

Constraints on cortical and thalamic projections: the no-strong-loops hypothesis

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The many distinct cortical areas of the macaque monkey visual system can be arranged hierarchically, but not in a unique way. We suggest that the connections between these cortical areas never form strong, directed loops. For connections between the visual cortex and particular thalamic nuclei, we predict that certain types of connections will not be found. If strong, directed loops were to exist, we suggest that the cortex would go into uncontrolled oscillations.

The macaque cerebral cortex has many visual areas that can be distinguished on the basis of connectivity, architectonics and receptive field organization. In a well-known review paper, Felleman and Van Essen¹ arranged these areas in a rough hierarchy, with area V1 (also called the striate cortex or area 17) at the bottom. It is a unique feature of the cerebral cortex that it consists of regions of quite similar structure than can be connected in series. This is in marked contrast to other major brain systems, such as the thalamus, the basal ganglia and the cerebellum, which deal with many different parallel inputs but do not form repeating serial sets of connections. The different regions of the thalamus, for example, are not directly connected to each other in series.

In the mammalian visual system, a cortical area higher in this serial hierarchy can form representations of complex visual objects that are built up from less complex visual features at lower stages. The ability to add additional areas to such a hierarchy, while still allowing the system to learn, is probably the secret of the success of the cerebral cortex in evolution.

Felleman and Van Essen¹ constructed their hierarchy by using a set of rules (Fig. 1) based on an earlier suggestion². A connection between two cortical areas is considered as ascending in the

hierarchy if it terminates mainly in cortical layer 4, especially if it originates in the supragranular cortical layers (layers 2 and 3). It is considered as descending in the hierarchy if it avoids layer 4, and terminates strongly in layer 1 and possibly in layer 6 as well. These are their strong rules.

They also considered what they called lateral connections, which connected cortical areas at the same level in the hierarchy, for instance between areas MT and V4. The connections could originate in all layers that project out of the cortical area (that is, from all layers except layers 1 and 4) and could terminate in all layers. This is their weak rule. Here we will consider only their strong rules.

Felleman and Van Essen¹ placed the (mainly) visual areas on a hierarchy having ten distinct levels, but they admitted that there were irregularities. In their words, these irregularities “raise the issue of whether the cortex is inherently only a ‘quasi-hierarchical’ structure that contains a significant number (perhaps 10%) of bona fide irregularities and exceptions to any set of criteria that can be devised. Alternatively, the visual cortex might contain an essentially perfect anatomical hierarchy that has been imperfectly studied using inherently ‘noisy’ methods of anatomical analysis.”

The idea of a unique hierarchy has been criticized by Hilgetag,

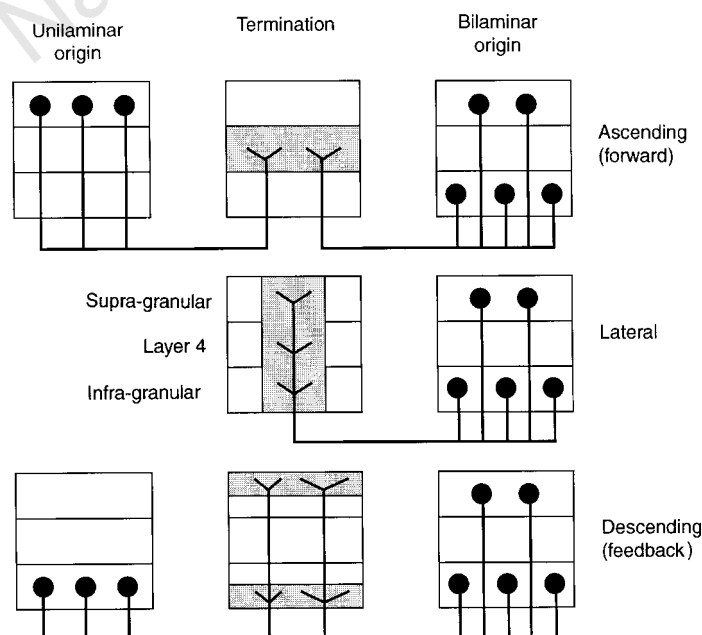


Figure 1 Rules used by Felleman and Van Essen¹ for deciding whether a projection between two cortical areas in the macaque monkey is ascending, descending or lateral (based on Fig. 3 of ref. 1).

