

arrive in spring to produce 1–2 local generations of hoverflies that are split almost equally between midsummer (40%) and autumn (40%). This is the equivalent of 380 *Episyrphus* for every hectare of land in the southern UK.

Such enormous numbers move serious amounts of nutrients into the UK: 30–80 tonnes of biomass, 1,000–2,500 kg of nitrogen, 100–250 kg of phosphorus and 50–150 GJ of energy. They also consume serious numbers of aphids during development. We have many estimates of how many each larva can consume, which of course varies with aphid size and species, and only about 2% of these larvae survive to emerge as adults but have, of course, still eaten many aphids before dying themselves. Reasonable guesstimates of these numbers leads to a total figure of 6.3 trillion aphids eaten by the first generation of hoverflies derived from the spring migrants, an average of 900,000 aphids eaten per hectare. *Episyrphus* is a particularly important predator of cereal aphids, and Wotton *et al.* estimate that it eats about 20% of the cereal aphids present in the crops in early summer.

If this wasn't enough, the migrants carry about 10–11 pollen grains of 1–3 plant species each when flying into the UK, and hence in spring transport 3–8 billion pollen grains into southern Britain, and 3–19 billion back out again in autumn.

The actual numbers for these estimates may be even larger because the radar data come from heights between 150 and 1,200 m above ground level. Insects are unlikely to fly higher than 1,200 m because it is too cold, but there may be more of them flying below 150 m.

True migrants like *Episyrphus*, which are rather few among the hoverflies, make a stark contrast with other species. Migrants appear tailor-made to be able to respond flexibly to the challenges of climate change. Just what is it that makes them different from sedentary species that can only shift their ranges very slowly through colonisation at the range margins? A very rare hoverfly such as the golden hoverfly, *Callicera spinolae*, may have colonised successfully only once, and now only survives by establishing a new population just before the old one dies out [13]. The hornet-mimicking hoverfly *Volucella zonaria* was an extremely rare vagrant to southern Britain before 1940, occasionally breeding but

always dying out again. Then it established itself, and now has spread widely throughout the south and the Midlands but has taken 60 years to do so [14]. While all the time, vast numbers of their relatives arrived unseen every year by migrating high above them.

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Cerebellar Function: Multiple Topographic Maps of Visual Space

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New evidence from the Human Connectome Project has revealed multiple maps of visual space in human cerebellum. While some features of these maps adhere to the topographic organizational principles shared among the multiple maps in cerebral cortex, some properties appear idiosyncratic.

A human being's thoughts, actions, and emotions are supported by a brain containing about 85 billion nerve cells [1]. To

the layperson, and even perhaps to many cognitive neuroscientists studying the cerebral cortex, it may come as a surprise



