

larger the better — is absolutely vital. Without sentries, meerkats cannot feed safely; without helpers, they cannot breed successfully; without strength in numbers, they cannot hold territory. Through cooperation, individuals can increase the size and success of their group, and in so doing, improve their own individual prospects for survival and reproduction.

#### **Do all meerkats help equally?**

No, research has shown that the amount of help provided typically depends on the ability to help: well-fed individuals are more likely to expend energy for the benefit of others. But this is not to say that meerkats simply help indiscriminately. Female helpers, for example, preferentially feed female pups — probably because these pups, being the philopatric sex, represent the future workforce that might one day help to raise the helpers' own litters.

#### **How is it that we know so much about meerkats?**

Meerkats' striking sociability and their tendency to become habituated to the presence of human observers, make them eminently tractable model organisms for investigations into the evolution of social behaviour. A large-scale, long-term field study of meerkats in the southern Kalahari was initiated in 1993 by Tim Clutton-Brock of the University of Cambridge. This project, involving hundreds of thousands of man-hours of detailed behavioural observations coupled with long-term pedigree and life-history information has provided a wealth of data on cooperative breeding behaviour and constitutes the best database of such information that exists today for social mammals.

#### **What else have we learned from meerkats?**

Apart from serving as a model for the evolution of cooperation, the Kalahari meerkats have provided unique opportunities for research in other areas of biology too. Through observation and experiments, Marta Manser and her group at the University of Zurich have 'decoded'

many of the 30 or so calls, and the numerous postures, displays and olfactory signals that meerkats use. This work extends our understanding of animal communication and cognition. For example, meerkat alarm calls, which categorise threats according to both class and urgency, exhibit a level of complexity more typically associated with humans. Other behavioural studies have used meerkats to investigate why animals play, and recently they were used to neatly demonstrate that animals can, and do, actively teach their young. On the ecological front, meanwhile, meerkats have provided insight into the demographics, dispersal, and population genetics of social carnivores. For instance, long-term population data clearly demonstrate the "Allee effect": if meerkat group sizes fall too low, recruitment tails off rapidly and local population crashes can ensue. Finally, at a physiological level, meerkats are helping us to better understand the energetics, endocrinology and thermoregulation of small desert-adapted mammals.

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## Primer

# Structure and function of the cerebral cortex

Stewart Shipp

The grey matter of the cerebral cortex is a convoluted, layered sheet of tissue, 2–3 millimetres thick in man but with a surface area of several hundred square centimetres. This is not an adaptation to promote gaseous exchange, or heat loss — rather, if the grey matter is compact in at least one dimension, it is outgoing axons that may readily escape it; once outside, they club together and form the cortical white matter. If grey and white were intermixed, the average separation of neurons would be greater, creating extra neural 'wiring'. The speed of cortical computation would suffer accordingly.

The principle of economic wiring can also be invoked to account for regional specialisation of function across the surface area of the cortex. Put simply, neurons performing similar roles need to communicate, and do so more efficiently if nearby. When microelectrodes were first used for cortical recordings, an immediate discovery was that neurons in a radial column — a column perpendicular to the plane of layering — shared similar response properties: their receptive fields might all be located on the same patch of skin, or be selective for the same orientation of a contour at a certain location in the image on the retina. Moving tangentially through the sheet (parallel with the plane of layering) the discovery was that neighbouring columns have neighbouring receptive fields — the ensemble of columns ultimately giving rise to a cortical map of the relevant sensory surface. In sensory cortex, this engenders the 'one map, one area' principle for parcelling the cortical surface into discrete areas, each of which is thought to have some nuance of functional

specialisation. Cortical areas are richly interconnected — with each other and with subcortical structures — and the layering of the cortex reflects the radial organisation of all these input–output relationships. Indeed, the layered pattern is rather uniform over the expanse of the sheet, as if to serve basic ‘housekeeping’ operations that generalise across cortical applications as diverse as colour vision, speech and music.