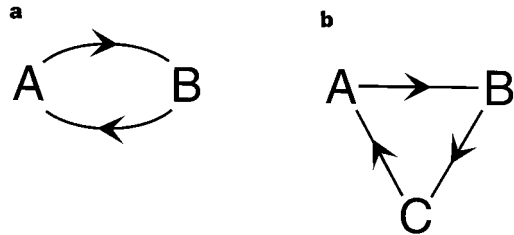


Figure 2 Forbidden cortical loops. A, B and C represent distinct cortical areas. Arrows represent strong driving connections into cortical layer 4. **a**, Binary loop; **b**, tertiary loop. The examples shown are not found in the macaque visual cortex, at least in the lower parts of the visual hierarchy.

O'Neill and Young³, who have used an evolutionary optimization algorithm to find hierarchies that have the fewest departures from a perfect hierarchy. They showed that many hierarchies were possible, each with a number of violations of the rules. They noted that if 36 of the less-reliable constraints were excluded, then there were only two violations. They concluded, "The primate cortical visual system is therefore surprisingly strictly hierarchical, but it is nonetheless not possible to determine the exact hierarchy."

The no-strong-loops hypothesis

We address the question: are there any constraints on the type of connections that can be used to form a hierarchical system? Our suggestion is that the system must avoid strong connections that connect areas in a closed loop.

What do we mean by 'strong connections'? In quantitative terms, this is, at present, a vague idea. In qualitative terms, we would like to believe that an appreciable connection into layer 4 is a driving connection (which we consider to be strong), and a connection to layer 1—mainly to the apical dendrites of pyramidal cells—is a modulating connection (which we consider to be weak). By driving inputs, we mean one or more inputs that, by themselves, can make the relevant neurons fire strongly. By modulating inputs, we mean one or more inputs that, by themselves, cannot make the relevant neurons fire strongly, but can modify the firing produced by the driving inputs. It can be argued that the driving inputs contribute mainly to the classical receptive field of a neuron, and the modulating inputs largely to the non-classical receptive field.

We shall call the first type of connection a D_{cc} connection and the second an M_{cc} connection (the subscript cc means cortex-to-cortex). Our cortical hypothesis is that if we consider only D_{cc} connections between visual cortical areas, they will never form a directed loop, either a binary loop (Fig. 2a) or a tertiary loop (Fig. 2b), nor any higher-order loop. Notice that we are talking about connections between cortical areas, not connections between individual neurons.

Close inspection of the data of Felleman and Van Essen¹ shows that this rule is always obeyed. As far as we know, there does not appear to be any more recent experimental evidence that contradicts it, at least for the earlier parts of the visual hierarchy, although the evidence for the later parts is very skimpy.



Figure 3 An acyclic digraph with eight nodes (A to H), drawn so that all the arrows point upwards. In **a**, the nodes are all drawn at different levels. Many other arrangements of levels are possible. In **b**, these nodes have been drawn using the minimum possible number of levels (five). In this case, there are two other possible ways of doing this. The one shown exhibits the unique numbering of levels used by mathematicians. (Notice that it would make no difference to the levels if there were an additional arrow from A to D.)

Digraphs

A hierarchy without directed loops is not necessarily unique. This follows from the mathematical theory of directed graphs, or digraphs as they are often called⁴. A digraph consists of a series of nodes (in our case, cortical areas) connected by lines, each line having an arrow on it to show its direction. If a digraph has a directed loop, then it is not possible for the nodes to form a hierarchy of levels. If it has no directed loop, the nodes can form a hierarchy, but it may not be a unique one.