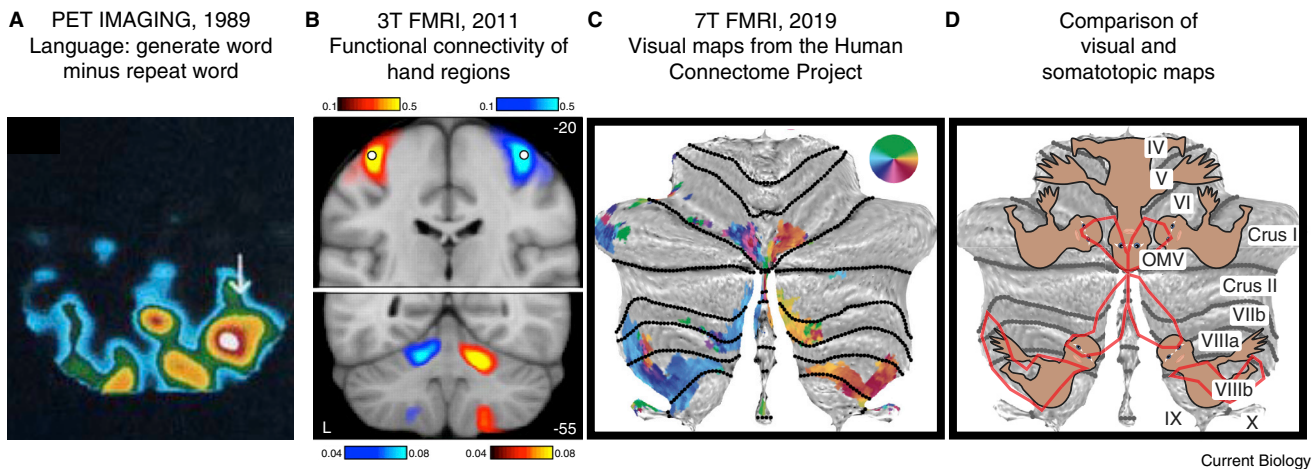


Figure 1. Progress in neuroimaging of the human cerebellum.

(A) Positron emission tomography (PET) imaging of the cerebellum from showing increased activation in right, lateral cerebellum for the generation of words compared to repeating a word, indicating a role for the cerebellum in language cognition. Reproduced with permission from [10], © Peterson *et al.* [10] *J. Cog. Neurosci.* MIT Press. (B) Resting state correlations between cerebellum and cerebral cortex show that hand regions in left and right cortex (white circles) are correlated with multiple, distinct contralateral regions in the cerebellum. Reproduced with permission from [12]. (C) Multiple visual maps in the cerebellum, from [2]. The underlay is a flattened representation of the cerebellum, and the color overlay shows the polar angle representation from the pRF model fits. Note the limited amount of green, meaning limited coverage of the upper visual field. (D) A comparison of visual and somatotopic maps in the cerebellum. The underlay is identical to (C). The red lines show the locations of the visual maps from (C). The brown drawings are cartoon depictions of the approximate representations of the body in the cerebellum, adapted from [18]. Note that the visual maps mostly overlap the eye regions.

that most of these neurons — about 80% — are in the cerebellum, a relatively small structure in the back of the head, dwarfed by the much larger twin cerebral hemispheres. What does the cerebellum do and how is it organized? A paper published recently in *Current Biology* by van Es *et al.* [2] reports evidence for multiple visual maps in the human cerebellum, an intriguing finding in the context of historical views of the cerebellum.

Since the early 19th century, the dominant view of cerebellar function has been that it coordinates movement. Flourens' [3] ablation experiments showed that animals lacking a cerebellum could execute movements, but the actions were irregular and uncoordinated. Gordon Holmes [4], analyzing gunshot wounds to soldiers in the first world war, found that cerebellar damage often caused impairments in posture, speech, gait and other forms of movement [4]. Interestingly, Holmes found no conclusive evidence of functional specialization in different regions of the cerebellum. This contrasts with his groundbreaking work in cerebral cortex using similar methods, in which he described a map of the visual field on the occipital lobe surface [5], expanding on the earlier findings of Inouye [6].

The idea that the cerebellum might be involved in more than motor coordination

took hold in the later 20th century. The detailed studies of cerebellar circuitry by Eccles and colleagues [7] in the 1960s were incorporated into computational theory by David Marr [8], who proposed that cerebellar circuits perform error-based motor learning via Hebbian plasticity. Marr's theory was influential because it linked a circuit description to behaviorally relevant computation. And by emphasizing learning, it opened the door to the possibility that cerebellar circuits are well suited to the general task of learning and memory, with the specific domain determined by connectivity to cerebral cortex. Indeed, anatomical tract tracing between cerebellum and cerebrum in monkeys [9] and positron emission tomography in humans [10] (Figure 1A) supported the idea that the cerebellum has different functional modules, and that it contributes to many aspects of cognition in addition to motor coordination [11], both conclusions in contrast to Holmes.

The advent of functional magnetic resonance imaging (fMRI) in the last 25 years has enabled a far more detailed study of the human brain. While our understanding of cerebellar organization and function derived from fMRI lags that of the cerebral cortex, it is perhaps starting to catch up. Buckner and colleagues [12]

leveraged knowledge of the cerebral cortex to study the cerebellum with fMRI. They used correlated fluctuations in the fMRI time series during rest to reveal a precise mapping between cerebellum and cerebrum (Figure 1B) and to propose a functional parcellation of the cerebellum. The resting state analyses have been complemented by high-resolution fMRI measures of stimulus- and task-evoked responses, which also support functional specialization [13,14]. Both resting state and task-evoked neuroimaging studies suggest that one cognitive domain of the cerebellum is visuospatial attention, perhaps in conjunction with eye movements. Areas of cerebral cortex involved in vision and visual attention are often organized in maps of the visual field. Does the cerebellum also contain visual maps?

