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Decomposing and Localizing Vision: An Exemplar for Cognitive Neuroscience

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To date the greatest successes in developing a brain-based model of a cognitive process have been in the domain of vision. As chapter 12, above, by Van Essen and Gallant, makes clear, by now at least 33 different cortical areas involved in visual processing have been identified in primates, with a highly complex pattern of connectivity between them. Their figure (12.2, this volume) strongly conveys the idea that different visual areas each carry out different types of processing, and that the ability to see the world is the product of a complex system in which information processing tasks are divided up, but in which the specialized components collaborate. Although not all the component operations and brain areas involved in vision have been discovered, and the account offered so far is subject to revision in the face of new research, it is nonetheless relatively complete and well supported. Moreover, from studying figure 12.2, one develops an understanding of how processes in the brain make it possible for us to see the world. As such, it offers what Thomas Kuhn refers to as an exemplar – a example of successful research which provides a model to be emulated by other domains of cognitive science.

The account of visual processing that has emerged fits the framework of *mechanistic explanation* we introduced in chapter 1, this volume – it decomposes seeing into a number of different operations and localizes each of them in different parts of the brain. Analyzing the history of research that led to this account provides us an exemplar in a second sense – an exemplar of the path cognitive neuroscience research is likely to take. The previous three chapters in this section represent major stages in the development of current mechanistic explanations of vision. But they represent only some of the steps in the overall process by which researchers arrived at this understanding of how the visual system works. In this chapter I will relate additional components of that history to illustrate important steps in developing mechanistic explanations.
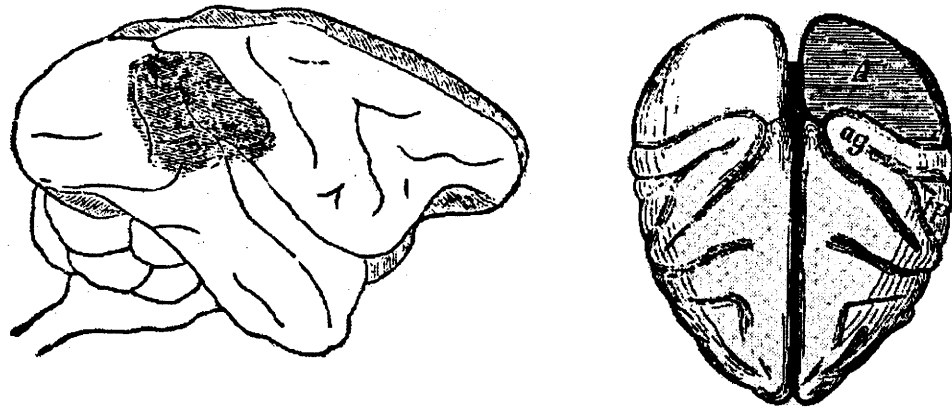
Figure 13.1 Competing proposed localizations of visual processing based on lesions made in monkeys. David Ferrier claimed that lesions to the angular gyrus (left) resulted in blindness whereas Hermann Munk argued that lesions to the occipital lobe (right) generated blindness.

Our experience of vision is simply one of opening our eyes and seeing what is before us. We are not aware of intermediate operations that the brain is performing. But this should not be surprising. Natural systems typically work very smoothly and fail to reveal their components. Thus, it takes active intervention to reveal the component operations. One especially important way of revealing component operations is to break the system, or find instances of broken system, where we can identify the operation that fails and the operations that can still be performed without the broken elements. This is the strategy of lesion research we described in chapter 4, above. While many of the cleavages in the visual system were first identified through lesion studies, researchers did not widely accept the decomposition until lesion research was complemented by single-cell recording research which could reveal more directly what the individual components were doing. Thus, a common pattern that we will observe is lesion research suggesting how the visual system is decomposed, and single-cell recording providing additional evidence and revealing in greater detail the component operations.

1   Getting Started: Identifying the Locus of Control

A common starting point in developing explanations of how a complex system carries out a particular function such as vision is the attempt to localize *that* function as a whole in a particular part of the system. Competing hypotheses as to the locus are often advanced, and the first stage in the inquiry is an attempt to adjudicate between them. In the case of vision, two loci were advanced in the nineteenth century: the angular gyrus located in the posterior parietal lobe and the occipital lobe (figure 13.1). Of these, the more popular locus was the occipital lobe. It was proposed as the cortical center for vision by the Italian investigator Bartolomeo Panizza (1855) on the

basis of a study of patients who experienced blindness after strokes damaged the occipital lobe, and lesion studies on several other species in which lesions to the occipital lobe produced blindness. His publications were largely ignored, perhaps because they only appeared in local Italian journals, but neuroanatomical studies in the same period by Pierre Gratiolet (1854) and Theodor Meynert (1870) indicated that the optic tract, which first projected to an area of the thalamus known as the *lateral geniculate nucleus* (LGN), projected on to the occipital lobe (Meynert traced the projections more specifically to the area surrounding the calcarine fissure), thereby supporting the occipital lobe locus.

The occipital lobe locus was opposed by one of the leading neurologists of the time, David Ferrier (1876). He was a pioneer in the use of mild electrical stimulation to identify loci in the brain associated with different functions, and found that stimulation of the angular gyrus (a region in the posterior parietal cortex) caused monkeys to move their eyes toward the opposite side. He further supported the angular gyrus locus through lesion studies in which he reported that bilateral lesions to the angular gyrus resulted in blindness, but that large lesions in the occipital lobe produced little impairment. Ferrier (1881) later moderated his claims, holding that both the angular gyrus and the occipital lobe figured in vision and that only lesions to both could produce complete and enduring blindness, but he continued to emphasize the angular gyrus.

In retrospect, it appears that the reason Ferrier's lesions of the angular gyrus produced deficits in vision was that his incisions cut deeply and severed the nerve pathways from the thalamus to the occipital cortex (Finger, 1994). Moreover, his failure to eliminate vision with occipital lobe lesions was due to incomplete removal of the visual processing areas in the occipital lobe. But these shortcomings in his technique were only established much later and did not figure in settling the conflict. Moreover, one should not just infer that Ferrier misapplied the lesion techniques because he cut too deeply since the functional difference between the underlying white matter and the gray matter first had to be appreciated and standards for conducting lesions research developed. Standardized methods are often the outcome of such scientific controversies – they cannot be appealed to in settling the controversies.

What seems to have established the occipital lobe as the *locus of control* for vision was the accumulation of reports from numerous investigators much like those originally put forward by Panizza. Many experimentalists (e.g. Munk, 1881; Schäfer, 1888b) described visual deficits after occipital lobe lesions in animals while clinicians (Henschen, 1893; Wilbrand, 1890) reported on patients who suffered visual deficits after damage to the occipital lobe.

