle, an alternative to representing these processes explicitly would be to generate a look-up table in which each motor command is paired to an expected sensory input. In practice, an adequate prediction model or look-up table could be acquired by learning. Obviously a complete and accurate model is rarely possible in practice (and seems unlikely to exist in an insect’s small brain) so any actual forward model is likely to be an approximation. However, there are many possible levels between accurate and detailed internal models and simple, approximate predictors. At what point on this continuum does the forward model view – that is, that the system implements a specific neural mechanism for calculating the predicted sensory input from the motor command – become unnecessary?

In many of the examples discussed so far, the modulation of the sensory input seems little more than the simple gating of a sensory channel, such as the inhibition of the optomotor response during

escape turns as seen in the locust [30]. This would not seem to require much calculation - although even this may require some prediction of the time-course of the expected input. There is likely, at the least, to be a time lag between the motor output and the resulting sensory input, so any internal gating signal should be similarly delayed. The reafferent effects of a motor signal might often have a longer time course than the signal itself, in which case the gating needs to be similarly extended in duration. In some cases it can be shown that the timing and duration of inhibitory effects seen in insect sensory neurons is precisely matched to the predicted sensory feedback, for example in cricket auditory perception (figure 1). Male crickets produce bursts of sound by closing their wings. In auditory interneurons, an inhibitory current driven by efferent signals occurs with the same temporal pattern and an appropriate delay, so as to reduce the response to each self-produced sound burst [31]. This appears to prevent auditory desensitisation, so that the cricket remains sensitive to other males singing in the vicinity.

In the case of the male cricket, however, it appears that the amplitude of the inhibitory current is not scaled to the amplitude of the wing movements that produce the sound. It would be very interesting to discover whether more complex predictive transformations can be found in an invertebrate preparation. Another way to approach this issue is to look for behavioural evidence that the animal reacts to altered feedback, in a manner consistent with a quantitative comparison between expected and actual feedback. This has been investigated to some extent using open- and closed-loop flight simulation in flies [13], which suggests, for example, that they selectively ignore visual feedback in the expected direction but respond to feedback in the opposite direction. Employment of this paradigm is complicated by the possibility that the animal is able to adapt, during the experiment, to the altered feedback. More recent refinements in this experimental paradigm (e.g. [32][33]) might enable more systematic investigation of these issues. For example it would be interesting to attempt to implement analogues of some of the recent behavioural experiments on humans that have been used to test the forward model hypothesis by using detailed temporal analysis of the behaviours [34][35].

Another interesting question is whether it can be demonstrated in insects that the prediction is involved in learning, or modified by experience. Kanou et al [36] show that crickets can adapt the directionality of their cercal escape response after damage only if they have experienced re-afferent input during free movement. The predictive mechanism required for more complex learnt behaviours might link various strands of evidence about the function of insect mushroom bodies. These distinctive structures in the insect brain are most often assumed to be principally involved in learning, particularly of olfactory discriminations [37]. But other lines of evidence suggest a role in multimodal integration and context-dependent behaviours. Evidence of efferent neurons that respond to specific stimuli combinations and sequences, and of recurrent connectivity, lead Li and Strausfeld [38] to argue that the mushroom bodies may "monitor motor actions or intended motor actions, differentiate self and imposed stimulation". This is just the role suggested for forward models in the cerebellum of vertebrates.

Conclusion

There are a number of examples of recent research in invertebrate neuroscience that may benefit from, and have relevance to, the current discussions of forward modelling in vertebrate neuroscience. The link between specific physiological circuits and behaviour can potentially be more directly explored in these 'simpler' animals. Already the consideration of how we might determine whether and how prediction is used in these systems has been helpful to focus the often vague discussions of 'efferent copy' and 'corollary discharge' and to indicate what might be the most critical lines of evidence to explore. These can be summarised by asking whether central modulation of sensory processes in invertebrates can be demonstrated to be:

i. specifically targeted to enhance or suppress behaviourally relevant stimuli;

ii. well-scaled in amplitude and timing to match the expected feedback, demonstrating non-trivial transformation of the motor output to predict the input;
iii. able to adapt to alterations in the motor-sensory linkages.