An example may make this clearer. Consider the digraph in Fig. 3a: it is easy to see that, for example, nodes B, D, E and G could all be drawn at levels above F (but below H), or that they could all be drawn below C (but above A). Many other arrangements of the exact levels of the nodes are possible, but each one is a possible hierarchy and none of them has directed loops. Even if one adds the constraint that the number of levels should be kept to a minimum⁵, there are in this case three possible hierarchies, each with five levels (one is shown in Fig. 3b). However, there is a unique way of numbering the levels of an acyclic digraph: each node is assigned an integer equal to the number of links in the longest path from the lowest level to it (Fig. 3b).

We will postpone a more general discussion of possible reasons for our hypothesis until we have considered a possible extension of it to connections between the cortex and the thalamus.

The visual thalamus

The dorsal visual thalamus in primates consists mainly of the well-known lateral geniculate nucleus (LGN) and the less-studied but much larger pulvinar. The visual pulvinar has at least three major parts: the inferior, the lateral and the medial pulvinar. Unfortunately, these divisions are not completely clear-cut because the evidence is very patchy.

This is partly because the divisions are sometimes based on architectonics, sometimes on their connections, and sometimes on physiological properties. Moreover, each of these major regions probably contains subregions. For example, a chemoarchitectonic (staining) description of the macaque inferior pulvinar⁶ (as defined by the authors) suggested that it had five possible subdivisions. It is likely that half a dozen or more separate maps of the visual environment exist in the various pulvinar nuclei⁷.

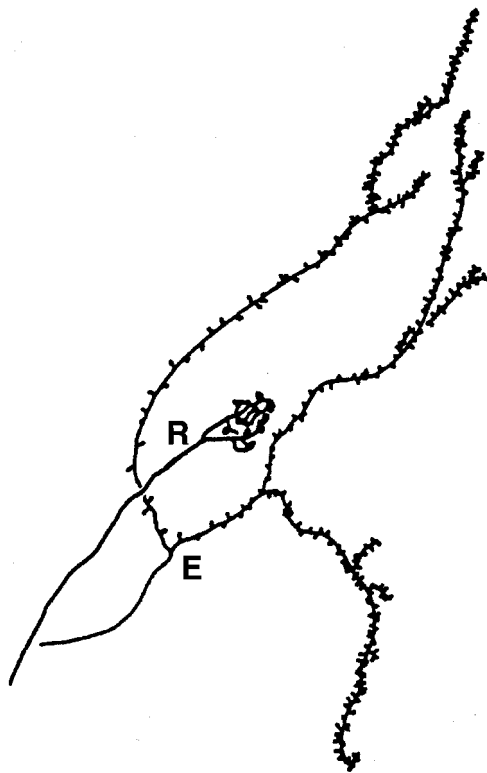


Figure 4 Termination of a typical R (round)-type corticopulvinar axon and an E (extended) corticopulvinar axonal termination. The diameter of the terminal field of the R-type axon is $\sim 100\ \mu\text{m}$. Based on data from the macaque monkey (taken from part of Fig. 24 of Rockland¹²).

There is good evidence that the asymmetric synapses formed by afferent inputs to the thalamus are of two main types^{8–15}. The axon terminals of one type are invariably concentrated in sharply delineated arbors; Rockland¹² calls these R (round)-type terminations. The other type are densely arrayed along axons of slightly smaller calibre, which Rockland calls E (extended). The two types are shown in Fig. 4.

R-type terminals are beaded and characteristically large ($3\ \mu\text{m}$ in diameter), although variable in size and actual shape. They conform to the classical type-2 endings, as described in specific thalamic nuclei¹⁶. The associated axonal terminations are concentrated in sharply delimited, round arbors and carry of the order of 100 terminals, that typically end on proximal dendrites.

E-type axons have stalked or spinous terminations of classic type-1 corticothalamic endings¹⁶. Their axonal terminal fields are elongated and quite extended ($1\text{--}3\ \text{mm}$) and carry between 500 and 1,000 E terminals that typically end on distal dendrites.

In the LGN, the driving input from the retina is provided by R-type axon terminals, with type-2 synapses; the input back from cortical area V1 has E-type axon terminals, with type-1 synapses. We shall tentatively assume that the latter is a modulating input, in spite of the fact that there are many more E-type than R-type axons. In part, this is based on the fact that eliminating or transiently inactivating primary visual cortex has only weak, secondary effects on the receptive field properties of geniculate cells^{17–19}.