One might assume that, if outputs to different destinations arise from separate levels in a column, there should be some differentiation in function to match. Thus, in principle, the study of cortical layers is the study of cortical specialisation in the radial dimension, and how it is conserved from area to area. Of course, there are subtle variations in the laminar structure across the cortical sheet, which form a complementary means of identifying separate areas, as for example in Brodmann’s century-old scheme for human cortex. Sometimes the laminar variations are not so subtle — the contrast between primary motor and primary visual areas (M1 and V1) being the most emphatic (V1 showing the highest degree of laminar differentiation, and M1 the least). These variations in cortical architecture have long been treated purely cartographically, betraying a lack of any analytic insight into the way different applications might modulate layer structure and function. This is largely because, as documented below, our appreciation of layers is still rooted rather more securely in anatomical than physiological cortical characteristics.

#### Cellular machinery

Neurons come in two main forms: excitatory (pyramidal) and inhibitory. Pyramidal neurons are named for their prominent apical dendrite, which typically points superficially. Customarily, a neuron ‘belongs’ to the layer in which its cell body is sited — even if the apical and basal dendrites, between them, span several more layers, picking up a broader range of signals. Pyramidal

neuron dendrites are covered in spines (specialised postsynaptic structures) and the density of spines, coupled to the degree of dendritic branching within a layer, indicate the parent neuron’s commitment to sample signals from that layer.

Inhibitory neurons, despite being in a minority (20%), are rather more diverse in their morphology. Some forms have attracted familiar names, for example basket cells and chandelier cells, on account of their characteristic axonal ramifications, forming ‘baskets’ around cell bodies, or making multiple strings of contacts (‘chandeliers’) around axon initial segments. The names are not simply fanciful, because the contact region on the target cell — axon, cell body, proximal or distal dendrites — is a useful component of a systematic classification. Inhibitory neurons are also known as local circuit neurons, or simply interneurons, because, in the cortex at least, their axons are purely ‘intrinsic’ — they do not enter white matter and make only short-range, local connections. Some pyramidal cells act similarly, but others make both short and long range connections. The latter are carried by axons passing through white matter termed ‘extrinsic’.

In a classic of the developmental literature, the cortex is created ‘inside out’, as newborn pyramidal cells migrate, radially, away from the proliferative zone to form layer 6 first, and layer 2 last. Layer 1, which in adults is largely cell free, originates from the marginal zone of the developing cortical plate, a likely source of the signalling molecule, semaphorin 3A, known to polarise the initial growth of apical dendrites. Inhibitory cells have diverse origins, migrate tangentially, and at least one major class displays an ‘outside-in’ gradient of neurogenesis. The genetic mechanisms controlling this process are beginning to be unravelled; for instance, different sets of transcription factors are found to regulate the generation of neurons destined for layers 6 and 5, and those later destined for layers 4, 3 and 2. As we shall see, there are several sets of extrinsic

connections that make a similar distinction.

#### How cortex connects to itself

The diagram in [Figure 1](#) is billed as the connectivity of a generic, primate, non-primary visual area (also incorporating knowledge of rat and cat sensory cortices). A perverse choice, perhaps, given that details are scarce and there is, without exaggeration, an order of magnitude more information available concerning the intrinsic connectivity of primate V1 than for any other visual area. Yet V1 is just about the most exquisitely laminar structure known to neurobiology, likely to possess many idiosyncratic features. The detection of generic principles requires a broader cortical survey.

We can make a start following the well-beaten tracks of cortico-cortical communication. [Figure 2](#) depicts a string of areas forming a serial pathway. Looking from left to right, the pathways arriving at an area carrying new sensory signals terminate in layer 4; there is then an internal relay to layer 3, which is the primary source of output to layer 4 of the next area in line. The sequence is initiated by input into layer 4 of the primary cortical area from a primary (or ‘first-order’) relay nucleus of the thalamus, and is known as an ascending pathway. There is also, typically, a descending (or feedback) pathway issuing from layers 6 and 5, and terminating in layers 6, 5 and 1 of the area below.

