Object vision and spatial vision: two cortical pathways

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Evidence is reviewed indicating that striate cortex in the monkey is the source of two multisynaptic corticocortical pathways. One courses ventrally, interconnecting the striate, prestriate, and inferior temporal areas, and enables the visual identification of objects. The other runs dorsally, interconnecting the striate, prestriate, and inferior parietal areas, and allows instead the visual location of objects. How the information carried in these two separate pathways is reintegrated has become an important question for future research.

Thirty-five years ago Lashley concluded that visual mechanisms do not extend beyond the striate cortex. He was led to this view after finding that 'None of the lesions in the prestriate region of the monkey has produced symptoms resembling object agnosia as described in man . . . Uncomplicated destruction of major portions of the prestriate region . . . has not been found to produce any disturbances in sensory or perceptual organization'[14].

We now know, of course, that Lashley's conclusion was wrong. Tissue essential for vision extends far beyond striate cortex to include not only the prestriate region of the occipital lobe but also large portions of the temporal and parietal lobes. Neurobehavioral studies since Lashley's[3,6,20–23,28], together with converging evidence from physiological[1,6,10,24,30,44] and anatomical studies[5,31,39,41–43], indicate that these extrastriate regions contain numerous visual areas that can be distinguished both structurally and functionally. Moreover, recent work from our own laboratory[40] suggests that these multiple visual areas are organized hierarchically into two separate cortical visual pathways, one specialized for 'object' vision, the other for 'spatial' vision.

Two pathways

The two cortical visual pathways are schematized in Fig. 1. One of them consists of a multisynaptic occipitotemporal projection system that follows the course of the inferior longitudinal fasciculus. This pathway, which interconnects the striate, prestriate, and inferior temporal areas, is crucial for the visual identification of objects[21]. Subsequent links of the occipitotemporal pathway with limbic structures in the temporal lobe[36] and with ventral portions of the frontal lobe[13] may make possible the cognitive association of visual objects with other events, such as emotions and motor acts.

The other pathway consists of a multisynaptic occipitoparietal projection system that follows the course of the superior longitudinal fasciculus. This pathway, which interconnects the striate, prestriate, and inferior parietal areas, is critical for the visual location of objects[40]. Subsequent links of the occipitoparietal pathway with dorsal limbic[26] and dorsal frontal cortex[13,26] may enable the cognitive construction of spatial maps, as well as the visual guidance of motor acts[8] that were initially triggered by activity in the ventral pathway. In contrast to the ventral pathway, which remains modality-specific throughout its course, the later stations in the dorsal pathway appear to receive convergent input from other modalities and so may constitute polysensory areas[10,32].

The notion that separate neural systems mediate object and spatial vision is not new[11,25]. In previous formulations, however, these two types of visual perception were attributed to the geniculostriate and tectofugal systems, respectively, rather than to separate cortical pathways diverging from a common striate origin. The shift to the present view is in keeping with the cumulative evidence that, in primates at least, all forms of visual perception, as distinguished from visuomotor functions, are more heavily dependent on the geniculostriate than on the tectofugal system.

Object vision

The anterior part of inferior temporal cortex, or area TE in Bonin and Bailey's terminology[2], is the last exclusively visual area in the pathway that begins in the striate cortex, or area OC, and continues through the prestriate and posterior temporal areas, OB, OA and TEO (Fig. 1). This ventrally directed chain of cortical visual areas appears to extract stimulus-quality information from the retinal input to the striate cortex[20], processing it for the purpose of identifying the visual stimulus and ultimately assigning it some meaning through the mediation of area TE's connections with the limbic and frontal-lobe systems[12]. According to this view, the analysis of the physical properties of a visual object (such as its size, color, texture and shape) is performed in the multiple subdivisions of the prestriate–posterior temporal complex[44] and may even be completed within this tissue. Such a proposal gains support from the striking loss in pattern-discrimination ability that follows damage to the posterior temporal