More recent evidence^{11,12,14} shows that the same two types of axon (and synapse) are also found in the macaque pulvinar. Thus we shall generalize our assumptions by postulating that the R-type is a driving connection (which we shall call d_{ct} , where the subscript means 'cortex to thalamus'), and that the E-type (though more numerous) is a modulating connection (which we shall call m_{ct}). The properties of the two types of corticothalamic connections are

summarized in Table 1. It is highly likely that all these connections are excitatory, using glutamate as neurotransmitter.

The E-type cortical axons probably derive from medium to small pyramidal cells in the lower cortical layers. The evidence available suggests that they are located in layer 6, and as a rule always have collaterals in the thalamic reticular nucleus. There is suggestive evidence^{12,13,20} that cortical R-type axons originate from pyramidal cells in cortical layer 5. In the case of rat V1, some of these cells project to the tectum and the pontine nucleus, whereas for V1 in the macaque, some of these layer-5 cells branch and project to both superior colliculus and the pulvinar²¹.

Thalamic projections to the cortex

Projections from the thalamus to the cortex also fall into two classes. The first type goes mainly into layer 4 or lower layer 3, with a minority also contacting processes in layer 6. The projection cells in the magno- and parvocellular laminae of the monkey LGN are prominent examples of such a connection that can very reliably drive cortical cells, despite their small number of synapses²². Note that a large number of synaptic inputs are not needed to drive a cell reliably. As few as 2.8% of all excitatory synapses on a layer 4C α spiny stellate cell originate from magnocellular cells in LGN²². To us, this is a prime example of a driving connection, so we will call it d_{tc} (where the subscript means 'thalamus to cortex'). The other type projects to layer 1, but not exclusively. We postulate that this is a modulating connection and call it m_{tc} . An example of this is shown by cells in the interlaminar zones of the LGN that project into the superficial layers of V1²³.

We can now state our extended hypothesis: in the primate visual system, if we consider only what we have called driving connections (that is, corticocortical connections of type D_{cc} , corticothalamic connections of type d_{ct} , and thalamocortical connections of type d_{tc}), then these connections never form a strong directed loop.

This extended hypothesis is supported by Jones' rule, put forward by Jones in his monograph on the thalamus²⁴. He suggested that connections between the cortex and the thalamus usually fall into two distinct classes, as shown in Fig. 5a. (1) If a cortical area projects to a thalamic region from cortical layer 6, then if there is a reverse projection, it goes mainly into layer 4 or lower layer 3; (2) if a cortical area projects to a thalamic region from cortical layer 5, then if there is a reverse projection it avoids layer 4 and often goes mainly to cortical layer 1. These thalamocortical projections are usually much more diffuse than the layer 4 projection.

It is not clear at the moment whether Jones' rule is always obeyed. Jones' rule is certainly obeyed in the case of V1. Here, the cortico-geniculate pathway originates in layer 6, whereas most geniculate axons terminate in layer 4 (ref. 15). The projection from V1 to the pulvinar originates in layer 5; the backprojections from the pulvinar to V1 appear to end superficially in layers 1 to 3, rather than in layer 4.

There is evidence that some of the projections from parts of the pulvinar to extrastriate cortex end in layers 3 and 4, and others mainly in layer 6, avoiding the middle layers²⁴. The precise details of the connections between the many visual cortical areas and the various subdivisions of the pulvinar are not known, except that the corticopulvinar pathways always originate in an infragranular layer^{12,25}.

What might Jones' rule mean in our terminology? Let us assume (as seems likely) that projections from cortical layer 6 are formed by

Table 1 The two main types of corticothalamic connections*

Axons	Synapses	Location on dendrites	Character
R type: few	Type 2, beaded	Proximal	Driving (?)
E type: many	Type 1, stalked	Distal	Modulating (?)

* See Fig. 4.