The ascending-descending (A-D) patterns are sufficiently regular to constitute ‘rules’ of cortical connectivity: for instance, there are no known instances where reciprocal connections between a pair of areas are both ‘A’ (or both ‘D’) in format. Hence the laminar patterns can be used to infer the relative hierarchical status of a pair of connected areas, even where the relative distances from the primary area are unknown. Ultimately, a hierarchical chart encompassing the entire system can be constructed with all the constituent areas allocated to a succession of tiers. Higher tiers may involve several areas interconnecting with a symmetrical, undifferentiated laminar pattern,

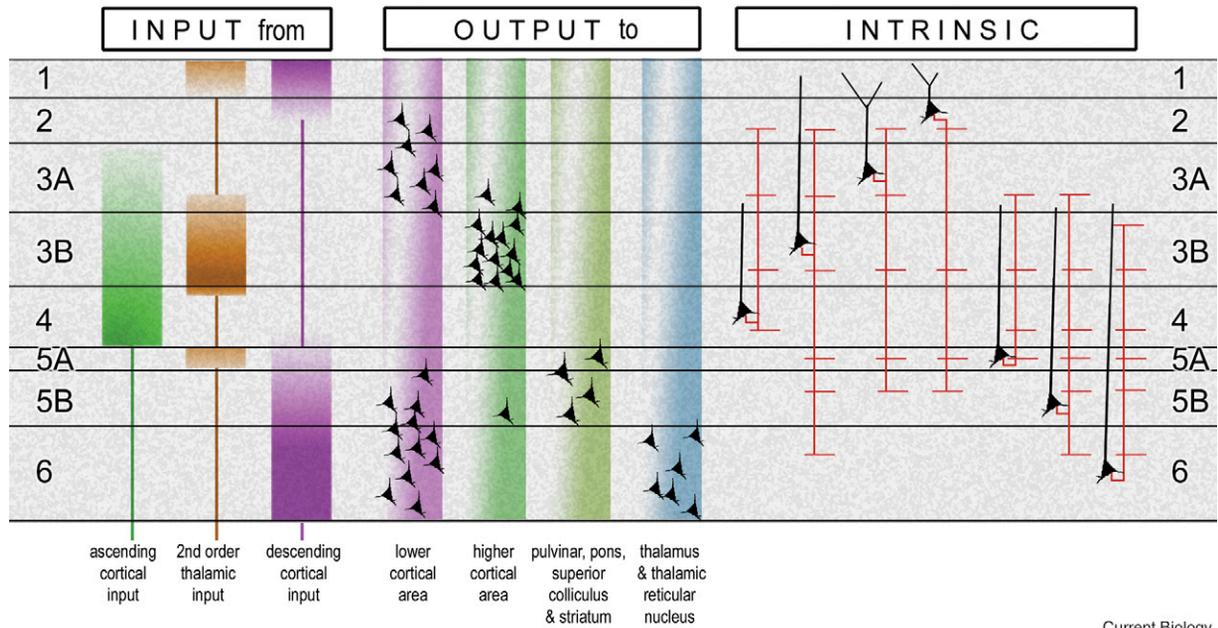


Figure 1. Summary of inputs, outputs and intrinsic excitatory connections of a generic, nonprimary visual area of primate cerebral cortex.

referred to as a 'lateral' connection. The exercise can be conducted for each of the visual, auditory and somatosensory systems and, to a degree, there are similar laminar patterns of connectivity within non-sensory frontal cortices.

There is, naturally enough, a rather greater degree of variability in laminar connectivity than the A-D scheme (as in Figure 2) admits. First off, connections can skip one or more levels in the hierarchy, and in so doing obey a 'distance rule': the connection actually adheres more tightly to the A-D laminar pattern the more levels it traverses. Connections between areas at immediately adjacent levels tend to be a little more liberal. For instance the ascending connection may include a component arising from neurons in layers 5 and 6, and it may terminate in layer 3 as well as layer 4. The descending connection may include a contribution from neurons in layers 2 and 3A, and terminate in a way that is less polarised toward the outer layers, 1 and 6. Second, where distinguishing A or D from L patterns becomes tricky, the laminar terminations are often more informative than the cellular origins. Third, where individual axons of a given connection are reconstructed in detail, there are

typically some details apparently unique to that connection (given that, to date, only a few connections have been scrutinised so closely). Overall, however, the systematics are unquestionably regular enough to begin to enquire how the A-D pathways work, and how they differ from each other.