During the same period as researchers were identifying a locus for vision at a macro level, neuroanatomists were making great progress in discovering the microstructure of the brain. Chapter 3, above, related the process by which the neuron doctrine was established and how researchers began to map the cortex in terms of neuroanatomical features such as the thickness of particular layers in various parts of the cortex. Even earlier, in 1776 Francesco Gennari, in the course of examining frozen sections of human brains, had identified a white stripe that was especially prominent in the posterior part of the brain (Glickstein and Rizzolatti,

1984). Subsequently Paul Flechsig (1896) identified this stripped area as the target of the projections from the LGN, and Grafton Elliot Smith (1907) named it the *area striata*; the area is now often referred to as the *striate cortex*. The area was also distinguished on cytoarchitectural grounds in a wide variety of species by Korbinian Brodmann (1909/1994), who assigned this area the number 17 since it was the seventeenth cortical area he had examined. Much later the terms *primary visual cortex* and *V1* also came to be applied to this area which, by the beginning of the twentieth century, was generally accepted as the locus of visual processing.

2   From Simple Localization to Mechanistic Explanation

As controversial as it often is to establish, a proposal of a locus of control for a function is generally only a preliminary step toward explaining it. A simple identification of a function with a structure does not really explain the function since it provides no account of how the function is accomplished. Explanation requires decomposition into component functions, which usually results either from (1) discovering other structures that are involved in carrying out the same function (thereby revealing that the first site was not the sole locus of control and provoking the question of what more specific contribution that location makes), or (2) discovering components within the structure in question (and then asking what activities each of these performs). In twentieth-century research on visual processing, both of these played a critical role – the discovery of structure within the striate cortex provided one clue to the division of labor in processing visual stimuli and the discovery of a variety of other visual centers in the brain provided another clue.

Beyond direct localization: complexity within striate cortex

A first step beyond simply identifying striate cortex as the locus of control was already made in a detailed study Salomen Henschen (1893) made of lesion sites which produced vision deficits in humans. He showed that deficits in different parts of the occipital lobe produced blindness in different parts of the visual field and proposed that the occipital lobe must be topographically organized so that different parts of the retina projected on to different areas of the visual cortex (leading him to refer to it as the *cortical retina*). The occipital lobe map that Henschen proposed lays the projections out in the reverse manner of what is now accepted. While it might seem surprising that someone could discover a topological structure, and yet get all the locations reversed, such developments are surprisingly common in the history of science. It is indicative of how difficult it is to extend beyond individual, highly suggestive findings to generate a systematic account.

Discovering the correct topographical layout of striate cortex resulted from amassing many more data. Tatsuji Inouye was able to study 29 individuals who sustained highly focal damage to the occipital lobe during the Russo-Japanese war (as a result of new bullets introduced by the Russians; see Glickstein, 1988), and with the
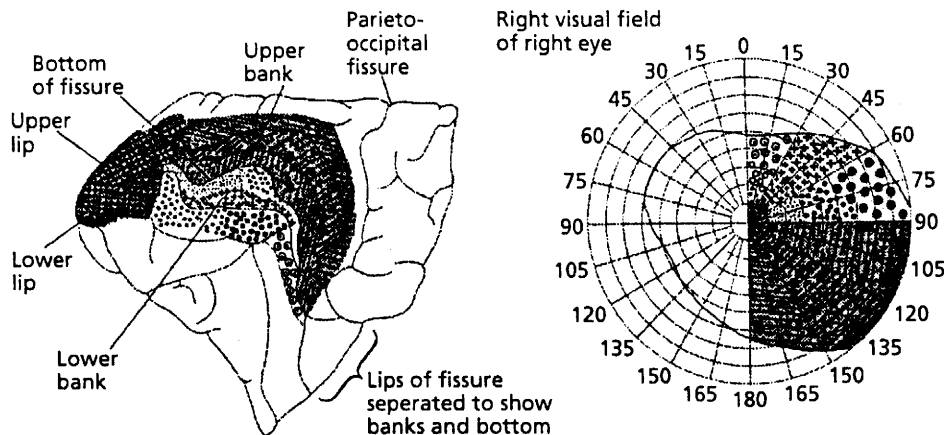
Figure 13.2 Gordon Holmes's (1918) map of how locations in the visual field (right) project onto parts of the primary visual cortex, based on studies of soldiers injured during World War I.

additional data points was able to determine that the central part of the visual field projects to the rear of the occipital lobe and the peripheral parts to the front. A similar study by Gordon Holmes and William Tindall Lister during World War I generated an even more detailed and accessible diagram of the topographical projection of parts of the visual field on to the visual cortex (see figure 13.2).

Micro-lesion studies could reveal topographical organization, but not the actual function performed by cells in striate cortex since the result of lesions was complete blindness. To make additional progress, researchers needed to determine what cells in striate cortex actually contributed to visual processing. For this, the key technique was single-cell recording. Here the strategy is to determine what kinds of stimuli cause a cell to fire most actively and then to assume that the cell is representing that stimulus (see chapter 18, this volume).[1] The pioneer for this approach was Steven Kuffler, who employed dark and light circles as stimuli while he recorded from ganglion cells in the retina; from this he discovered that the receptive fields of these cells were organized so that a cell might respond when a stimulus was in the center of its receptive field but not in the surrounding area (an *on-center* cell) or the reverse (an *off-center* cell).

Kuffler extended his research to the LGN, but it was two researchers in his laboratory at Johns Hopkins, David Hubel and Torsten Wiesel, who succeeded in extending this technique to striate cortex cells. While working at Walter Reed Army Institute, Hubel had developed a tungsten microelectrode and began using it to record from both sleeping and waking animals. He had succeeded in finding a few cells that responded when he moved his hands back and forth in front of the cat, but found he could not influence most cortical cells. After Hubel and Wiesel began their collaboration in the spring of 1958 they soon made the discovery that cells in striate cortex responded most vigorously not to spots of light but to oriented lines
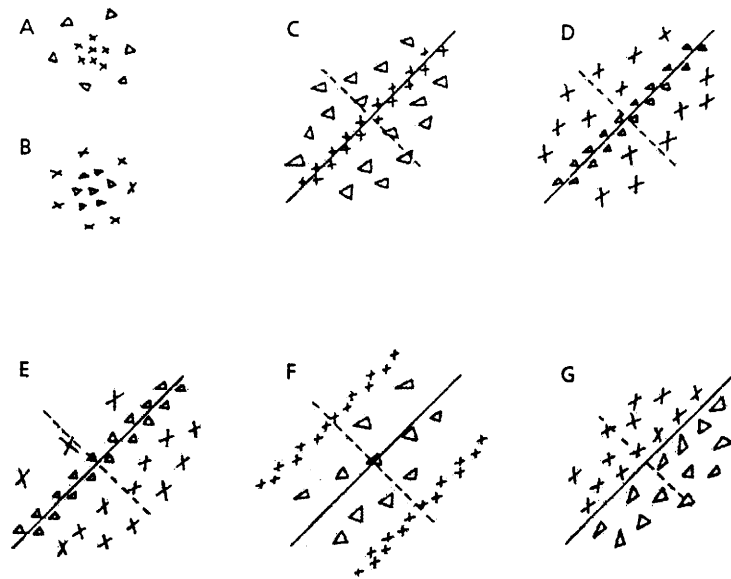
Vision

Figure 13.3 Examples of Hubel and Wiesel's (1962) mapping of receptive fields of cells in the lateral geniculate (A–B) and simple cortical cells (C–G) in the cat. X indicates an area producing excitatory responses and ∆s an area producing inhibitory responses.