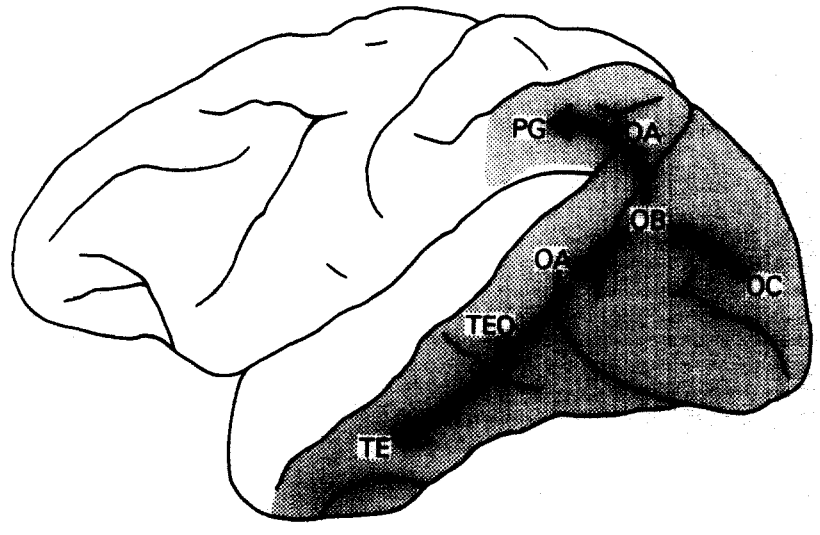

Fig. 1. *Lateral view of the left hemisphere of a rhesus monkey. The shaded area defines the cortical visual tissue in the occipital, temporal and parietal lobes. Arrows schematize two cortical visual pathways, each beginning in primary visual cortex (area OC), diverging within prestriate cortex (areas OB and OA), and then coursing either ventrally into the inferior temporal cortex (areas TEO and TE) or dorsally into the inferior parietal cortex (area PG). Both cortical visual pathways are crucial for higher visual function, the ventral pathway for object vision and the dorsal pathway for spatial vision.*

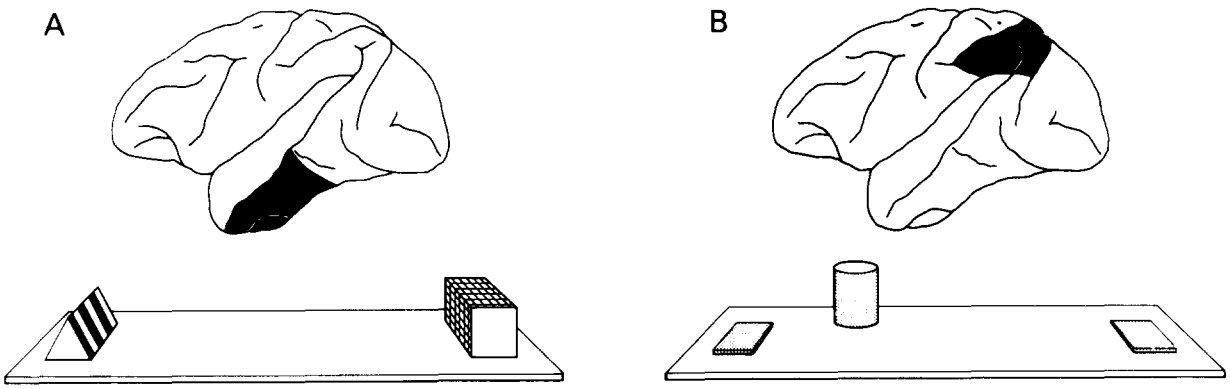

Fig. 2. *Behavioral tasks sensitive to cortical visual lesions in monkeys.* **(A)** *Object discrimination. Bilateral removal of area TE in inferior temporal cortex produces severe impairment on object discrimination. A simple version of such a discrimination is a one-trial object-recognition task based on the principle of non-matching to sample, in which monkeys are first familiarized with one object of a pair in a central location (familiarization trial not shown) and are then rewarded in the choice test for selecting the unfamiliar object.* **(B)** *Landmark discrimination. Bilateral removal of posterior parietal cortex produces severe impairment on landmark discrimination. On this task, monkeys are rewarded for choosing the covered foodwell closer to a tall cylinder, the 'landmark', which is positioned randomly from trial to trial closer to the left cover or closer to the right cover, the two covers being otherwise identical.*

area[20]. But the synthesis of all the physical properties of the particular object into a unique configuration appears to entail the funnelling of the outputs from the prestriate–posterior temporal region into area TE[21]. This postulated integration of the coded visual properties of an object within area TE would make TE especially well suited to serve not only as the highest-order area for the visual perception of objects but also as the storehouse for their central representations and, hence, for their later recognition.