Recent methodological advances have enabled the identification of dozens of visual maps in cerebral cortex, many of which are outside the occipital lobe [15]. It is now possible to identify multiple visual maps in the human frontal and parietal association cortices using population receptive field (pRF) modeling of responses to combined visual stimulation and spatial attention [16]. Nonetheless, it was not until last year that visual maps were discovered in the cerebellum.

Brissenden *et al.* [14] used pRF modeling to identify a visual field map in lobule VIIb/VIIIa of the human cerebellum that represents ipsilateral visual space and is active during spatial attention and working memory. This was an important finding with many possible applications. Maps enable researchers to reliably and repeatedly find precise locations in a person's brain and to thereby study an area in great depth. Maps often serve as the basis by which we compare measurements across labs, populations, and tasks, and maps underlie many theories of sensory function.

The new work by van Es *et al.* [2] exploits the power of the retinotopy data from the Human Connectome Project (HCP) to further characterize the visual topographic organization of the cerebellum. Benson *et al.* [17] provided pRF model solutions for 181 HCP participants, both for individuals and for the surface-aligned group average. These data are freely available to the public (<https://osf.io/bw9ec/>) and the new paper is a striking example of the promise of the shared resource. Using the HCP group-average data, van Es *et al.* [2] have obtained evidence for three visual clusters in the cerebellum arranged in five maps (Figure 1C).

One map identified by van Es *et al.* [2] overlaps with the one reported by Brissenden *et al.* [14], but appears to be restricted to lobule VIIb. The maps in the oculomotor vermis (OMV) and VIIIb appear to each contain two adjacent maps due to the reversals in the representation of polar angle in visual space. The authors confirmed the reliability of the maps using a split-half approach from the HCP dataset. Furthermore, they confirmed that these maps can be produced in individual subjects given a sufficient amount of data is collected.

Some features of the maps in cerebellum resemble those in cerebral cortex. For instance, angle and eccentricity representations within maps are largely orthogonal [6], and multiple maps border one another at polar angle reversals. As for maps in the cortex [15], van Es *et al.* [2] found a positive correlation between the size and eccentricity of modeled voxel receptive fields.

There are some differences as well. Unlike cortical maps, the cerebellar maps contain representations of the ipsilateral

visual field, consistent with the known lateralized organization of the cerebellum. Moreover, the maps do not cover the visual field as systematically and completely as maps in cortex. Namely, the OMV map appears to represent only the very central portion of visual space (less than the 1° fovea!), and all maps are heavily biased towards the lower visual field. And because the stimulus-evoked fMRI signal from these areas is noisy, the cerebellar maps are not clearly visible in most individuals scanned for typical retinotopy sessions (~30 minutes), unlike maps in occipital cortex.

Why were multiple maps in the cerebellum not found previously? Perhaps the challenging nature of imaging the cerebellum has hampered progress. Indeed, the cerebellum is situated deep in the head far from the radio-frequency coils MRI uses to make sensitive measurements, it moves with each heartbeat and breath, and requires specialized procedures to spatially align individuals for group averaged statistics [18]. And because of its small size, a typical MRI voxel in the cerebellum averages over diverse neural populations, reducing stimulus sensitivity. Just as important as the technical limitations, there are also likely functional limitations. Even in cerebral cortex, it has been challenging to measure maps in association regions such as parietal and frontal cortices, as they are not as powerfully responsive to simple visual stimuli as, say, primary visual cortex. Fully engaging these regions requires appropriate stimuli and tasks. The cerebellum is densely connected to parietal and frontal cortex [9], and so it is likely that it, too, will not be strongly driven by simple visual paradigms.

