

A forward model for the perception of movement

In neuroscience, and in control theory, a *forward model* is an internal model responsible for what performing calculations analogous to the dead reckoning discussed in the context of Kalman filters.

A well-known discussion of forward models is given in Wolpert et al. (1995). In this paper they give some, albeit quite circumstantial, evidence that the brain has a forward model for movement. In their experiment subjects are sat in the dark with one hand on a manipulandum, that is, a device you push around with one hand which can record your hand, restrict it to specific paths and exert a force against or with the movement of your hand. A manipulandum is shown in Fig. 1.

In this experiment the manipulandum is restricted to horizontal motion. At the start of each trial the location of the subjects hand is illuminated and it is assumed that at that time the subject knows exactly where their hand is. The subject is then asked to move their hand; there may be a force assisting or resisting this movement, in any case at the end a resistance force is used to force the subject to stop moving their hand at a point uniformly chosen between zero and 30 cm. The subject is then asked to use their other hand to indicate, using a mouse which moves a marker along the horizontal track, where they believe where their hand is. It turns out people consistently overestimate how far their hand has travelled.¹ In fact this overestimate has a distinctive timecourse shown in Fig. 2: the overestimate increases rapidly for movements that take a second or less and then decreases slowly for longer movements.

It is proposed in Wolpert et al. (1995) that this is evidence for a forward model. In their description the sense of hand position in the absence of visual feedback has two components, a dead reckoning component supplied by the forward model and a proprioceptive component coming from mechanoreceptors and joint receptors in the arm itself. The dead reckoning model is similar to what we saw before for the Kalman filter:

$$\mathbf{x}_d = F\mathbf{x} + U(t)\mathbf{c} + \mathbf{W} \quad (1)$$

¹This raises a plethora of questions; like if they then get visual feedback does the estimate improve? Is the overestimate the result of not modelling the braking force? This isn't dealt with in the paper and may work against its conclusions!

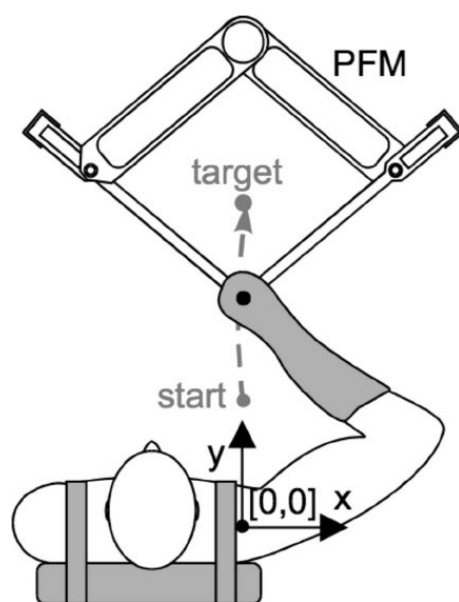


Figure 1: A manipulandum allows hand movements to be recorded and to be manipulated by applying a force. [Image from Mistry et al. (2013), the start and target labels don't apply to the experiment being discussed here].

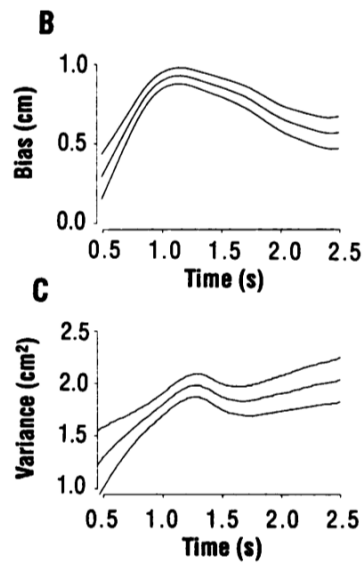


Figure 2: The bias in estimates of hand position; **B** shows the mean bias and **C** the mean variance. The middle line shows the mean and the two outer lines are standard errors indicating the variability of the measurement. The participants never stop moving their hands in less than 0.5 seconds so the graphs start there; after 2.5 second the bias stops changing; 1 second corresponds to 0.9 cm and 2.5 seconds to 2 cm. It should be noted that this is only a small fraction of the trials, the trials themselves are uniformly chosen from between zero and 30cm, we are told the result plateaus after 2.5 seconds. [Image from Wolpert et al. (1995)].