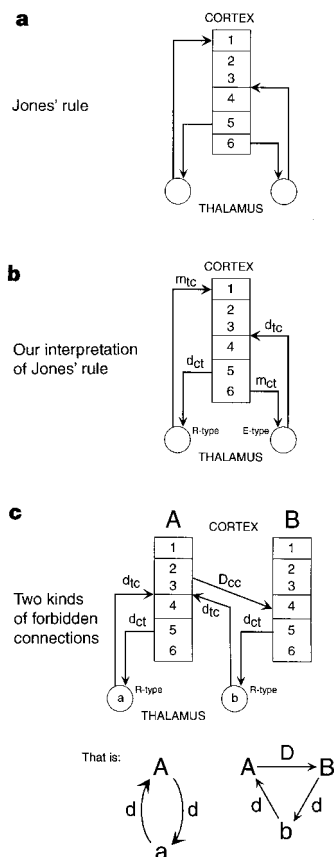


Figure 5 Permissible and forbidden connections between thalamus and cortex. **a**, Jones²⁴ described the two types of connections between thalamus and cortex he had observed, based on their layer of origin and termination. Rule 1 is illustrated on the right; rule 2 on the left. **b**, Our interpretation of these rules in terms of driving connections (d_{ct} into cortical layer 4 or d_{ct} from the lower layers and having R-type synapses) and modulating connections (m_{ct} into layer 1 or m_{ct} from layer 6 and having E-type synapses). **c**, Our no-strong-loops hypothesis rules out these types of strong connection between the thalamus and cortex. (In this pair of diagrams, the modulating pathways have been omitted to avoid confusion.)

E-type axons—which we called an m_{ct} connection—and projections from layer 5 by R-type axons, which we called a d_{ct} connection. Figure 5b shows our interpretation of Jones' rule. Jones' rule does not deal with the connections shown on the left of Fig. 5c, which is forbidden by our hypothesis, because it has two driving connections in a loop. In short, Jones' rule supports our hypothesis.

However, our hypothesis also extends to tertiary and higher interactions, where it states we should never find connections as those shown on the right-hand part of Fig. 5c. To test our extended hypothesis properly, it will be necessary to have a clean division of the pulvinar into distinct regions, and more experimental data on exactly how these various regions connect to the many cortical areas in the visual cortex.

Strictly speaking, our hypothesis applies to the type of axon (R or E), whereas Jones' hypothesis considers the cortical layer of origin. Although R-type cortical axons probably arise from layer 5 in most cases, there may be exceptions.

In formal terms, then, what we predict is that if a certain thalamic region, x , projects strongly to the middle layers of a certain cortical area, Z , then any projection x receives from R axons must come from a cortical area Y , which is lower in the cortical hierarchy than Z . That is, Z should not project (directly, or through cortical intermediaries) strongly into the middle layers of Y .

It might be considered that with so many connections between the cortex and the pulvinar, it would be difficult to avoid forming at least a few strong directed loops: this need not be the case. Noting that the postulated driving connection from layer 5 of V1 to the pulvinar is in an upward direction in the visual hierarchy, we can avoid directed loops if none of the strong connections projects downwards in the hierarchy. A simple example of such a set of permissible driving connections is shown in Fig. 6.

This hypothetical example hints that the strong connections are all of the feedforward type, and that the visual cortex is basically a feedforward system that is modulated by the various feedback connections. (This is not to say that such modulation may not be very important for many of its functions.) Whether this overall view of the macaque visual system is correct remains to be discovered. Notice that some of these postulated strong pathways go through the pulvinar, as has already been stressed¹⁴. This aspect of pulvinar connections has often been ignored.

Unfortunately, it is unclear what should be considered a single region of the pulvinar. It may be a fairly large volume defined, for example, by its staining properties⁶. However, from our point of view it might have a smaller volume, because the extent of axonal collaterals of thalamocortical cells within the thalamus appears to be minor, in contrast to cortex where intracortical connectivity can be quite extensive. Thus, to some extent, a small volume of the pulvinar might act largely independently of neighbouring volumes, and so might be considered a 'region' from the point of view of our hypothesis.