or bars. Like many important scientific discoveries, theirs exhibited a bit of serendipity. They began by trying a variety of circular stimuli comparable to those Kuffler had used to elicit responses in retinal ganglion cells, but failed to produce any strong results. But as they were inserting a glass slide into their projecting ophthalmoscope, Hubel reports that "over the audiomonitor the cell went off like a machine gun" (Hubel, 1982, p. 438). They soon figured out that it was not the dot on the slide that was having an effect, but the fact that "as the glass slide was inserted its edge was casting on to the retina a faint but sharp shadow, a straight dark line on a light background" (p. 439).[2]

Over the first ten years of their collaboration, Hubel and Wiesel probed the striate cortex of both cats (Hubel and Wiesel, 1962) and monkeys (Hubel and Wiesel, 1968) and discovered a rich organization of cells with different response patterns. What they termed *simple cells* had receptive fields with spatially distinct *on* and *off* areas along a line at a particular orientation (most typically, they had a long, narrow *on* area sandwiched between two more extensive *off* areas) (see figure 13.3). Hubel and Wiesel suggested how several cells with center-surround receptive fields (such as those found in the LGN) might all send excitatory input to a single simple cell. In this regard, it is salient that simple cells predominate in layer 4, which is the input layer to cortex. Whereas simple cells were sensitive to stimuli only at a given retinal location, what Hubel and Wiesel termed *complex cells* were responsive to bars of light at a particular orientation anywhere within their receptive fields (figure 13.4). Many
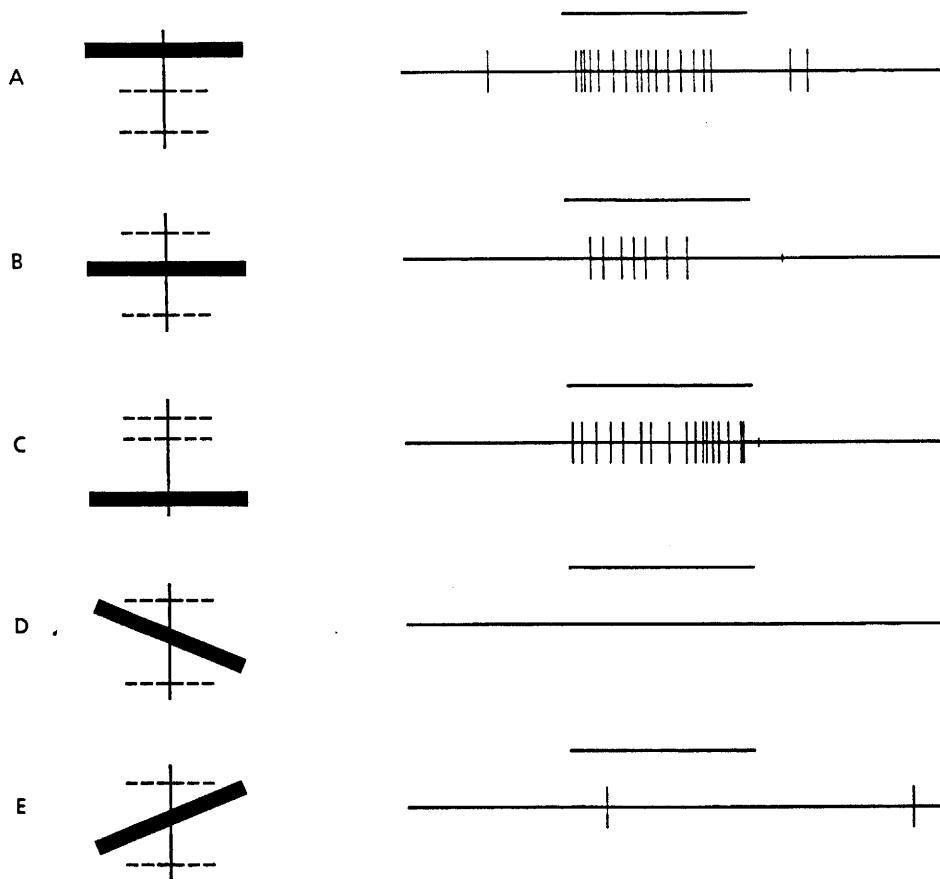
Figure 13.4 Response of complex cells in primary visual cortex to stationary, horizontally oriented black rectangles placed at different locations in the cell's receptive field (a) or moving through its receptive field (b). From Hubel and Wiesel, 1962, p. 111.

complex cells were also sensitive to the direction of movement of bars within their receptive field. Hubel and Wiesel identified these as *complex cells* since their response pattern could be explained if they received input from several simple cells, any of which would be sufficient to cause the complex cell to fire. Complex cells are found primarily in layers 2 and 3, and 5 and 6.[3] In their papers from this period Hubel and Wiesel also distinguished *hypercomplex cells* which responded maximally only to bars extending just the width of their receptive field.[4]

Having identified three types of cells with different response properties, Hubel and Wiesel, proposed a decomposition of processing within striate cortex, with one type of cell supplying information to other cells and each carrying out its own information processing (although they also acknowledged that all three types of cells sent processes to other parts of the cortex). They also proposed the discovery of the
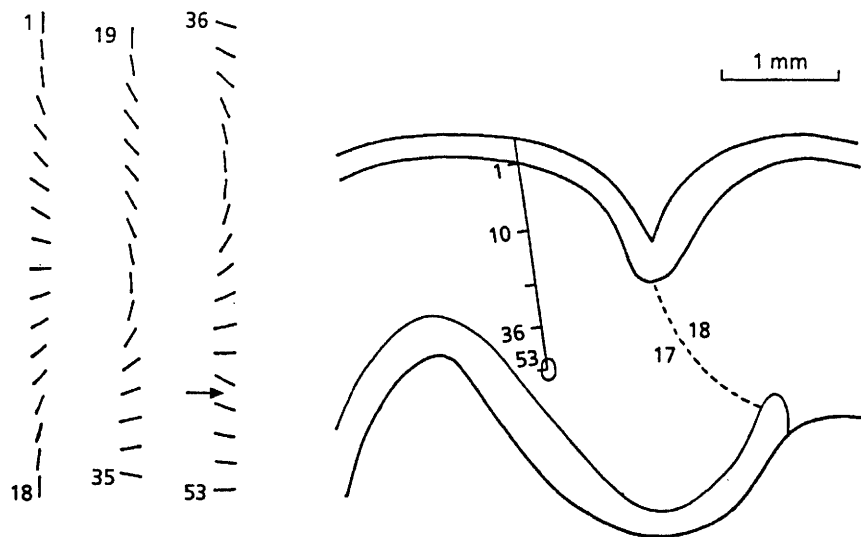
primary function of striate cortex, but with a prophetic caveat: "The elaboration of simple cortical fields from geniculate concentric fields, complex from simple, and hypercomplex from complex is probably the prime function of the striate cortex – unless there are still other as yet unidentified cells there" (Hubel and Wiesel, 1968, p. 239).