That area TE is important for the retention of some form of visual experience has been suspected for decades[18]. Numerous behavioral studies[6] have demonstrated that bilateral removal of inferior temporal cortex in monkeys yields marked impairment both in the retention of visual discrimination habits acquired prior to surgery and in the postoperative acquisition of new ones. This impairment, which is exclusively visual, appears in the absence of any sensory loss and thus has long been considered a higher-order, or 'visuopsychic', dysfunction.

But that the impairment is in fact a visual retention disorder was demonstrated only later when it was found that area TE lesions impair performance on visual tests that tax memory even more than they do on visual tests that tax perceptual ability[3]. Now, having examined the ability of monkeys with TE lesions simply to remember the visual appearance of newly presented objects, we have uncovered what is perhaps the most dramatic impairment of all[21]. After just a few days of training, normal monkeys shown an object only once will demonstrate that they recognize that object when it is presented several minutes later (Fig. 2A). Thus, somewhere in the visual system the single presentation of a complex stimulus leaves a trace against which a subsequently presented stimulus can be matched. If it does match, i.e. if the original neural trace is reactivated, there is immediate recognition, as demonstrated by the monkey's highly accurate performance. The area in which the neural trace appears to be preferentially established is area TE, since lesions here – but not lesions elsewhere in the cortical visual system – nearly abolish the monkey's ability to perform the recognition task. Apparently, area TE contains the traces laid down by previous viewing of stimuli, and these serve as stored central representations against which incoming stimuli are constantly being compared. In the process, old central representations may either decay, be renewed, or even be refined, while new representations are added to the store.

It is significant that by virtue of the extremely large visual receptive fields of inferior temporal neurons[6] this area seems to provide the neural basis for the phenomenon of stimulus equivalence across retinal translation[7]; i.e. the ability to recognize a stimulus as the same, regardless of its position in the visual field. But a necessary consequence of this mechanism for stimulus equivalence is that within the occipitotemporal pathway itself there is a loss of information about the visual location of the objects being identified.

Spatial vision

The neural mechanism that enables the visual location of objects also entails the transmission of information from striate through prestriate cortex; however, the prestriate route in this case, as well as the rest of the pathway for spatial vision, appears to be quite separate from the pathway for object vision (Fig. 1). Evidence in support of this dichotomy of cortical visual pathways has come from our studies of posterior parietal cortex.

In the initial study of the series, Pohl[28] demonstrated a dissociation of visual deficits after inferior temporal and posterior parietal lesions. That is, whereas the temporal but not the parietal lesion produced severe impairment on an object-discrimination learning task, just the reverse was found on tests in which the monkey had to learn to choose a response location on the basis of its proximity to a visual 'landmark' (Fig. 2B). These results provided compelling evidence that 'the inferior temporal cortex participates mainly in the acts of noticing and remembering an object's qualities, not its position in space. Conversely, the posterior parietal cortex seems to be concerned with the perception of the spatial relations among objects, and not their intrinsic qualities'[20].

The effective lesions in Pohl's study were large, since they included not only inferior parietal cortex, or area PG, but also dorsal prestriate tissue within area OA. To test for the possibility of a further localization of function within this region, additional experiments were performed with more restricted lesions[22]. The results, however, failed to reveal any evidence of a cortical focus serving spatial vision; rather, the severity of impairment on the landmark task was found to depend on the amount of tissue included in the lesion, completely independent of the lesion site. Since damage to the same region, no matter how extensive, failed to produce any impairment in the acquisition of a visual pattern discrimination, it appears that the entire posterior parietal region, including dorsal OA cortex, participates selectively in the processing of visuospatial as distinguished from visual object-quality information.