As there are likely to be fewer large regions of the pulvinar than cortical areas to which it connects, it will be of interest to discover exactly which subset of cortical areas receives a d_{ct} connection from a particular pulvinar region. It is possible that all of these cortical areas can be considered to occur at one particular level in the visual hierarchy.

Theory

Assuming that further experimental evidence confirms our no-strong-loops hypothesis, what could be the reason for it? The obvious explanation is that a strong excitatory loop would throw the cortex into uncontrolled oscillations, as in epilepsy. It could be contended that there is enough local inhibition in the system to choke off such oscillations, but the fact that epilepsy does occur suggests there are limits to the control that inhibition can have over nascent oscillations. We thus think it likely that the reason no strong loops are observed (if this is true) is that the system could not constrain their effects, possibly because neurons are usually kept in a jittery state near the edge of excitation in order to make them respond more promptly, so that the amount of inhibition in the system is limited. The obvious test would be to construct a strong loop in some way, but this is beyond our present experimental capabilities.

It is well known to neural-net modellers (H. White, personal communication) that although neural nets can be constructed with feedback connections that form loops, they do not work satisfactorily if the excitatory feedback is too strong (for several special cases, see refs 26, 27). This was also true for early radio sets that emitted howls (caused by positive feedback) if the volume control was turned up too high. However, it is almost impossible at the moment to use detailed neural network models to prove our hypothesis, because too little is known about many of the connections and parameters involved.

Possible generalizations

Our hypothesis is sufficiently plausible that it could be extended to other parts of the nervous system. We have considered only the visual system of primates, but it could be extended to all parts of the cerebral cortex, and to all parts of the thalamus, including the intralaminar nuclei, and to other mammals and other vertebrates. It

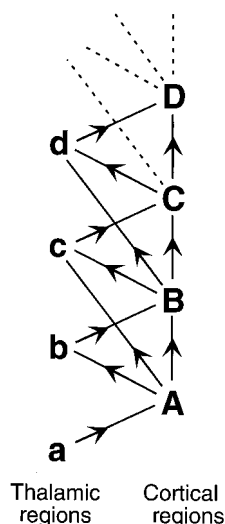


Figure 6 A hypothetical set of connections lacking strong directed loops. A, B, C and D represent cortical areas; a, b, c and d represent thalamic regions. Only strong (driving) connections are shown. Because no arrow points downwards in the hierarchy, no strong directed loops can occur. It is easy to add further strong connections, provided they all point upwards. Note that this diagram suggests that each thalamic region can be assigned a unique level.

might be instructive to consider to what extent connections of the superior colliculus, the claustrum, the cerebellum and the basal ganglia into or out of the cortex and thalamus can be classified as driving or modulating.

Does our no-strong-loops hypothesis rule out the existence of a significant number of directed loops between two individual neurons (as opposed to areas)? An example of such a two-neuron loop would be a thalamocortical projection neuron making a driving connection in layer 4 onto the apical dendrite of a layer-5 cell that drives the thalamic cell. We leave all these topics for further consideration.

Discussion

Our division of the connections into ‘driving’ and ‘modulating’ connections may well be too simple. In the first place, although it is probably that a ‘driving’ connection does excite the recipient neurons to fire, it is less certain that a ‘modulating’ connection can only modulate and not, under some circumstances, fire the recipient neurons by itself. This is why we called them D/d and M/m, to indicate that our idea of their exact function is only rather tentative. (See experiments on the anaesthetized squirrel monkey²⁸ and on the anaesthetized cat²⁹, and a critique of these experiments³⁰.) However, under natural circumstances, we think that the D/d connections are likely to produce a stronger excitation than the M/m ones. Also, the timescale of their effect might differ, with the M/m pathways acting as a ‘bias’ over a much longer timescale than the D/d pathways. The exact nature of the receptors involved might also be different.

Our general point is that all the different types of connection should not be regarded as having the same character and the same ‘strength’. Although it is not true that “everything is connected to everything else”, the connections between cortical areas are very extensive (see discussion in ref. 1). It is therefore important to try to classify the connections into different types, in the hope that by doing so the behaviour of the system can be comprehended more easily. Connections may differ in many important ways apart from their layer of origin and destination: for example, how widely their

axons arborize, the type and dendritic location of the synapses they form, the receptors involved, and so on.