By inserting electrodes gradually and recording from cells at different depths in the cortex, Hubel and Wiesel also discovered two additional features of the organization of striate cortex. First, when they inserted an electrode at an angle of 30° and recorded at successive locations, the preferred stimulus orientation for cells gradually changed (figure 13.5). Over the first 18 locations (approximately 1 mm) the preferred orientation varied through a full 180°. As penetration continued, a point was reached (arrow) where the variation in preferred orientation suddenly reversed. Second, they discovered that complex cells in striate cortex generally received binocular input, although they tended to be more responsive to input from one eye than the other. If the electrode were inserted perpendicularly rather than at an angle, all the cells encountered would respond to the same orientation with the same eye dominance, leading Hubel and Wiesel to adopt Vernon Mountcastle's proposal of a columnar organization of cortex. They proposed that in one direction successive columns (each 0.5 mm wide) were dominated by alternate eyes (ocular dominance columns) while in the other direction successive columns were responsive to different orientations of the stimulus.

Chapter 10, by Hubel and Wiesel, provides a summary of the major discoveries they and others made in the 1960s and 1970s about the organization of primary visual cortex. In this research we see clearly the emergence of a mechanistic analysis in which different operations are identified in the processing of visual inputs, each localized in a different cell type. Although one consequence of this research was to reveal complexity within striate cortex, another, perhaps more important consequence, was to demonstrate that it was not the sole locus of visual processing, since detecting oriented bars of light is not yet perception. This focused a question for further research: where else is visual information processed, and what does each of these areas contribute. Accordingly, Hubel and Wiesel conclude their 1968 paper with the prophetic comment:

> Specialized as the cells of 17 are, compared with rods and cones, they must, neverthe-less, still represent a very elementary stage in the handling of complex forms, occupied as they are with a relatively simple region-by-region analysis of retinal contours. How this information is used at later stages in the visual path is far from clear, and represents one of the most tantalizing problems for the future.   (Hubel and Wiesel, 1968, p. 242)

Beyond direct localization: identifying prestriate visual areas

The second means of moving beyond direct localization is to discover additional components that contribute to the function. However, although in the nineteenth century there were suggestions of additional visual processing areas,[5] there was an influential factor working against the identification of other brain areas involved in visual processing. In the first half of the twentieth century brain research was dominated by an anti-localizationist sentiment that construed most of the cortex as jointly subserving cognitive capacities, without any particular part playing a specialized role. This view was supported by experiments, some performed by Pierre Flourens in the early nineteenth century in response to phrenology and others performed in the early twentieth century in response to neo-phrenological localizationists, which suggested that individual parts of the cortex could be removed without loss of any particular cognitive ability. What mattered was how much was removed; cognitive performance seemed to decline roughly proportionately to the amount removed. Karl Lashley termed this the principle of mass action and applied it in particular to the area immediately surrounding the striate cortex, an area for which he coined the term *prestriate region*. He denied that prestriate cortex played a specifically visual function, insisting: "visual habits are dependent upon the striate cortex and upon no other part of the cerebral cortex" (Lashley, 1950). Prestriate cortex could be involved, along with other association areas, in higher processes resulting from visual perception, but were not involved, according to Lashley, in visual processing *per se*.

For many researchers, one sign of the lack of differentiated function beyond striate cortex was the lack of evidence that these areas were topographically orga-

nized in the manner of striate cortex. The very lack of a topographical organization was construed as support for the idea that these areas played a holistic, integratory role. Thus, one of the first indications of visual processing beyond striate cortex was Alan Cowey's (1964) discovery, using surface electrodes to record evoked responses, of a second topographically organized area in Brodmann's area 18 (which immediately adjoins area 17); this area came to be known as V2, with striate cortex being designated V1. Using single-cell recording, Hubel and Wiesel (1965) confirmed the topographical organization of this area and identified yet a third area, V3, in Brodmann's area 19. By tracing degeneration of fibers from discrete lesions in striate cortex to areas in surrounding cortex, Semir Zeki (1969) offered collaborative evidence for the existence of these additional areas. Zeki (1971) then extended this approach by creating lesions in V2 and V3 and tracing degeneration forward into areas on the anterior bank of the lunate sulcus in which "the organized topographic projection, as anatomically determined, gradually breaks down" (p. 33).[6] Zeki labeled these areas V4 and V4a.[7]

For the discovery of these additional areas to advance the functional decomposition of vision, it was necessary to link them with functions distinct from those associated with V1. As with V1, single-cell recording played the major role. Zeki (1973) recorded from cells in V4 and found "in every case the units have been colour coded, responding vigorously to one wavelength and grudgingly, or not at all, to other wavelengths or to white light at different intensities" (p. 422). Using a similar procedure as Hubel and Wiesel did in studying V1, Zeki recorded from successively encountered cells in a perpendicular penetration and found they responded to the same wavelength while successively encountered cells in an oblique penetration responded to different wavelengths. Zeki interpreted this as evidence of a columnar organization. The next year Zeki (1974) reported on a study recording from cells on the posterior bank of the superior temporal sulcus, an area he would later label V5 and others would designate MT. He found that cells in this area responded primarily to movement, with some firing in response to movements in any direction, but with most being sensitive to the direction, and sometimes the shape of the moving stimulus. As with V5, he found evidence of a columnar organization of movement-sensitive cells, with adjacent cells exhibiting slight changes in their preferred orientation (figure 13.6). Soon after the topography of these areas was ascertained through single-cell recording, neuroanatomical staining studies revealed that the connections to area V4 were primarily from V2 (Zeki, 1978) and those to area V5 were from V1 (van Essen et al., 1981).

Zeki's discovery of a color area made explicable the earlier reported clinical cases of achromatopsia (the inability to see objects as colored; see note 5). These patients had presumably suffered lesions in V4. In 1983 Zihl et al. (1983) reported on a patient who, as a result of vascular damage, could not perceive motion. To the patient activities such as coffee being poured into a cup appeared as contiguous shapes, like a glacier. Zeki's discovery of motion detection by V5 or MT could likewise explain this patient's deficit as due to damage to that area. The advent of neuroimaging techniques (chapter 4, this volume) has made it possible to identify the areas of increased
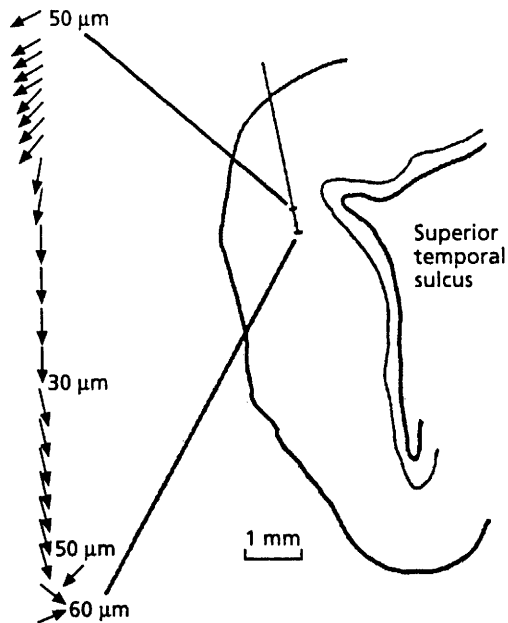
Figure 13.6 Zeki's (1974, p. 563) reconstruction of a penetration into the posterior bank of the superior temporal sulcus showing the preferred direction of movement of successive cells from which recordings were made.

blood flow when humans are presented with colored and moving stimuli; in confirmation of the decomposition suggested by single-cell recording in monkeys, Zeki et al. (1991), using PET, found distinct loci of increased blood flow in color- and motion-processing tasks. Since it is not yet feasible to differentiate areas such as V4 and V5 in humans on purely neuroanatomical grounds, these neuroimaging studies provide one of the best indications as to where these areas are located in the human brain.