#### The ascending pathway

The primary target of the ascending pathway, layer 4, is defined cytoarchitecturally by the dense packing of small cells and is also known as the 'granular layer'. Layer 4 cells in turn relay signals to layers 3 and 2. However, there is also a component of the ascending pathway that terminates directly within layer 3B, the primary source of the ascending output to the next stage. Does this mean that there is, minimally, a monosynaptic relay through each area? A shrewd guess is that this not so, although this is only known definitively for area V1, where the minimal relay (of thalamic signals) is disynaptic. The purpose of the pathway is to process rather than simply 'relay' signals, which requires more elaborate synaptic interactions.

The granule cells of layer 4 include a minority of inhibitory types, whose postsynaptic

structures can be recognised by electron microscopy, forming about 10–20% of all contacts made by the ascending axon terminals. Most of these terminals contact the dendritic spines of excitatory cells; however, fewer than 5% of excitatory synapses with spines in layer 4 are actually formed by the ascending input. The remainder are intrinsic connections between layer 4 pyramidal cells, and this may be a means of amplifying the incoming signal.

There are also extensive lateral connections formed between pyramidal cells in layers 3 and 2. Typically these are patchy in appearance, as if nests or clusters of cells with certain properties in common — such as similar orientation tuning, in visual cortex — selectively connect with each other. There is, in addition, the bewildering diversity of selective connections made by inhibitory neurons to ponder. It is reasonable to suspect that certain basic neural operations, known in shorthand as a 'canonical microcircuit', are repeated over and over again in the serial chain of areas — ultimately resulting in the synthesis of such exemplars as face selective neurons — but the details are little understood.

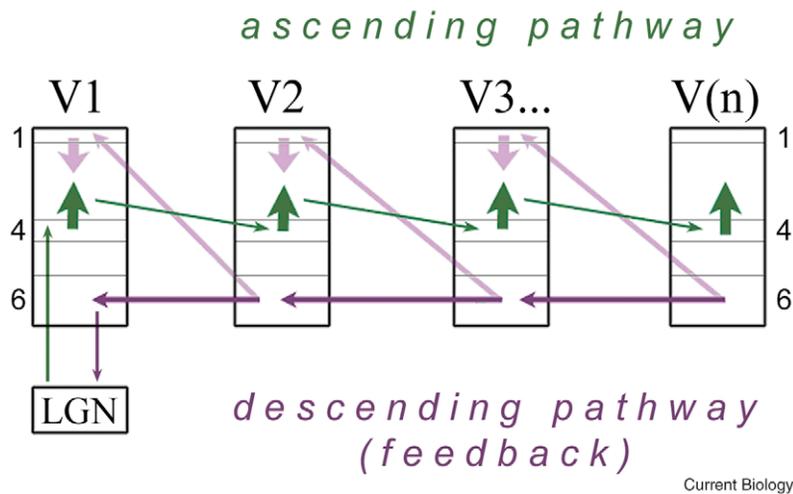


Figure 2. The laminar characteristics of ascending and descending connections along a serial (hierarchical) pathway of sensory areas in primate cortex.

Although layer 4 is a distinct cytoarchitectural structure, it is valid to question how far it, or any other layer, acts as a discrete functional sub-unit, as there are so many ways in which both excitatory and inhibitory neurons show total disregard for layer boundaries. For example, layer 4 contains spiny apical dendrites of layer 5 pyramids, and spiny basal dendrites of layer 3 pyramids; furthermore, the apical dendrites of layer 4 pyramidal neurons pass into layer 3. A valid functional subcompartmentation should show some systematic discontinuities in connectivity across layer boundaries, and these can be hard to identify. One good example is the absence of excitatory, intrinsic feedback from layer 3 to layer 4. Not only do the pyramidal cells of layer 3 fail to make synaptic contacts as their axons pass through layer 4 toward white matter, but their collateral axons ramifying within layer 3 also avoid contact with the apical dendrites of layer 4 pyramidal neurons. This clearly effects some degree of separability between neural operations within the two layers, consistent with a minimal 'two-stage' processing within each tier of the ascending cortical pathway.