And can we uncover the actual pathways and mechanisms by which the motor signal is transformed and transported so as to interact with the sensory input?

Outstanding questions

- Can some of the behavioural experiments that have strongly supported the forward model hypothesis be used as paradigms for invertebrate investigations?
- Can more examples of direct motor output to sensory areas be found, so that neural circuitry of these mechanisms can be understood?
- Are the mushroom bodies, or some other brain structure in insects, carrying out a non-trivial and learned prediction process?
- What are the implications for understanding cognitive processes in insects [39]?

Box 1: What is a forward model?

The term ‘forward model’ comes from control theory, the study of how to control the behaviour of dynamical systems. The principle is illustrated in figure 1. Consider a simple example, such as ‘cruise control’ in a car, where the aim is to control the speed of the vehicle with a motor command (normally given by the ‘gas’ pedal) that changes the throttle position. The change in wheel speed (the motor output) will be a complex function of factors such as the engine characteristics, the current speed, and the coupling from engine to wheels. The change in speed of the car (the effect of the motor output on the world) will also depend on the road surface, the wind resistance of the vehicle and so on. The actual speed can be measured by a sensor such as a tachometer, which itself has certain characteristics. In theory, all these factors could be represented in a ‘forward model’ that takes the motor command as input and, by simulating the relevant processes, predicts the speed that will be measured by the tachometer (the ‘sensory input’).

Why not just run the system and observe the consequences? There are several advantages to making the prediction as well, as control engineers have discovered. One is the potential time lag involved in sensory feedback. For example, if the cruise controller waited till the tachometer reached the speed limit before closing the throttle, the adjustment could come too late to avoid exceeding the speed limit. Another is that a comparison between the prediction and the observation can be used to distinguish external disturbances from expected feedback. For example, if the car has a flat tyre, we don’t want the controller to keep increasing output to try to reach the desired speed despite the additional friction, but rather to detect that some significant change to the system dynamics has occurred. Differences between prediction and feedback can also be used to learn and improve the generation of control signals, e.g. that are well-tuned to the specific vehicle.

Another potential function of a predictor is that it can be run off-line to test out whether a particular control input is viable or leads to bad consequences, e.g. that changing the throttle position too rapidly might cause the engine to stall. This notion of a ‘decoupled’ forward model is an important one, but it is important to note it is not an essential component of the forward model concept, at least as discussed in this paper. That is, claiming that a nervous system is using a forward model to predict is not the same as claiming it is able to use it to plan.

Box 2 How do forward models relate to efference copy and corollary discharge?

Descartes was perhaps the first to explicitly note that passive motion of the eye produces an impression of world motion when deliberate movements do not [40]. Pukyne and Helmholtz are usually credited as the first to suggest that this might involve motor output (or 'effort of will') being copied internally to interact with sensory input - that is, we don't see the world move if we can predict from the motor command to the eye that the scene is about to change - and Mach and von Uexkull were among the first to depict the idea in the form of feedback diagrams [40]. The concept was more clearly formulated in 1950, simultaneously and independently, as 'efference copy' by von Holst and Mittelstaedt [11], and 'corollary discharge' by Sperry [41].

It is clear from reading the latter formulations that both were describing the same principle as that outlined in box 1 as forward modelling. Sperry describes corollary discharge "into the visual centers [allowing] anticipatory adjustment...specific for each movement with regard to its direction and speed". Von Holst and Mittelstaedt describe efference copy as being compared to the sensory re-afference like a ``photo-negative". Sperry focusses on the advantages of being able to predict input in advance, whereas Von Holst and Mittlestaedt emphasise the potential for using the difference between the predicted and actual feedback to control behaviour. What is not so clear is whether 'efference copy' and 'corollary discharge' were intended to be the input to a forward model or the output of a forward model. If ‘efference copy’ means (as the name suggests) a copy of the efferent motor command, then this is the input to a forward model; but if ‘efference copy’ is to be compared like a “photo-negative” to the sensory re-afference, then it must be the output of a forward model, i.e. the predicted sensory consequences of the motor command, not the motor command itself. ‘Corollary discharge’ is even more ambiguous: is it the discharge from the motor areas (the input to a forward model) or the discharge into the sensory areas (the output from a forward model)? This issue reflects the tendency, still common in many discussions of efference copy and corollary discharge, to neglect the problem of how the motor output is to be transformed into a signal that can be compared to the sensory input, as it is by no means obvious why these should be comparable. One advantage of the forward model terminology is that it makes this problem explicit.