where, as before

$$F = \begin{pmatrix} 1 & t \\ 0 & 1 \end{pmatrix} \quad (2)$$

but here there is in addition a control vector corresponding to the force the subject applies to the manipulandum.

$$\mathbf{c} = \begin{pmatrix} 0 \\ 1/m \end{pmatrix} \quad (3)$$

and $U(t)$ is the work done on the manipulandum, so $U(t) = \int_0^t u(t)dt$ where $u(t)$ is the force on the manipulandum, both from the subject and, possibly, from the added force applied to the manipulandum during the experiment. Finally \mathbf{W} is the noise. Basically, the difference from what we saw before is the extra control term modelling the acceleration of the manipulandum. In this picture this force is something the brain knows about, they are the motor commands whose effect is begin modelled. In any case, the details here are not important, the main thing is that in this model the brain models the consequence of the motor commands and produces a prediction based on dead reckoning of where the hand is. One detail is important, the covariance of \mathbf{W} grows with time, if W is the covariance matrix then $W = wt$ for some w .

Overall the model has a prediction from the forward model and sensory information from proprioception; these are combined to give a new estimate of the position \mathbf{x}_n

$$\mathbf{x}_n = \mathbf{x}_d + K(\mathbf{x}_s - \mathbf{x}_d) \quad (4)$$

where \mathbf{x}_s is the sensory estimate of the position and K is the Kalman gain.²

In this picture of motor control the movement of the hand is under continuous feedback control; as the hand is moving the forward model is predicting where the hand will soon be so the motor areas can issue instructions for what the muscles must do next to move from that point to the one beyond. This continuous feedback is a more adaptable and robust model of motor control than one involving a backward model; in a backward model the desired final location of the hand is the input and the output is the required motor commands.

²All this is described in position space, as if in the brain the sensory information is converted into position information; a more likely picture is that the forward model outputs a sensory prediction. However, this doesn't change the picture being presented here.

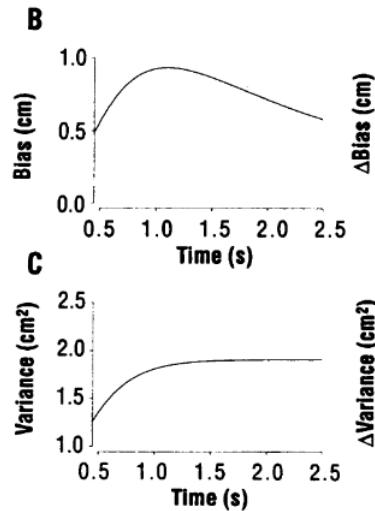


Figure 3: The model bias in estimates of hand position; **B** shows the mean bias and **C** the mean variance. These show some similarity to the experimental results; it is clear though that the Kalman model doesn't show a plateau as with the experimental result unless it is assumed the sensory result, like the dead reckoning result, has a bias, just a smaller one and one that doesn't grow with movement. [Image from Wolpert et al. (1995)].

An additional advantage of a forward model is that it can help with sensory perception; if there is a prediction of how the sensory consequence of a model command then this can be used to separate the expected sensation from the unexpected. Some aspect of the unexpected sensation will, of course, be attributable to errors in the forward model, but some will be related to the environment. In fact, there is a complicated story here, the brain uses differences between the forward model and the sensory perception to correct its understanding of, in this case, the hand's location, it uses it to improve sensory perception of the environment and it uses it to correct the forward model itself. How it balances these different aspects based on how often an error occurs and the information, encoded in neuromodulation, of which is likely to be appropriate, is an interesting open question.

Lets return to the experiment. In a Kalman filter the size of the Kalman gain depends on the variance in the two estimates. If the variance in the dead