#### The descending pathway

As mentioned above, both the origins and terminations of the descending pathway tend to

avoid the middle layers. Layer 1, often the principal target of this pathway, is a unique stratum almost entirely devoid of neuronal cell bodies, apart from a few inhibitory neurons. It is composed largely of incoming axonal ramifications and the branching apical dendrites of pyramidal cells, mostly those of the upper layers but some sited as deep as layer 6. The remaining component is a rich contingent of glial cells, perhaps signifying a distinct local blend of neurochemistry, but one whose physiological significance remains wholly mysterious.

Sourcing the origins of the descending pathway, the major inputs to layer 5 come from layers 2/3, often formed by extensive collateral branches of output axons heading toward white matter. The input from layer 2/3 to layer 6 is, by comparison, rather weaker, and more restricted to underlying neurons in the same radial column. Layers 5 and 6 themselves are interconnected but, of the two, layer 6 appears less intensively integrated into the local intrinsic circuitry; conversely, layer 6 is typically a richer source and target zone for the extrinsic circuitry of the descending pathway.

The action of the descending pathway is often termed 'feedback', an implicit assumption that it is triggered as an echo of ascending signals. However, the simple overview of A-D systematics

(Figure 2) immediately suggests that each pathway, using a distinct set of layers, is capable of some autonomy. Anatomically, an independent chain of activation relayed backwards from layer 6 to layer 6 looks possible. Or, in a cognitive context, the descending pathway could serve as a conduit for top-down effects related to attention. Using the visual system as an example, there are many indications that attention to particular objects, features or locations in the visual scene is associated with increased activity of the neurons with matching receptive field characteristics. In a similar vein, the descending pathway could mediate expectations, or higher level hypotheses as to what may be present in the retinal image (imagine looking for a familiar face in a crowd). The intrinsic interactions across layers could then be viewed as a matching process, between visual signals looking for an explanation and visual hypotheses searching for evidence.

The fact that this is couched in semi-theatrical terms reveals a paucity of any more profound mechanistic understanding of the interaction between these two streams. One proviso to the above scheme is that descending connections are generally considered to be 'modulatory' rather than 'driving' in action — capable of modifying ascending activity, but not of initiating activity *de novo*. The ascending pathway appears to have a driving character, as illustrated by the systematic growth in receptive field size caused by spatially convergent connections from one level to the next. The neurons at each level are capable of being activated by a small subset of their afferents. There is at least as much, if not more, spatial convergence in the descending pathway, and if the synaptic efficacy were also no different, receptive fields at the lower level would soon inherit the pooled size of the higher level fields. As this is not observed — in any layer of any area of any species so far studied — it is relatively safe to conclude that the synaptology of the ascending and descending pathways must differ significantly.

The strict implication is that descending activity cannot normally propagate across levels in the absence of an ascending substrate with which to interact. But if, in abnormal circumstances, it were to have this capacity, we might be looking at a hallucination.

#### Variants of architecture

If the A-D system and its proposals for layer specialisation of function has any claim to provide a general account of the cerebral cortex, it must survive a stiff challenge from the motor system. The root of the problem is that motor cortex is, rather famously, agranular, and the lack of a layer 4 hinders the systematic diagnosis of A-D laminar patterns. If seeking to explore an analogy with sensory cortex, it is also unclear, *a priori*, which direction along the motor pathway is 'ascending': is it (a) from primary motor cortex (M1) to premotor cortex, on the grounds that M1 is closer to the effectors (spinal motoneurons), and has the simpler motor fields; or (b) the opposite, on the grounds that the higher premotor centres should 'drive' the motor commands issued by M1?

In terms of anatomy, model (a) is more correct, in that connections from higher to lower premotor areas, and to M1, show identifiably 'D' patterns of laminar connectivity. It is, however, difficult to find any good examples of a classical 'A' pattern of connection between motor areas. Instead, connections from M1 to premotor areas target all layers roughly equally (in the manner of a lateral connection in sensory cortex). Evidently, the lack of a clear ascending system relayed through a granular layer 4 might reflect the lack of a stream of input data that requires serial re-processing in a way analogous to sensory cortex. But how, then, can the full A-D model be adapted to the operation of motor cortex?