Beyond direct localization: expanding visual analysis into temporal and parietal cortexes

The discovery of visual processing areas surrounding V1 which analyzed distinct visual properties such as color and motion both significantly advanced the functional decomposition of vision and posed a major question: where is the information about edges, colors, and motion put to use to permit the recognition of objects and events in the world? To address this question researchers had to expand the quest for specialized visual processing areas into more anterior parts of the temporal and parietal lobes. The first suggestions that areas in the temporal lobe played a specific role in visual processing was a study by Edward Schäfer (1888a) ostensibly devoted to

showing that, contrary to Ferrier's claims, the temporal cortex was not the locus of an auditory center. In monkeys in which either the superior temporal gyrus or nearly all the temporal lobes were removed, Schäfer reports no detectable loss of hearing but describes a deficit in recognizing visually presented stimuli:

> the condition was marked by loss of intelligence and memory, so that the animals, although they received and responded to impressions from all the senses, appeared to understand very imperfectly the meaning of such impressions. This was not confined to any one sense, and was most evident with visual impressions. For even objects most familiar to the animals were carefully examined, felt, smelt and tasted exactly as a monkey will examine an entirely strange object, but much more slowly and deliberately. And on again, after only a few minutes, coming across the same object, exactly the same process of examination would be renewed, as if no recollection of it remained.   (p. 375)

Little attention was paid to Schäfer's observations until after a study by Heinrich Klüver and Paul Bucy in the late 1930s, in which removal of the temporal lobe in monkeys resulted in a condition they described as *psychic blindness* or *visual agnosia* in which "the ability to recognize and detect the meaning of objects on visual criteria alone seems to be lost although the animal exhibits no or at least no gross defects in the ability to discriminate visually" (Klüver, 1948). The effects of the lesions induced by Klüver and Bucy were referred to as a syndrome since the monkeys exhibited a variety of other behavioral changes, including loss of emotional responsiveness and increased sexual behavior. Pribram and Brashaw (1953) addressed the question of whether these different deficits were due to a common process in the same brain area. By demonstrating that different lesions in temporal cortex could generate one or another deficit they showed that the various deficits were due to interrupting different processes. In particular, they traced visual agnosia to lesions of the amygdala and adjacent cortex. Subsequently, Pribram collaborated with Mortimer Mishkin in localizing visual agnosia specifically to lesions in inferotemporal cortex (Mishkin and Pribram, 1954). Subsequently, through a complex set of lesions involving the striate cortex in one hemisphere and the inferotemporal cortex in the other and the sectioning of the forebrain commissures, Mishkin (1966), succeeded in separating striate and inferotemporal cortex, and demonstrated that the deficits in visual learning and memory result when inferotemporal cortex is cut off from earlier visual processing. He also demonstrated that TE and TEO, areas within inferotemporal cortex that von Bonin and Bailey (1951) had distinguished on cytoarchitectonic grounds, produced differential deficits, with TEO lesions producing greater deficits in single-pattern discrimination tasks and TE lesions generating greater deficits on learning to perform multiple discriminations in parallel.

Again, the lesion studies indicating separate processing areas were complemented by single-cell recording studies that sought to determine what stimuli generated specific responses in inferotemporal cortex. Charles Gross, together with Carlos Eduardo Rocha-Miranda and David Bender (1972), found cells in the inferotempo-

ral cortex of the macaque which responded most vigorously to shapes such as hands. (Like Hubel and Wiesel's, their discovery resulted from serendipity: after failing to find a light source that would drive a particular cell, they waved a hand in front of the stimulus screen and produced a vigorous response.) Although nearly a decade passed before further research was published confirming different areas where individual cells were responsive to specific shapes,[8] in the 1990s there has been an explosion of reports of specific areas in inferotemporal cortex responsive to different specific shapes (see Tanaka, 1996, for a review).

A similar pattern of first lesion studies, then single-cell recording studies, emerged in research on the parietal cortex.[9] Ettlinger and Kahlsbeck (1962) analyzed deficits in monkeys with lesions in posterior parietal cortex and revealed deficits in visual orientation and reaching, indicating that these areas are involved in analysis of the location of objects in the visual field. In the early 1970s Hyvärinen and Poranen began recording from neurons in posterior parietal cortex, where they found cells which they interpreted as involved in visuospatial guidance of movement.

> ...when a sensory stimulus which interested the animal was placed in a specific location in space where it became the target of the monkey's gaze or manual reaching, tracking or manipulation.... Some cells were clearly related to eye movements whereas others appeared to discharge in response to visual sensory stimuli. (Hyvärinen and Poranen, 1974; quoted in Gross, 1998, p. 203)

The link Hyvärinen and Poranen found between activity of parietal cells and eye movement suggested a motor function for parietal cortex cells, a suggestion that was further developed by Vernon Mountcastle and his colleagues, who identified parietal cells linked not just to eye movement and visual tracking of objects, but to arm and hand manipulation (Mountcastle et al., 1975). Mountcastle interpreted these cells as involving motor commands linked to selective attention. Other research, however, suggested that the posterior parietal cortex was primarily involved in visual analysis since some cells are responsive in the absence of any motor activity (Goldberg and Robinson, 1980). But importantly, Richard Andersen and his colleagues demonstrated that cells in posterior parietal cortex mapped stimuli in terms of spatial location, a feature to which temporal lobe cells are relatively unresponsive (Andersen et al., 1985).[10]

3 Proposing a Complex, Organized System

The research described in the last two sections clearly advanced the efforts to functionally decompose and localize visual processing. Whereas initially only V1 seemed to be involved, it now appeared that much of the back half of the brain was devoted to analyzing visual inputs, with different areas analyzing different aspects of visual scenes. As discoveries piled up, a possible outcome was a theoretical morass — the

discovery that the brain consisted of many special-purpose processing areas with no systematic organization. But Mortimer Mishkin and Leslie Ungerleider introduced what proved to be a powerful organizing principle (see chapter 11, this volume). They proposed that visual processing beyond V1 was organized into two pathways, one progressing dorsally into posterior parietal cortex that was involved in analyzing *where* objects are in the visual field, the other, progressing ventrally down into inferotemporal cortex, that is involved in analyzing *what* objects are present in the visual scene. The distinction between *what* and *where* processing had been advanced previously by Schneider (1967) and Trevarthen (1968) for subcortical areas, but by proposing it for cortical areas Mishkin and Ungerleider offered a macro-level organizing principle for visual areas that integrated the findings related in previous sections.