An analogy may help here. In organic chemistry, the atoms making up one molecule are bonded together and also, less strongly, to the atoms in neighbouring molecules. Although the details of the different bonds vary from atom to atom, it is useful to distinguish strong bonds, such as homopolar and coulombic bonds, from weak bonds, such as hydrogen bonds and those due to van der Waals forces. Moreover, each of these types of bonds has its own character. It would be impossible to understand the structure of, say, a protein molecule if all these ‘bonds’ were considered to be on an equal footing.

In the same way, one should attempt to classify the interactions between neuronal groups (such as those in a single cortical area) into different types, in order to obtain a general picture of what is going on. Our classification above should be regarded as a tentative step in that direction.

Are there likely to be significant exceptions to our no-strong-loops hypothesis? It is possible that most directed loops are weak loops but that there may be some loops that are of intermediate strength. These might allow sustained activity of finite duration. Not surprisingly, we have wondered whether such intermediate-strength loops might form the neural correlate of consciousness; in particular, we would draw attention to some of the loops between the frontal cortex and the higher visual cortical areas³¹. There is already a hint that the laminar connections there are not what might have been expected. A paper by Ungerleider and colleagues³² stated, “... it may be that the rules that have been used for establishing hierarchical relationships within both the visual and somatosensory systems¹ do not extend, in any simple way, to connections with frontal lobe areas.”

Conclusions

Our hypothesis is relatively easy to test experimentally, at least in its neuroanatomical form. It is based on certain neuroanatomical connections that have already been established and predicts the general nature of other connections that have not yet been established definitively. It seems very likely that it is true for the corticocortical connections in at least the lower levels of the macaque visual hierarchy. More experimental data are needed to test it for the higher levels of the visual hierarchy (and especially the connections to frontal cortical areas) and for the many connections between the pulvinar and the visual cortex.

Although neuroanatomy can by itself confirm our prediction of the absence of certain connections, it cannot confirm our explanation for these absences unless there is good neurophysiological evidence that what we have called driving connections are in some significant sense stronger than the connections we have termed modulating. ‘Strength’ implies that a strong connection fires those neurons more effectively than a weak one. It is possible that the reason for the strength of connections to cortical layer 4 is the amplification produced by local lateral connections³³. The evidence suggests that the strength of a connection cannot be gauged by merely counting the number of axons involved. In the long run, we need to know not only the ‘strength’ but something of the general character of the effects produced by each type of connection; for instance, whether they originate from neurons that fire in bursts³⁴.

If our cortical hypothesis is true, it might explain why the hierarchy in the visual cortical areas may be only a rough one, and would call a truce on discussions as to which version of the hierarchy is the best. If our extended hypothesis, which includes the thalamic connections, turns out to be true, it may suggest an unambiguous hierarchy for at least most of the visual cortical areas. Our hypothesis is, however, a negative one: it predicts which types of connections will not be found. It says very little about the complex processing, involving all the types of connections, that allows an animal to see and to act on what it sees. It does

not explain the function of modulatory m_{ct} or m_{tc} connections or of corticocortical feedback connections. To study this, we need much further work and probably new ideas; our hypothesis merely attempts to clear the ground for such endeavours. □

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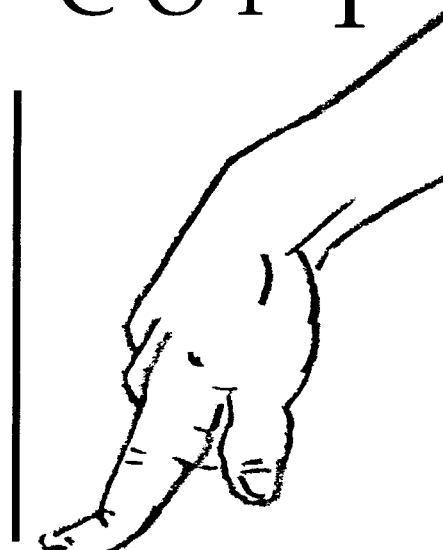
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