There are, in fact, ascending cortical inputs to motor areas — if defined, anatomically, by terminating in the middle layers — and these derive from bimodal visual/somatosensory regions of cortex. The sensory processing is thought to convert external object locations into body coordinates (object

location as specified in terms of shoulder, elbow and wrist joint angles required to grasp that object). The sight of an object by itself is sufficient to drive some premotor neurons — as if to code a potential act of grasping that is not necessarily executed. Another interesting category of premotor activity is demonstrated by 'mirror neurons' that can be activated by the sight of an action performed by another individual, when it is congruent with the neuron's own specificity in the production of body movement.

The premotor activity could thus be thought to represent motor concepts that might be translated into action by a descending or modulatory influence upon M1. It makes sense that this should not be a deterministic, driving action upon M1, because the appropriate use of muscles will depend on the current body posture and limb dynamics. Hence, the evolution of the motor output signal might depend on another kind of distributed matching process — between external object and internal body-related activity filtering through the intrinsic circuitry of motor cortex. This permits a provisional common framework for considering cortical communications within both the sensory and motor systems.

#### How cortex connects subcortically

The output from motor cortex to spinal motor neurons derives entirely from layer 5 pyramidal cells. In fact, layer 5 qualifies as the 'motor' output layer over the entire cortex, because nearly all signals directing behaviour emanate from this layer. Corticospinal neurons in layer 5 may be densest in M1 but are distributed amongst several somato-motor areas and in visual cortex, for instance, layer 5 is the source of output to the superior colliculus, a midbrain centre governing head and eye movements. The same layer of frontal eye field, meanwhile, has direct output to brainstem oculomotor centres. Other targets of layer 5 include the cerebellum (via the brainstem pontine nuclei), the striatum and the thalamus.

As mentioned above, layer 5 is closely integrated with layers 2 and

3, as if to sample the activity of these superficial layers. Generally speaking, layer 5 neurons have relatively large receptive fields, and are 'trigger-happy' — their high spontaneous activity reflects a resting membrane potential that is relatively close to the threshold for initiation of an action potential. The best-documented example is the output from V1 to superior colliculus, which is found to arise from large pyramidal neurons with apical dendrites rising to layer 1. Compared to other layers, or even other layer 5 neurons, these cells are less selective for the orientation and direction of a visual stimulus and totally insensitive to its colour. These are rational characteristics for an output signal that basically serves to provide spatial coordinates for the acquisition of target objects by the oculomotor system. A sophisticated target description (apart from basic details concerning location/size/shape) is, presumably, irrelevant to the ocular or skeletomotor apparatus, and can be locked up in cortical circuitry for the unique appreciation of our cognitive faculties.

Layer 6 also connects to the thalamus (including its inhibitory sheath, the thalamic reticular nucleus) — but as this is merely the outgoing component of a cortico-thalamo-cortical loop, layer 6 does not act as an alternative gateway for cortical signals to directly influence behaviour. As a rule, neurons making either cortical or subcortical connections form separate populations. There is considerable diversity within each population, although the picture is confused by the fact that the outputs are frequently carried by axons bifurcating toward two or more targets: much or all of the layer 5 output to thalamus, for instance, is formed by collaterals of axons travelling toward the brainstem. There is one prominent set of neurons, the giant Meynert cells of primate primary visual cortex, that manage to flout all the above generalisations, in that they: are sited in layer 6; connect, via bifurcating axons, to both the superior colliculus and a higher cortical area, V5/MT; and have short, stubby apical dendrites.

