forward models. A forward model is one that describes the causal relationship between actions and their consequences. The ability to predict the consequences of our actions is fundamental for action and also for many cognitive functions. In this brief review we discuss the role of forward models underlying *prediction* in sensorimotor control and in higher cognitive functions, including *agency,* which is integral to *conscious experience.

Prediction refers to the estimation of future states of a particular system. In sensorimotor control, we are primarily interested in predictive processes in systems that are directly and immediately influenced by our motor commands; for example, predicting how our arm moves in response to a motor command. Skilled action relies on accurate predictions of both our own body and objects with which we interact (such as a tool) because sensorimotor feedback loops are simply too slow because of the significant delays that arise in receptor transduction, neural conduction, and central processing. An influential idea in sensorimotor control is that the brain predicts the consequences of action by simulating the dynamic response of our body and environment to the outgoing motor command. Such as system is termed an *internal forward model* as it is internal to the central nervous system, models the behaviour of the body, and captures the forward or causal relationship between actions and their consequences.

A fundamental role of forward models in motor control is to monitor performance by comparing predicted sensory outcomes to actual outcomes. For example, when I lift an object my brain predicts the timing of lift-off as signalled by mechanoreceptors in the skin and reacts rapidly if these signals occur either earlier (if the object is lighter than expected) or fail to occur (if the object is heavier than expected) (for a review see Flanagan and Johansson 2002). Moreover, these prediction errors can be used to update forward models themselves with a view to improving future predictions. Thus forward models are not fixed entities but are updated through experience. Well-established computational learning rules can be used to translate the prediction error into changes in synaptic weights which will improve future predictions.

Another important function of forward models is state estimation. Knowing our body's state, e.g. 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 and provide information which is corrupted by random processes, known as *noise*. An approach that deals with these obstacles 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 due to noise inherent in both the sensory and motor signals. An example of such state prediction is seen in object manipulation. When moving grasped objects, people modulate grip force in precise anticipation of the changes in load caused by acceleration of the object (Flanagan and Wing 1997). Sensory detection of the load is too slow to account for this increased grip force which instead relies on predictive processes.

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, which is known as *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 (Blakemore et al. 1999). This mechanism has been supported by studies in which a time delay is introduced between the motor command and the resulting tickle. 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 agency—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. 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 on the basis of 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 underlie delusions of control in *schizophrenia, in which it appears to the patient that their body is being moved by forces other than their own (Frith et al. 2000).

Forward models, used to predict the consequences of motor commands, may be distinguished from *inverse models* that are used to estimate in advance the motor commands required to achieve desired consequences. A study of grip force control has shown that when learning to manipulate an object with novel properties the brain learns to predict the consequences, as measured by grip force, before learning how to control the object so as to achieve a desired trajectory (Flanagan et al. 2003). This suggests that the brain maintains distinct forward and inverse models for prediction and control. Whereas in delusion of control normal movements are made but are perceived as coming from an external source, in *anarchic hand abnormal movements are made and are attributed by the patient as self-generated. This suggests that in delusions of control the inverse model functions normally and the forward model is faulty, whereas in anarchic hand syndrome the inverse model is impaired and produces an non-desired movement, but the normal forward model correctly predicts the consequences and thereby attributes the movements as self-generated (Frith et al. 2000).

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. For example, forward models can be used in mental practice to predict the sensory outcome of an action without actually performing the action. In this way mental practice could improve performance by tuning controllers or selecting between possible mentally rehearsed actions. *Functional brain imaging and behavioural studies have shown that brain areas active during mental rehearsal of an action are strikingly similar to those used in performing the action. Similarly, in social interaction, a forward social model could be used to predict the reactions of others to our actions (Wolpert et al. 2003). It may be that the same computational mechanisms that developed for sensorimotor prediction, which largely lie outside the conscious domain, may have been adapted for other cognitive functions, some of which are integral to conscious experience.

Acknowledgements
This work was supported by grants from the Human Frontiers Science Programme, the Wellcome Trust, the Natural Sciences and Engineering Research Council of Canada.

DANIEL M. WOLPERT AND J. RANDALL FLANAGAN

Blakemore, S. J., Frith, C. D., and Wolpert, D. M. (1999). 'Perceptual modulation of self-produced stimuli: the role of spatio-temporal prediction'. *Journal of Cognitive Neuroscience,* 11.

Flanagan, J. R. and Johansson, R. S. (2002). 'Hand movements'. In: Ramachandran, V. S. (ed.), *Encyclopedia of the Human Brain,* Vol. 2.

—— and Wing, A. M. (1997). 'The role of internal models in motor planning and control: evidence from grip force adjustments during movements of hand-held loads'. *Journal of Neuroscience,* 17.

——, Vetter, P., Johansson, R. S., and Wolpert, D. M. (2003). 'Prediction precedes control in motor learning'. *Current Biology,* 13.

Frith, C. D., Blakemore, S. J., and Wolpert, D. M. (2000). 'Abnormalities in the awareness and control of action'. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences,* 355.

Wolpert, D. M., Doya, K., and Kawato, M. (2003). 'A unifying computational framework for motor control and social interaction'. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences,* 358.