Our findings support the accumulat-

ing neurobiological evidence that parietal area PG, rather than being a purely tactual association area as was once thought, is a polysensory area to which both the visual and tactual modalities contribute[10,24,30]. The findings are thus consistent with the proposal[33] that area PG serves a supramodal spatial ability that subsumes both the macrospace of vision and the microspace encompassed by the hand. According to this proposal, visuospatial and tactual discrimination deficits, as well as the inaccuracies in reaching that also follow inferior parietal damage, are different reflections of a single, supramodal disorder in spatial perception.

Polysensory area PG is presumed to depend for its visual input on the modality-specific prestriate area OA, which appears to serve visual spatial functions selectively. Such a hierarchical model for spatial perception suggests, in turn, that the source of the critical visual input for the entire dorsal prestriate–parietal region is, again, the striate cortex. The alternative possibility, namely, that the source of the critical input is the superior colliculus, found no support in a study of the effects of tectal lesions on performance of the landmark task; even complete bilateral destruction of the superior colliculus failed to produce a reliable loss in retention. We therefore examined the contribution of striate inputs to the visuospatial functions of posterior parietal cortex[23], using a disconnection technique analogous to the one used originally to examine the contribution of striate inputs to the object-vision functions of inferior temporal cortex[19]. Our results suggested that the posterior parietal cortex, like the inferior temporal, is totally dependent on striate input for its participation in vision; but unlike the inferior temporal, the posterior parietal cortex does not seem to receive a heavy visual input via the corpus callosum. It therefore appears that each posterior parietal area may be organized largely as a substrate for contralateral spatial function, which could account in part for the symptom of contralateral spatial neglect that has so often been reported after unilateral parietal injury in man[4,9,17].

A second difference in the organization of visual inputs to posterior parietal and inferior temporal cortex was uncovered in an experiment that compared the effects of selective removals of striate cortex[23]. In this experiment, monkeys received bilateral lesions of the striate areas representing either central vision (lateral striate) or peripheral vision (medial striate). The results indicated that while inputs from central vision are the more important ones for the object-recognition functions of inferior temporal cortex, inputs from central and peripheral vision are equally important for the visuospatial functions of posterior parietal cortex.

In summary, interactions with striate cortex are critical for the parietal just as they are for the temporal area, but the striate inputs to these two cortical targets are organized differently: relative to inferior temporal cortex, posterior parietal cortex receives a greater contribution from inputs representing both the contralateral and the peripheral visual fields. These differences, which are seen also in the visual receptive field topography of inferior temporal vs. posterior parietal neurons[6,30], presumably reflect differences in the sensory processing required for object vs. spatial vision.

Metabolic and anatomical mapping

The evidence from our behavioral work demonstrates that the neural mechanisms underlying object and spatial vision depend on the relay of information from striate cortex through prestriate cortex to targets in inferior temporal and inferior parietal areas, respectively. We have now mapped the full extent of both cortical visual pathways combined, using the 2-[^{14}C]deoxyglucose method[15]. By comparing a blinded and a seeing hemisphere in the same monkey we have found that the entire visual system can be outlined on the basis of differential hemispheric glucose utilization during visual stimulation. Reduced glucose utilization in the blind as compared with the seeing hemisphere was seen cortically throughout the entire expanse of striate and prestriate cortex (areas OC, OB and OA), inferior temporal cortex as far forward as the temporal pole (areas TEO and TE), and the posterior part of the inferior parietal lobule (area PG). These results, which are in remarkably close agreement with our neurobehaviorally derived model of the two cortical visual pathways, have allowed us to delineate the exact limits of the entire system[16] (Fig. 1).

To trace the flow of visual information within each system we undertook a series of studies using autoradiographic and degeneration tracing techniques. Our goal in these anatomical investigations was to identify the multiple visual areas within the prestriate cortex, explore their organization, and map their projections forward into both the temporal and parietal lobes.

The findings indicated that the striate cortex is indeed the source of two major cortical projection systems. The first system begins with the known striate projection to the second visual area, V2[31,35,42,43]. We found that V2 in turn projects to areas V3 and V4[38]. These three prestriate areas are arranged in adjacent 'belts' that nearly surround the striate cortex, and, like striate cortex, each belt contains a topographic representation of the visual field. Area V2 corresponds to prestriate area OB, while V3 and V4 are both contained within prestriate area OA, exclusive of its dorsal part. Area V4 in turn projects to both areas TEO and TE in the inferior temporal cortex[5].