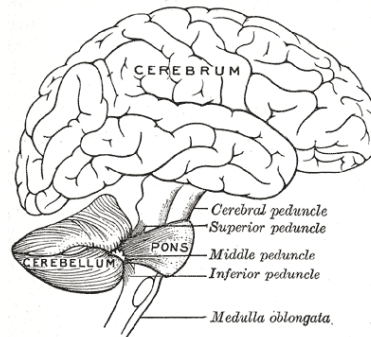


Figure 4: A drawing showing where the cerebellum is in the brain. [Picture from wikipedia which in turn got it from an old edition of *Gray's Anatomy*]

reckoning estimate is low compared to the variance in the sensory estimate then the Kalman gain is near zero; conversely if the dead reckoning variance is large compared to the sensory variance the gain is near one. In the authors' account of their experimental result they imagine that because of the conditions of the experiment the dead reckoning estimate has a positive bias which increases with movement.³ The effect of this bias is seen in the overestimate. However, the Kalman gain increases over time; the variance in the dead reckoning estimate starts at zero and increases, again getting larger and larger with movement, and so the estimate of the position becomes more and more reliant on the sensory estimate as time passes, so the bias reduces. In fact the result of the Kalman filtering model is seen in Fig. 3 and gives a good qualitative agreement with experiment. The key point is that the bias stops increasing because the Kalman gain orchestrates a switch from the dead reckoning estimate to the sensory estimate.

The cerebellum

This leaves open the question as to where the forward model might be maintained. The obvious answer is the cerebellum.

The cerebellum is found at the back of the brain, see Fig. 4; it is well conserved across vertebrate species and is known to be involved in movement. The cerebellum has a number of striking features; it has a more stereotypical

³There is no explanation as to why this might be; this is a weakness of the analysis.



Figure 5: A drawing by Santiago Ramón y Cajal of a Purkinje cell. [Picture taken from http://en.wikipedia.org/wiki/Golgi's_method]

structure than most brain area and this structure is conserved across species. It also has one of the brain's largest cells, the Purkinje cell, and its most numerous, the granule cell.

Purkinje cells have a distinctive structure with a huge, highly branched, but flat dendritic arbor, see Fig. 5; this allows an extensive connectivity with each Purkinje cell receiving inputs from around 100,000 other cells. In the cerebellum the Purkinje cells are lined up like pages in a book, with their arbors lying in parallel planes. They receive two excitatory inputs, weak inputs from parallel fibres, axons that run perpendicular to the planes of the Purkinje cell dendritic arbors, and a strong input from a climbing fibre, a single axon which winds around the Purkinje cell and makes multiple contacts with it, see Fig. 6.

Another peculiarity is that the Purkinje cell has different responses to

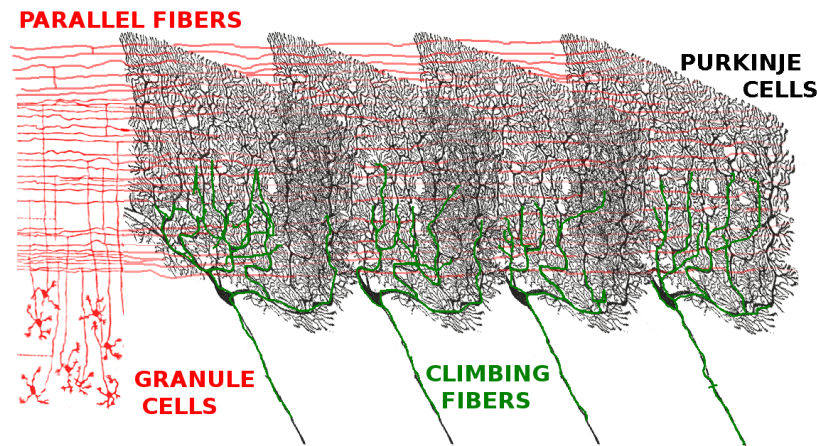


Figure 6: A cartoon of the cerebellar circuitry. A vertical axon rises from each granule cells, splits once and then extends horizontally in two directions making connections with multiple Purkinje cells. Each Purkinje cell has its own climbing fiber which winds up around it.

different inputs; in response to multiple weak inputs from the parallel fibers it fires a normal sort of spike, called in this context a *simple spike*; in response to single spike from the climbing fiber it fires a special spike, called a *complex spike*, with a leading spike, a number of small ‘spikelets’ and a sustained after-period of depolarization; this is illustrated in Fig. 8.

If there is a forward model it seems likely to be supported by the cerebellum (Gao et al., 1996). The cerebellum receives input from the motor areas. The Purkinje cells receive a huge number of input and so appear to be capable of calculations akin to large matrix multiplications. Finally, the Purkinje cell has a second input type and this is thought to communicate an error signal allowing the cerebellum to perform supervised learning, in other words there seems to be a mechanism for updating the forward model (Marr, 1969; Albus, 1971).