Current research on forward models generally uses the term ‘efference copy’ to refer to the output of the motor command system that is fed into the predictor, and ‘corollary discharge’, where used at all, to refer to the output of the predictor, i.e. the signal fed into the sensory system. However there is an alternative tradition in neuroethology that defines `corollary discharge' as "any neural signal that branches off centrally from an efference signal" [42]. ‘Efference copy’ is then taken to be that subset of corollary discharge in which the signal is “exactly proportionate to the efference signal” and thus used to “exactly counterbalance the reafference” [42] – though note, as mentioned above, it is not actually so evident that being proportionate to the motor signal will correctly predict the sensory signal. However it is also not uncommon to find the terms ‘efference copy’ and ‘corollary discharge’ used interchangeably in invertebrate neuroethology.

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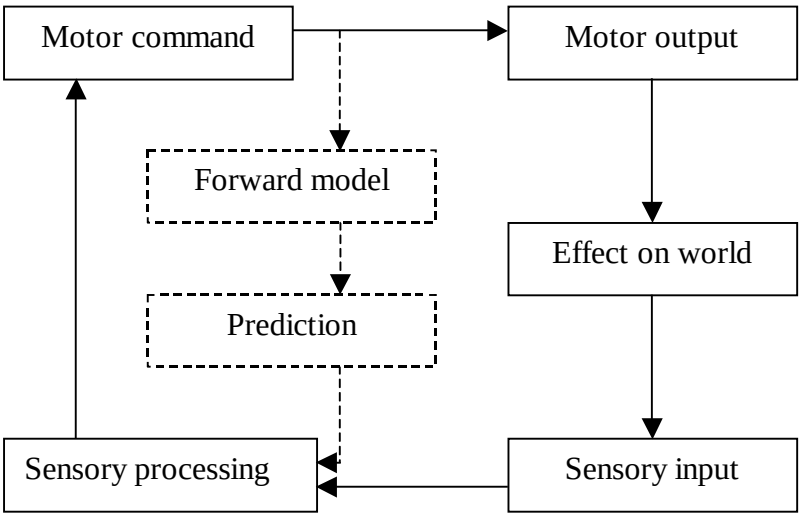

Box 1 Figure 1: Schematic representation of a sensory-motor system with a forward model. The solid arrows indicate the loop by which a motor command is translated into motor output, has some effect on the world, causing some sensory input, which the system can process to generate the next command. The forward model is an internal loop that takes the motor command, and predicts the expected sensory input, which can be used to modulate the processing of the actual input. A classic example is that moving our eyes causes the image on the retina to move, but we perceive a stable world because the image movement is predictable from the eye movement command.

Legend for main text Figure 1:

(Poulet & Hedwig 2003 [31], figure 10, reprinted with permission). Male crickets produce a calling song by rubbing one wing against the other, producing a series of sound bursts. The omega neuron (ON1) is an identified auditory interneuron in the prothoracic ganglion that normally has a strong response to the sound of cricket song, but this response is reduced for self-generated song. A: If the male cricket's own song is made silent (by removing one wing) and it is presented with an external acoustic stimuli, the spike frequency observed in ON1 to this stimuli is significantly reduced during silent singing movements (dots represent the maximum spike frequency, the black line the average spike frequency, plotted against the average wing movement). B: During normal singing, the wing movements produce four bursts of sound (lower graph) which results in four spike bursts in ON1 (shown as a PST histogram) with a 15-20ms latency. The grey bars indicate that the response reduction seen in A is closely matched to the timing of the peaks of the response to self-generated sound as seen in B. Thus the ON1 neuron will fire significantly less to the male cricket's own song while maintaining sensitivity to external sources of sound.