For Mishkin and Ungerleider, the separation of two the pathways began in pre-striate cortex. Other researchers soon proposed extending the scheme back into V1, LGN, and the retina, generating a model of two processing streams from the very earliest visual input. An important piece of evidence for projecting the two streams further back was a distinction between two different cell types in the retina and the LGN. Enroth-Cugell and Robson (1966) had differentiated two types of cells in the cat retina, which they named *X* and *Y cells*. X cells had small receptive fields (hence, they were sensitive to high spatial frequencies), medium conductance velocities, and responded as long as the stimulus was present. In contrast, Y cells had large receptive fields, rapid conductance velocities, and responded transiently. A similar distinction of retinal cell-types was advanced for primates. $P\alpha$ (or P ganglion) cells correspond to the X cells in the cat while the $P\beta$ (or M ganglion) cells correspond to the Y cells in the cat. Research on old-world monkeys revealed that this scheme is maintained in the LGN where the cells in the two inner layers have large cell bodies (the layers are thus known as *magnocellular* or *M layers*) while those in the outer four have small cell bodies (thus called *parvocellular* or *P layers*). The M layers of the LGN receive projections from the M ganglion cells, while the P layers receive input from the P ganglion cells (Dreher et al., 1976).

One challenge was how to link the two precortical pathways with the two corti-cal pathways. The early studies of Hubel and Wiesel and others had suggested that V1 had a homogeneous cytoarchitecture; if this were the case, the two precortical pathways would converge in V1 and then two other pathways would diverge beyond V1. But, in accord with the caveat in the passage quoted above from Hubel and Wiesel, a new technique, involving the application of cytochrome oxidase stains (developed by Margaret Wong-Riley, 1979), revealed additional complexity in V1. Cytochrome oxidase is an enzyme critical to the oxidative metabolism of the cell; staining for it reveals areas of high metabolic activity. In layers 2 and 3, and 5 and 6 of V1 these showed up as "blobs"[11] which indicated regions of particularly high metabolic activity. Recording separately from cells in the blob regions and in the interblob regions, Livingstone and Hubel (1984) found orientation-selective cells only in the interblob regions, and wavelength-sensitive cells in the blobs, indicating a separation of processing within V1. On the basis of this differentiation, Living-

stone and Hubel proposed extending Mishkin and Ungerleider's two pathways to account for all visual processing from the retina on.

As Van Essen and Gallant's chapter (12, this volume) makes clear, the integrating scheme of two processing streams receives support from the neuroanatomy. The M layers of the LGN project to layer 4B in V1, where there are no blobs, whereas the P layers of the LGN project, via layers 4A and 4Cb, to layers 2 and 3 of V1, where there are both blob and interblob regions. Cytochrome oxidase stain also revealed a differentiation in V2 of alternating thick and thin stripes with interstripe areas between them. The differentiation in V1 is maintained, with the thick-stripe regions receiving their input from layer 4B, the thin-stripe regions from the blobs of layers 2 and 3, and the interstripe regions from the interblob regions in V1. From the differentiated areas in V1 and V2, processing largely separates into the *what* and *where* pathways originally distinguished by Mishkin and Ungerleider (see figure 12.2).

The proposal of two processing streams has provided an organizing framework for research on visual processing in the brain and, as we shall see, has influenced computational and psychological investigations of perception. But it is important to note that, like most integrating schemes, this one is subject to a variety of qualifications. Van Essen and Gallant draw attention to the fact that the two streams are not entirely independent – there are neural connections between areas such as MT and V4, which appear in different streams, and processing in the later parts of one stream continues even when its primary input is removed. Moreover, there is considerable interaction between the two precortical streams so that processing in each stream can continue even if the supposed precortical input is removed. Furthermore, the characterization of the two streams as processing *what* and *where* information has been questioned. Milner and Goodale (1995) argue that the dorsal stream receives information about the identity of objects (revealed in the ability of individuals with temporal lobe lesions to grasp objects appropriately for their use) and propose that what is distinctive about it is that it is primarily concerned with coordinating information about visual stimuli for action. In their view, the ventral stream is principally involved in extracting information about visual stimuli required for higher cognitive processing. Even with such qualifications, though, the idea of two visual streams plays an important integratory role in theorizing about visual processes, providing for a relatively coherent and graspable account of how the brain processes visual information.

4   What is Still Needed: A Computational Analysis

I have characterized the model of vision presented in figure 12.2 as providing an exemplar of successful explanation in cognitive neuroscience, and have used its history to provide an exemplar of how mechanistic models of cognitive processes can be developed. However, it is important to bear in mind that the account is still incomplete. One way it can be filled in is to discover more processing components

and figure out what operations they seem to be performing. But another way is to develop computational models of visual processes that specify the operations to be performed by each component in the proposed pathways of visual processing — models that specify how the firing patterns of neurons in one area encode specific information about distal objects and how later neurons are able to extract yet other information by operating on the firing patterns of the first set of neurons.

Many computational modelers, including many who now refer to themselves as computational neuroscientists, are currently engaged in developing just such models. But the effort is not new. One of the most influential proponents of applying computational modeling to vision was the British physiological psychologist turned MIT AI researcher David Marr. Marr began his career as an enthusiastic supporter and active contributor (Marr, 1969, 1970) to the approach of attempting to understand the visual system by discovering the responsiveness of individual cells, but he gradually became disenchanted with it. He was dissatisfied not only because the exciting initial discoveries, such as Hubel and Wiesel's discovery of edge detectors, had not yet been followed by similar discoveries of higher-level correlates of perception (his negative assessment here might have been premature), but also because of a recognition that such discoveries would not suffice to *explain* perception. As he worked out his final position in his posthumously published book, *Vision* (Marr, 1982), an explanation of perception, as opposed to a description of how the visual system behaved, required figuring out what the visual system was doing and how the various processes contributed to doing it:

> The message was clear. There must exist an additional level of understanding at which the character of the information processing tasks carried out during perception are analyzed and understood in a way that is independent of the particular mechanisms and structures that implement them in our heads. This was what was missing — the analysis of the problem as an information processing task. Such analysis does not usurp an understanding at other levels — of neurons or of computer programs — but it is a necessary complement to them, since without it there can be no real understanding of the function of all of those neurons.   (p. 19)

In fact, Marr went on to argue that there are "three levels at which any machine carrying out an information processing task must be understood." The highest of these levels is what he called the *computational theory* where one specified both (a) "what is computed and why" and (b) "that the resulting operation is defined uniquely by the constraints it has to satisfy" (p. 23). Marr illustrated what he was seeking by providing the computational theory for a cash register: *what* a cash register does is arithmetic, and the reason it does it is because the operations of arithmetic are those we "intuitively feel to be appropriate" for combining prices (p. 22). The constraints it must satisfy are principles such as associativity and commutivity. In the case of vision, he contends, "the underlying task is to reliably derive properties of the world from images of it; the business of isolating constraints that are both powerful enough to allow a process to be defined and generally true of the world is a central theme of our inquiry" (p. 23).

The second level focuses on how the machine carries out its information-processing task by specifying the *representations* it uses at the input and output level, and the *algorithms* it uses to transform input representations into output representations. Marr notes that the representations and algorithms must be appropriately coupled since particular kinds of operations are suited for specific kinds of representations, but that there often are many kinds of representations that can be selected for a given computation (one can represent the number one with binary or digital numerals) and, even given a choice of representations, different algorithms can perform the computation.