References

Albus, J. S. (1971). A theory of cerebellar function. *Mathematical Biosciences*, 10(1-2):25–61.

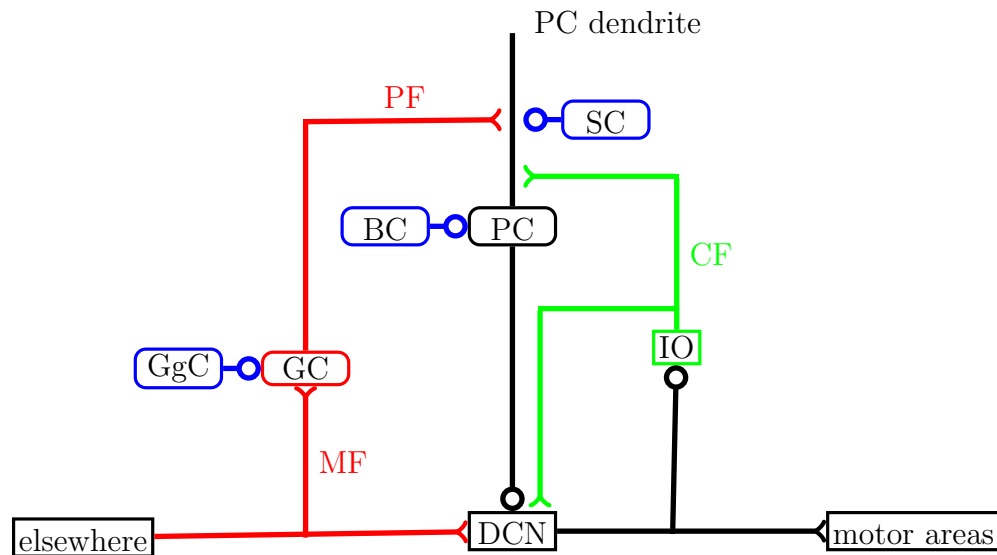


Figure 7: A schematic of the cerebellar circuit. The granule cells (GC) receive input from a diverse range of other parts of the brain along the mossy fibers (MF). Each granule cell will combine input from just three or four mossy fibers and do this in lots of different combinations. The parallel fiber (PF) carries spikes from the GC to the Purkinje cell (PC) whose large dendrite is drawn as a line. The PC also receives input from a climbing fiber (CF) coming from Inferior Olivary Nucleus (IO). In turn it sends an inhibitory signal to the Deep Cerebellar Nucleus (DCN); the DCN has inhibitory neurons which act on IO and excitatory neurons which act on the motor system. The basket cells (BC), the Golgi cells (GgC) and the stellate cells (SC) are all local inhibitory cells.

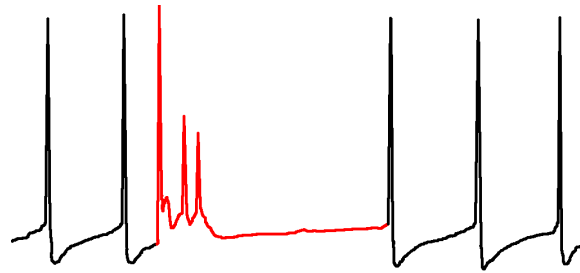


Figure 8: A complex spike. This drawing shows a simple spikes in black and a complex spike in red. The complex spike is followed by a long refractory period during which spiking is not possible. This is a sketch, not an actual recording, but a typical time scale would have this refractory period 50 ms long.

- Gao, J.-H., Parsons, L. M., Bower, J. M., Xiong, J., Li, J., and Fox, P. T. (1996). Cerebellum implicated in sensory acquisition and discrimination rather than motor control. *Science*, 272(5261):545–547.
- Marr, D. (1969). A theory of cerebellar cortex. *The Journal of physiology*, 202(2):437–470.
- Mistry, M., Theodorou, E., Schaal, S., and Kawato, M. (2013). Optimal control of reaching includes kinematic constraints. *Journal of neurophysiology*, 110(1):1–11.
- Wolpert, D. M., Ghahramani, Z., and Jordan, M. I. (1995). An internal model for sensorimotor integration. *Science*, 269(5232):1880–1882.