Going forward, it will be critical to establish the degree to which the idiosyncrasies in these visual field maps in the human cerebellum provide clues to their functions. In the macaque OMV, for example, the rate and timing of spiking in populations of Purkinje cells with directional selectivity encodes the amplitude (and velocity) of saccades [19]; saccade direction is encoded in different cells (a “place code”), whereas saccade distance is encoded in different spike patterns (a “rate code”). This seemingly agrees with the presence of a polar angle map but lack of eccentricity

gradients reported in the human OMV map. Likewise, the bias towards lower visual field representations in the cerebellar maps may provide insights that connect with our traditional theories of cerebellar function emphasizing motor processes and somatotopic organization. Indeed, our limbs and almost all of our body lie below our line of sight in our lower visual field. Perhaps these maps reflect the topography of visual inputs into the circuits involved in cerebellar-dependent visuomotor learning [20], and provide a visual interface to the well-known somatotopic maps (Figure 1D).

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Plant Genetics: Advances in Regeneration Pathways

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Two recent studies highlight the role of stem cell activation as a response to tissue damage and wounding.

Plants regularly encounter tissue damage during their lifetime. Their confinement to the place where they germinated makes it impossible to avoid wounding by abiotic and biotic factors, such as wind, extreme temperatures, grazing and trampling animals, or underground soil particles, which can cause wounding of the root. Not being able to escape those stresses, plants have evolved as masters of tissue regeneration. On the other hand, we use their regeneration abilities regularly in agriculture, where we can modulate plant growth by pruning without killing the plant, and also by grafting, a very common practice of combining high-yield shoots with pathogen-resistant root stocks.

Consequently, various approaches have been undertaken to understand regeneration of plant tissues. The first experiment demonstrating the role of regeneration capacity and positional signalling in determining the identity of the root cells was carried out by laser ablation [1]. That experiment was followed by others focusing on *de novo* organ regeneration, callus induction, grafting, and wounding response in *Arabidopsis* and other plant species. Xu *et al.* [2] and

Sena *et al.* [3] showed that the well-established stem cell niche maintenance genes *PLETHORA 1 (PLT1)*, *2*, *SHORTROOT (SHR)*, *SCARECROW (SCR)* and *WUSCHEL-RELATED HOMEODOMAIN 5 (WOX5)* also regulate wound healing after laser ablation and root tip excision. Later, research on callus induction and lateral root development suggested that the molecular programs governing callus development are similar to those in root establishment, even if the callus is derived from non-root tissue. There are also parallels to the first steps of lateral root induction and key players include *SCR*, *SHR*, *WOX5* and *ABERRANT LATERAL ROOT FORMATION 4 (ALF4)* [4]. A cell ablation experiment with bleomycin lead to the observation of *ETHYLENE RESPONSE FACTOR 115 (ERF115)*-governed cell divisions replacing the dead cells [5]. The network around *ERF115* – including the *PLTs*, *WOX5* and *WOUND-INDUCED DEDIFFERENTIATION 1 (WIND1)* – was studied further after laser ablation and hydroxyurea treatment to induce cell death. Heyman *et al.* [6] observed that the replenishing cell divisions were derived from the neighbouring cells after *ERF115*

induction. Using lineage tracing, Efroni *et al.* [7] saw that the dividing cell is usually the inner neighbour of the dead cell. Furthermore, the group stated that embryonic regulatory networks of root patterning are involved in re-specifying the root after excision.

De novo organogenesis experiments on leaf explants showed that the stem cell regulators *WOX11* and *12* and *LATERAL BORDER DOMAIN (LBD)* genes are involved in the specification of a hypophysis-like root founder cell following an auxin maximum after wounding and induce activation of *WOX5* and *7* [8,9]. Auxin biosynthesis by *YUCCA (YUC)* genes and polar auxin transport are essential in this process [10–12]. Aside from auxin, cytokinin has an important role in this process, and both hormones regulate each other to correctly position the stem cell niche both during *de novo* root organogenesis as well as during root tip regeneration [7,13]. Further genes functioning in wound healing have been revealed by grafting experiments and have put auxin transport, *ALF4* and *WIND1* in the centre [14]. Finally, a recent study used an enhanced version