Finally, the third level addresses the question of how the representation and algorithm are physically realized. It is here that appeal to neural mechanisms is relevant, but Marr wants to stress two points: (1) any explanation of what the neurons are doing requires specifying the computation being performed and the representational system and algorithms employed; and (2) there is only a loose coupling between these levels so that details about the neural architecture constrain but do not determine the representations and algorithm, and the computation being performed.

As Marr noted in a passage quoted above, much of his concern was with identifying the constraints operating on vision, as well as with specifying a representational system and sets of algorithms that could carry out the computation. Computer programming provided him one means of examining various representational systems and exploring what algorithms might operate on them, and he identified psychophysics as a major source for evaluating the empirical adequacy of such accounts. The task Marr set for himself was to determine how, from low-level feature detection, a system could come to recognize objects. His positive proposal was that the system constructs three successive representations of each visual scene which he termed the primal sketch, a 2½-D sketch, and a 3-D model representation. The primal sketch is a two-dimensional representation in which lines correspond to intensity changes in light reaching the retina and larger configurations are constructed by grouping the resulting lines. The 2½-D sketch is a viewer-centered representation that specifies the depth and orientation of visible surfaces in the world. Finally, the 3-D model representation is an object-centered representation of volumetric primitives which facilitates recognition of the objects present. Marr specified computational procedures (e.g. algorithms in his three-level account) for producing each of these. For example, especially important for creating the primal sketch is a procedure for identifying zero-crossings (areas in the scene in which the second derivative of the intensity function changes sign), and Marr proposed a procedure whereby this could be done through local computation by neurons such as Hubel and Wiesel's simple cells in V1. To create a 2½-D sketch from a flat image, Marr proposed independent procedures that relied on information in the primal sketch about, for example, motion, stereopsis, optic flow, and surface texture, to determine properties of surfaces and their relation to the viewer.

As he proceeds to the 3-D model representation and the process of identifying objects, Marr's account becomes more sketchy and he offers fewer proposals as to the neural substrates involved in the hypothesized processes. More recently, psy-

chologist Irving Biederman (1995) has put forward a proposal as to how object recognition could proceed quickly from an object-oriented representation such as Marr's 3-D model representation. He proposes that primitive volumes correspond to one of 24 basic shapes known as *geons* that are created by varying four attributes of a cone shape. He argues that combinations of two or three geons (produced by varying their attributes, e.g. orientation, and relations to each other) can uniquely specify objects. Although the details of the geon theory extend beyond what can be evaluated at the neural level, Biederman does appeal to evidence by Tanaka (1993) that cells in area TE in the inferotemporal cortex respond to complex object features.

One thing that is striking about Marr's work is, once he became dissatisfied with traditional neuroscience approaches, how much he dissociated the development of computational models from the attempt to develop neural grounding. His approach was rather to propose algorithms that could compute a 3-D model from the low-level information available to the nervous system, evaluating his proposals largely by whether they could compute a 3-D model. The wealth of information now available or soon to be forthcoming about how the brain decomposes the computational process, however, can provide an additional important constraint on computational modeling. A further important consideration that Marr did not address was whether real organisms ever compute a 3-D model of their environment. Recently a number of theorists have in fact questioned this, arguing that in fact visual processing extracts only partial information from a scene as it is needed (Ballard, 1991; Churchland et al., 1994).

Despite these shortcomings in the way he executed his project, Marr's insistence on an information-processing analysis as a critical component of an explanation is well taken. Currently, many of the computational models being developed employ connectionist or artificial neural networks. These are computational models in which the primitive elements (units) are simple processors modeled loosely on neurons. Instead of exhibiting a pattern of spiking, units take on activation values. They are connected to each other by weighted connections so that activation in one unit can excite or inhibit activation in other units. Programs running on standard computers can determine how activation values of units in a network will change in response to inputs and interactions within the network. Such programs can also implement a variety of rules for changing the strengths of the connections between units; such changes alter how the network will respond to inputs and provide a way of implementing learning. In many of the early neural network models processing is only in one direction from input to output units (such networks are spoken of as *feed-forward*); increasingly, though, researchers are exploring models in which there are also backwards or recurrent connections and collateral connections (Bechtel and Abrahamsen, 2000).

Building neural networks can often provide insight into the reasons for and importance of decomposition found in the brain. An example of the utility of this approach is found in two network models that were developed to understand the reasons for the brain's decomposition into *what* and *where* pathways. Rueckl, Cave, and Kosslyn
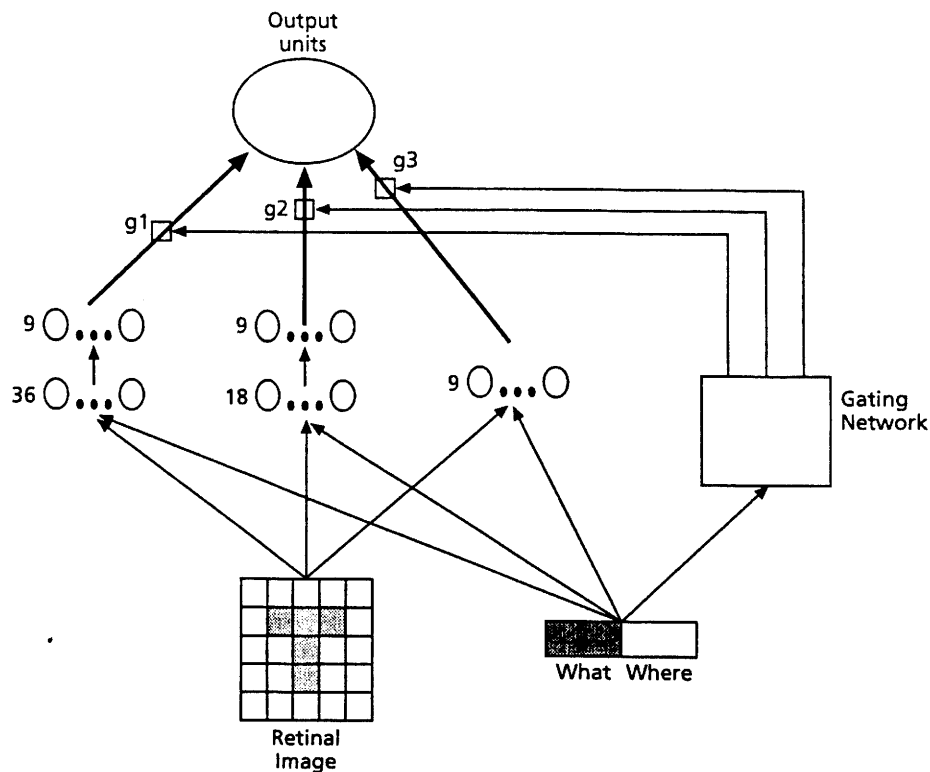
Figure 13.7 Jacobs et al.'s (1991) network that learned to employ different modular networks to determine the identity or location of the object specified on the artificial retina. The modular networks differed in whether they employed hidden units or not and the number of hidden units. The gating network learned to recognize which network produced the best answer for *where* and *what* questions and gated the output from the modular networks so that only the best-performing network would be allowed to control the output units.

