

PERSPECTIVES

Cerebellar forward models to control movement

John Stein

Department Physiology, Anatomy and Genetics, University of Oxford, Oxford OX1 3PT, UK

Email: john.stein@dpag.ox.ac.uk

Because negative feedback control is too slow, most of our movements are pre-programmed. These programmes require the generation of internal representations (neural 'models') of the sensorimotor transformations required to generate the set of motor commands that will execute a desired movement. Two kinds of model can be distinguished conceptually. 'Forward' models transform a set of motor commands into a prediction of their outcome in terms of the sensory reafference the movement will generate, the 'sensory consequences of the movement'. After it has been completed, these will eventually signal how the movement actually turned out, so the forward model, if it is accurate, can rapidly predict whether a motor programme will achieve its goals before it is carried out, and adjust it if it is unlikely to do so. After the movement has taken place it can be updated by comparing its predictions with what actually transpired. The inverse model then inverts the information flow of the forward model by inputting the desired goal of the movement, i.e. its desired sensory consequences, and back calculating the motor commands that would be required to achieve this. In other words it is the inverse model that actually generates the programme of motor commands to make the movement.

Of course the fact that we can conceptually separate these two aspects of the

internal representation of preprogrammed movements does not mean that they are necessarily located in separate regions or even different neurones in the brain. Nevertheless beginning with the theoretical arguments of Giles Brindley, David Marr and James Albus, and after 50 years of inactivation, recording and imaging experiments there is now a strengthening consensus that the cerebellum plays a crucial part in representing them. But in a complex system like this there can be no single experiment that unequivocally proves that the cerebellum is the site of internal models, and many still doubt that it is helpful to view it as instantiating these models rather than simply adjusting programme parameters such as 'the site, timing and magnitude of muscular contractions' in the words of Gordon Holmes. Actually the latter is exactly what you would expect the models to achieve. So none of the experiments that show that the cerebellum is involved in motor adjustments, such as coordination, learning new skills, conditioning or other reflex adaptations directly bear on whether it does these things by building up internal models or in some other way.

Ideally we would like to be able to demonstrate directly that cerebellar neurones carry out the information processing operations necessary for the generation of an internal model. Kawata's group (Imamizu *et al.* 2000) showed that there are localized increases in cerebellar activity after acquisition of skilled use of a new tool, probably reflecting the incorporation of the tool into a forward model. Liu *et al.* (2003) interpreted single unit activity in the lateral cerebellum of monkeys tracking a visual target as mediating a forward model. But neither result proves that the recordings represent an internal model rather than simply reflecting the movement itself.

In contrast the study by Cerminara *et al.* (2009) in this issue of *The Journal of Physiology* presents some of the first direct evidence that Purkinje cells can predict upcoming sensory feedback. They trained cats to track a moving target with their paw half a second after the target began moving. During this period the cats were predicting where the target would be when they got the go signal to reach out. They recorded from neurones in lateral cerebellar zone D2 because David Armstrong's group at Bristol had demonstrated that D2 neurones receive visual inputs but have no direct relation to limb movements (M-Horvat *et al.* 1998). The Bristol group's unique knowledge about the physiology of the zonal organisation of the cerebellum was thus seminal to Cerminara *et al.*'s work. The discharge of these D2 neurones were found to predict the movement of the target. Crucially they continued to do so even when the cat's view of the target was occluded. Thus this paper shows that neurones that had no direct relationship to the paw movements nevertheless predicted movement of the visual target even when the visual signals that originally enabled that prediction were no longer available. This is exactly what you would expect of a cerebellar forward model.

References

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