The second major system begins with both striate and V2 projections to visual area MT[31,35,39,41-43], which is located in the caudal portion of the superior temporal sulcus, mainly within dorsolateral OA. Area MT in turn projects to four additional areas in the upper superior temporal and the intraparietal sulci[37]. Although the total extents of these four areas are not yet completely established, the more anterior one in the intraparietal sulcus clearly falls within area PG. Thus, one major system of projections out of striate cortex is directed ventrally into the temporal lobe, while a second is directed dorsally into the parietal lobe. Furthermore, the divergence between these two systems appears to begin almost immediately after striate cortex, i.e. in its initial projections.

The two multisynaptic projection systems that we have traced provide not only the anatomical substrate for our two functionally defined visual pathways but also a partial solution to the puzzle that was presented at the outset, namely, why extensive removals of prestriate cortex in monkeys have repeatedly failed to yield the expected losses in either object or spatial vision[14,29,40]. If prestriate cortex constitutes an essential relay in both a striate–temporal and a striate–parietal pathway, then damage to this relay should yield effects at least as severe as damage to both its target areas. Yet such dramatic effects have not been found. The reason appears to be that no prestriate lesion to date has produced a total visual disconnection of the temporal and parietal lobes, since all removals have spared varying extents of prestriate tissue that could continue to relay visual information. Comparison with our anatomical maps indicates that the portions of prestriate cortex that have consistently escaped damage are those parts of both the belt areas and the MT-related areas that represent the peripheral visual fields. Thus, just as we had found from sparing in striate cortex, sparing of peripheral-field representations in prestriate cortex will protect both object and spatial vision from serious losses.

Objects in spatial locations

A major question posed by the present analysis is how object information and spatial information, initially carried together in the geniculostriate projections but then analysed separately in the two cortical vis-

ual pathways, are eventually reintegrated. As already noted, both pathways have further connections to the limbic system and the frontal lobe, and each of these target areas therefore constitutes a potential site of convergence and synthesis for object and spatial information. This theoretical possibility has not yet been sufficiently tested. Preliminary work does indicate, however, that one such site of reintegration may be the hippocampal formation and that one of its functions may be to enable the rapid memorization of the particular locations occupied by particular objects[27,34]. Further application of this concept of reintegration to research on the limbic system and the frontal lobe could throw new light on some old questions of local cerebral function.

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The cerebellum and control of rhythmical movements

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During rhythmical locomotory and scratching movements the cerebellum receives information both about the current state of the peripheral motor apparatus and about the activity of the spinal rhythmical generator. Comparison of cerebellar input and output signals suggests that the cerebellum 'selects' essential information concerning the activity of the motor mechanisms. On the basis of this information, the cerebellum regulates the transmission of signals from various motor brain centres and receptors to the spinal cord. This paper elaborates the hypothesis that the cerebellum co-ordinates different motor synergisms and adapts them to the environment.

The spino-cerebellar loop

Recently, a new approach to the study of cerebellar functions has been developed which involves recording cerebellar input and output signals accompanying movements. This approach is based on two different methods. In chronic experiments the activity of cerebellar neurons is recorded in animals which are awake and which have been trained to perform certain movements[11]. Alternatively, neurons in the cerebellum and structures related to it are recorded from acute decerebrate cats 'automatically' performing locomotor or scratching movements[2–7,10,17,18]. Though this second technique limits investigations to brain-stem–cerebellar and spinal mechanisms, it has the advantage of providing greater possibilities for analytical studies. Studies of the scratch reflex were especially fruitful. This reflex can be easily evoked in immobilized cats ('the fictitious scratch reflex')[12], and immobility of the animal facilitates microelectrode recordings. In addition, by comparing the activity of neurons of the cerebellum (and of other structures) during actual and fictitious scratching, one can estimate the relative roles of central and peripheral factors in generating cerebellar inputs and outputs.

Fig. 1 illustrates the main structures in decerebrate cats concerned with the control of hindlimb movements during locomotion and scratching. Spinal structures generating rhythmical movements are 'switched on' by signals arriving either from the supraspinal structures or from the upper spinal cord. When these spinal mechanisms are opera-