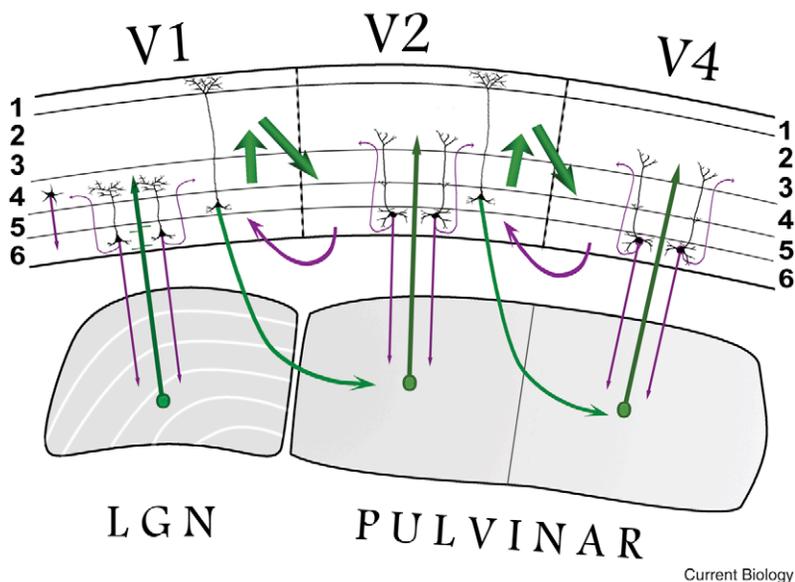


Figure 3. Schematic treatment of the driving and modulatory interactions between visual cortex and visual thalamus.

Green connections are inferred to be driving, in the sense of being capable of initiating activity *de novo*. Modulatory connections (purple) are thought not to have this capacity. The topographic arrangement of layer 5 and layer 6 afferents in pulvinar is not known to be quite so precise as illustrated here (specific territories governed by specific V2/V4 afferents). Also omitted are known geniculate afferents to V2 and V4.

#### How do layers 5 and 6 differ?

A comparison of the respective thalamic connections is highly instructive in regard to the differing functional roles of the subcortical outputs issuing from layers 5 and 6. The former is regarded as ‘driving’ and the latter as ‘modulatory’, as mooted above for the action of the A and D cortical pathways, although the thalamic evidence is the more robust. These differing characteristics are part and parcel of the distinction between first and second order thalamic nuclei, as shown in Figure 3. A first order nucleus is a classic ‘relay’ nucleus, such as the dorsal lateral geniculate nucleus (LGN) of the visual system, which feeds V1 and receives feedback from layer 6 of V1. Output from layer 5 of V1 does not terminate in the LGN, but only in the second order nucleus (i.e. the pulvinar nucleus within the visual system).

The second order nucleus is defined by the fact that it receives scant direct sensory input; instead, its driving inputs are provided from cortical layer 5. Anatomically, layer 5 terminals in the pulvinar match retinal terminals in the LGN. Each forms only a small minority of the

overall input to their respective nuclei, but the terminals are large and strategically placed on proximal dendrites (close to the cell body). It is the retinal terminals that confer their response characteristics upon geniculate cells, and layer 5 afferents to pulvinar are expected to achieve a similar driving effect. By comparison, terminals of layer 6 afferents are smaller, and terminate less focally.

The interaction between V1 and the LGN has been studied more intensively than any other feedback system. Cortical feedback appears to modulate the response of the geniculate neuron to a feature according to its context within the surrounding image. On a blank surround, the response is amplified (positive feedback). One such, notable, effect is a capacity to synchronise the responses of nearby LGN neurons responding to the same feature, such as an extended contour.

Within V1, there is a uniquely close association between layers 4 and 6 (which can be seen across species, and in other primary sensory areas too). Evidence for this association is that geniculate afferents terminate in layer 6 as

well as layer 4; there are direct outputs from layer 4 to layer 6, which are more prominent in primary cortices than elsewhere; the layer 6 pyramidal cells sending output to the LGN also sample layer 4 activity via branches of their apical dendrite within layer 4; and these same neurons also have ascending axon collaterals that arborise specifically within layer 4 (Figure 3). Anatomically, the 6-to-4 loop thus resembles a short-circuit amidst the cortico-geniculate feedback system, and there are reasons for thinking that it, too, is modulatory (it terminates mainly upon inhibitory neurons and, like monocularly driven LGN neurons, layer 4 neurons do not inherit layer 6 properties such as binocularity).