(1989) designed feedforward networks whose input was presented on an artificial retina comprising a 5 × 5 grid of cells, each of which supplied an input of 1 if the input pattern covered the cell and 0 otherwise (see figure 13.7). The input from the 25 cells was processed through a hidden layer[12] and projected on to an output layer which consisted of two sets of units, on one of which the network was to identify, by the pattern of activation produced, the shape of the input and on the other of which it was to specify the location of the shape on the artificial retina. The network was trained through an error correction procedure known as *backpropagation* in which information about how far off an output unit is from its target activation is propagated backwards through the network, and weights on connections are changed in a direction that will reduce that error in the future. Rueckl et al. compared two network designs. In the more distributed design, activation was processed through a single set of hidden units; potentially, every hidden unit could contribute to both

the *what* and *where* responses. In the more modular design that was inspired by the research of Mishkin and Ungerleider, the hidden units were partitioned into two sets: one set sent activation only to the *what* units, and the other set sent activation only to the *where* units. Rueckl et al. demonstrated that the dual task was learned more readily when there were dedicated sets of hidden units supplying the two sets of output units, a finding which suggests that the brain might have separated the processing of the two sorts of information for reasons of computational efficiency. Using a somewhat more complex network model, Jacobs, Jordan, and Barto (1991) showed that networks could discover how to decompose the task on their own (figure 13.7).

These neural network models represent early attempts to employ computational models in the effort to understand the operations performed by the different components in the visual system. As we have seen, the processing of *what* and *where* information in the brain is much more complex, involving many different brain areas, and different constituents within brain areas. Current computational research is often sensitive to these details, and attempts to develop biologically realistic neural networks. As successful computational models are developed, they will provide a critical complement to the details about the decomposition and localization of visual processing by allowing us to understand how a set of components found in the brain are able to jointly perform the tasks needed for us to see.

Conclusions

In this chapter I have treated neuroscience research on vision as an exemplar in two senses. First, vision research has reached a such level of maturity that it provides other domains of neuroscience with an exemplar which their research might emulate. Second, it provides a exemplar for philosophers of how mechanistic models that decompose and localize cognitive functions develop through time. The trajectory from direct localization, to discovering multiple components performing different functions, to developing integrated models supported by computational models, is one also exhibited in other disciplines of biology (Bechtel and Richardson, 1993). In each case there will be differences, in part as a result of the particular investigatory tools and information available to researchers at a time. But the challenges of figuring out what the parts of a system are, what they do, and how they interact, are common features of the development of mechanistic models.

Notes

1   One of the first positive results from recording from cells in striate cortex was actually simply to confirm its topographical organization. Talbot and Marshall (1941), working with lightly anesthetized cats and rhesus monkeys, recorded the responses evoked by bright light either from moist threads on the exposed pia or from insulated needles inserted into the cortex. They described their procedure as follows:

If the visual pattern is narrowed down to a band and then to a small square, a position can be found in the field where a movement of a degree or less will reduce the response at the cortical point. This response is observed periodically on a cathode-ray tube, and the stimulus moved by manipulating crossed slits, until the primary response shows maximum amplitude and minimum latency for the least stimulus area.   (p. 1255)

2   Hubel describes some of the sense of surprise at the finding that individual cells responded to a bar of light at a particular orientation: "This was unheard of. It is hard, now, to think back and realize just how free we were from any idea of what cortical cells might be doing in an animal's daily life" (1982, p. 439).

3   An important difference between the different layers is that they generally project to different brain areas: layers 2 and 3 to other cortical areas, layer 5 to the superior colliculus, pons, and pulvinar, and layer 6 back to the LGN.

4   Hubel and Wiesel (1965) identified such cells only in areas 18 and 19 of the cat and assumed that these cells received their inputs from complex cells. Later, though, they found them in area 17 in both cat and monkey. After Dreher (1972) found cells in cats that were location-specific like simple cells but whose response dropped off as the length of the stimulus exceeded an optimum length, they dropped the assumption that they received their inputs from complex cells.

5   By analyzing patients with cortical achromatopsia (the inability to see colors) whose lesions could be traced to the fusiform gyrus adjacent to the striate cortex, both Verrey (1888) and MacKay and Dunlop (1899) had provided evidence of a second visual area, one devoted to color perception, but most nineteenth century researchers dismissed these claims in favor of the supposition of one cortical center for vision in the striate cortex, which might produce achromatopsia with mild lesions and full blindness with more serious lesions. One finding supporting this interpretation was that most cases of achromatopsia also manifested scotomas or areas of total blindness, suggesting that one lesion produced both effects.

6   Zeki ends the paper with the following comment about projections to other brain areas: "How the prestriate cortex is organized in regions beyond (central to) V4 and V4a remains to be seen. It is perhaps sufficient to point out at present that the organization of the prestriate areas would seem to be far more complicated than previously envisaged and that the simplistic wiring diagram from area 17 to area 18, from area 18 to area 19 and from area 19 to the so-called "interior temporal" area will have to be abandoned. At any rate, we were not able in this study to find any projections to the "inferior temporal" areas from areas 18 and 19 (V2 and V3). (p. 34)

7   During the same period John Allman and Jon Kaas, through single-cell recording in squirrel monkeys, traced topographically organized visual areas not only into extrastriate regions but also into temporal and parietal cortexes.

8   Gross (1998, pp. 199–200) reports on the slowness of response:

for more than a decade there were no published attempts to confirm or deny these and our other early basic results, such as that IT cells have large bilateral fields that include the fovea and are not visuotopically organized. And unlike Panizza, the discoverer of visual cortex in the nineteenth century, we did not publish in obscure journals or from an unknown institution. Perhaps because of the general skepticism, we did not ourselves publish a full account of a face-selective neuron until 1981.

9   Both Ferrier and Yeo (1884) and their opponents Brown and Schäfer (1888) reported deficits from lesions to the angular gyrus in the posterior parietal cortex which fit the pattern of deficit in spatial localization identified in the 1960s. Ferrier and Yeo report that the lesioned monkey was "evidently able to see its food, but constantly missed laying hold of it" and Brown and Schäfer report that their monkey "would evidently see and run up to [a raisin], but then often fail to find it . . ." (both quotations from Gross, 1998, pp. 200 and 201). Based on studies of brain injuries in World War I veterans, Gordon Holmes (1918) identified deficits in spatial localization of objects that the veterans could easily identify visually.

10 Subsequent research has confirmed a close relation between parietal cells and motor action and investigations into whether these cells are directly involved in planning action or in maintaining attention on visual stimuli (Snyder et al., 1997; Batista et al., 1999).

11 Livingstone and Hubel introduced the term *blobs* to characterize their appearance, citing the *Oxford English Dictionary* for the term. These blobs are "oval, measure roughly 150 × 200 μm, and in the macaque monkey lie centered along ocular dominance columns, to which their long axes are parallel" (1984, p. 310).

12 These units are referred to as *hidden* since they neither receive external input nor constitute output units.

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