Corticogeniculate layer 6 neurons, and other layer 6 neurons (which may make intrinsic or extrinsic cortical connections) differ in some key respects. The latter have relatively widespread local axonal connections, contacting mainly other pyramidal neurons; the former (corticogeniculate) neurons have a more locally restricted axonal territory and a preference for contacting nearby inhibitory interneurons. The corticogeniculate neurons are therefore implicated in a local competition, mediated through the local inhibitory network. And, if competing with each other, this will effectively be a contest for the representation of a particular feature, for example between the orientations represented in adjacent cortical columns.

#### The functions of subcortical loops

Assembling the various pieces of this jigsaw, the picture is that of a corticogeniculate feedback system mediating a competitive process between the alternative features that might be represented at a particular image location, acting to select and amplify the dominant feature during any given period of eye fixation. Can such an interaction between V1 and LGN be used as a general model for the interaction between non-primary cortex and second-order thalamus? Given the lack of experimental data, this has to remain an open question. The obvious puzzle is that higher areas (nominally ‘V2’ and ‘V4’ in Figure 3) have a dual source

of likely driving inputs: from layer 3 of a lower area, relaying directly to layer 4, and from layer 5 of the same lower area relaying, via the thalamus, mainly to layer 3.

It is normally assumed that the hierarchical development of sensory representations is primarily constructed by the direct, ascending cortical pathways that represent a wider range of features at a higher level of precision. The second-order thalamic input should therefore adopt a different kind of role, and one reasonable inference is that it plays a part in spatial selective attention. Again, using the visual system for illustration, there is a well-documented anatomical and psychophysical overlap between the control of eye-movements and the deployment of covert attention, a consideration which helps to make sense of the fact that the layer 5 outputs to the pulvinar originate from neurons also communicating with the superior colliculus. Hence, assuming that the layer 5 outputs carry an object-selective signal, they could act via the pulvinar to exert a regulatory influence over the transcortical networks formed by the information-rich, superficial layers — specifically, perhaps, to propagate object-selective bias between the different kinds of object descriptions found in different visual areas.

The subsequent reciprocal interaction between layer 6 and the pulvinar could be more analogous to the corticogeniculate system, at least insofar as many layer 6 neurons have apical dendrites and axonal collaterals arborising within the pulvinar terminal zone (layer 3, as opposed to layer 4). The neural dynamics of the interaction are certainly unknown but, commensurate with an attentional process, it is at least worth noting that the topography of cortico-pulvinar relationships is considerably less precise than that of corticogeniculate relationships, permitting neural competition to develop over broader stretches of cortical maps, and hence between objects at separate, distinct spatial locations.

### Epilogue

The complexities of cortical circuitry are nothing short of fiendish, and

the problem of integrating genetic, morphological and physiological details from diverse cortical areas and across diverse species is a worthy challenge to the burgeoning science of neuroinformatics. Though inconsistencies abound, the fact that some trans-areal, trans-specific generalisations are possible, and justified, is a quite remarkable observation. Following the strategy of ‘know thine enemy’, it appears that the cortical fiend has some interesting habits, which we can usefully begin to tag with some shorthand, functional labels.

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# Rapid advancement of spring in the High Arctic

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Despite uncertainties in the magnitude of expected global warming over the next century, one consistent feature of extant and projected changes is that Arctic environments are and will be exposed to the greatest warming [1]. Concomitant with such large abiotic changes, biological responses to warming at high northern latitudes are also expected to outpace those at lower latitudes. One of the clearest and most rapid signals of biological response to rising temperatures across an array of biomes has been shifts in species phenology [2–4], yet to date evidence for phenological responses to climate change has been presented from most biomes except the High Arctic [3]. Given the well-established consequences for population dynamics of shifts in the timing of life history events [5,6], it is essential that the High Arctic be represented in assessments of phenological response to climate change. Using the most comprehensive data set available from this region, we document extremely rapid climate-induced advancement of flowering, emergence and egg-laying in a wide array of species in a high-arctic ecosystem. The strong responses and the large variability within species and taxa illustrate how easily biological interactions may be disrupted by abiotic forcing, and how dramatic responses to climatic changes can be for arctic ecosystems.

Most long-term records of phenological events are from north-temperate environments. Recent comprehensive studies from this region have reported