review

Branching Thalamic Afferents Link Action and Perception

R. W. Guillery

Department of Anatomy, University of Wisconsin, School of Medicine, Madison, Wisconsin 53706

Guillery, R. W. Branching thalamic afferents link action and perception. *J Neurophysiol* 90: 539–548, 2003; 10.1152/jn.00337.2003. Recent observations of single axons and review of older literature show that axons afferent to the thalamus commonly branch, sending one branch to the thalamus and another to a motor or premotor center of the brain stem. That is, the messages that the thalamus relays to the cerebral cortex can be regarded as copies of motor instructions. This pattern of axonal branching is reviewed, particularly for the somatosensory and the visual pathways. The extent to which this anatomical evidence relates to views that link action to perception is explored. Most pathways going through the thalamus to the cortex are already involved in motor mechanisms. These motor links occur before and during activity in the parallel and hierarchical corticocortical circuitry that currently forms the focus of many studies of perceptual processing.

INTRODUCTION

"If I could only move my hand about I should know what the things were."—Patient reporting on failure to identify objects by touch after removal of cortex limited to the precentral cortex (Horsley 1909).

The thalamus has for long been regarded as a "sensory relay" passing sensory inputs to the cerebral cortex for perceptual processing along corticocortical pathways (Fig. 1*A*). Evidence presented elsewhere (Guillery and Sherman 2002a), and briefly summarized below, shows that most axons carrying information to the thalamus are branches of axons whose other branch innervates motor or premotor centers (Fig. 1*B*). Some of these axons go to the thalamus along ascending (sensory) pathways; others come from the cortex itself. That is, the thalamus passes to cortex information that *copies* instructions being sent concurrently to motor or premotor centers (a corollary discharge; see Sommer and Wurtz 2002). This pattern of branching afferents leads to a focus on the close and potentially important link between the afferent, sensory messages, passed to the cortex for perceptual processing on the one hand, and to motor centers for concurrent motor action on the other. Although perceptual processing is today often treated as though it were an independent activity, based on what Churchland et al. (1994) for vision have aptly described as a "Theory of Pure Vision," there have been many earlier arguments to link perceptual processing closely to motor action. In the following review, current knowledge of thalamocortical pathways will be presented and related to views that link action to perception. Recent evidence about patterns of axonal branching in afferents to the thalamus will be summarized for the somatosensory and visual pathways. This evidence will then be related to older evidence and to views of perceptual processing.

AFFERENTS TO THE THALAMUS PROVIDE KEY FUNCTIONAL INPUTS FOR CORTEX

Essentially all areas of the neocortex receive afferents from the thalamus. For some cortical areas, such as primary visual or somatosensory areas (V1, S1), this thalamic input is seen to dominate the functional properties of the cortical cells. These thalamocortical afferents pass to the cortex the main, "driving input"[1] that the thalamic relay cells receive from the optic tract or medial lemniscus. The functional organization of these pathways, including cortex, has been studied in terms of the receptive field properties of their neurons. The fact, considered below, that many of the afferents to the thalamus are branches of axons that also innervate motor centers has not contributed significantly to an analysis of the message that is being passed to the cortex. The analysis has generally related to perception, not to action.

For most "higher" cortical areas, in contrast to V1 or S1, the functional role of the thalamic afferents (shown as interrupted lines in Fig. 1*A*) remains unexplored. However, these higher cortical areas also receive afferents from thalamic relay cells, and these relay cells are innervated from the cortex by axons that, like the lemniscal and optic pathways, also have branches to motor or premotor centers (Fig. 1*B*). All of these branching afferents to thalamus, both ascending and corticothalamic, can provide a new view of the messages that the thalamus passes to the cortex.

In most contemporary studies of the cortex, as illustrated in Fig. 1*A*, thalamocortical connections dominate the functional analysis of primary cortical areas (V1, S1, A1), whereas corticocortical connections dominate the analysis of higher cortical areas (e.g., Born 2001; Mishkin et al. 1983; Sereno et al. 2002; Van Essen et al. 1992). At present there are no reasons for treating the thalamic input to some cortical areas, such as V1, S1, or A1 as having prime importance, and ignoring this input for other cortical areas. There are only practical reasons for not including these other thalamocortical axons: much less is known about them and they have proved hard to study.

Recent evidence, based on filling and tracing corticothalamic axons shows that, whereas essentially all thalamic relays receive afferents from cortical layer 6 (not illustrated in the figure), only some receive afferents from layer 5 (e.g., Abramson and Chalupa 1985; Bourassa and Deschênes 1995;

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[1] The "driving input" can be defined as the input that determines the receptive field properties that are passed on to cortex by the thalamic relay cells. (More details in Sherman and Guillery 1998.)

Address reprint requests to R. W. Guillery (E-mail: rguiller@wisc.edu).

Bourassa et al. 1995; Gilbert and Kelly 1975; Ojima 1994). These two types of corticothalamic axon are distinct in their light and electron microscopic appearance, in the pattern of

their thalamic synaptic contacts (Guillery 1995; Guillery and Sherman 2002b; Rouiller and Welker 2000; Sherman and Guillery 2001; Vidnyánsky et al. 1996), and in their known functional roles. Whereas layer 6 axons have small terminals that contact peripheral dendritic segments and modulate transmission in the thalamus, layer 5 axons are large, resemble the contacts of lemniscal or retinal afferents, contact proximal dendritic segments (Feig and Harting 1998; Guillery et al. 2001; Mathers 1972), and act as "drivers" (footnote 1, and Guillery 1995; Sherman and Guillery 1998, 2001, 2002). That is, where the function of layer 5 cells has been tested by silencing their cortical origin, they are seen to transmit receptive field properties to the thalamus (Bender 1983; Chalupa 1991; Diamond et al. 1992), and in this they differ from layer 6 afferents (Geisert et al. 1981; Kalil and Chase 1970; Schmielau and Singer 1977).

CORTICOFUGAL AXONS ARISING FROM LAYER 5 PYRAMIDAL CELLS

The layer 5 axons innervate the thalamic relay cells that project to higher cortical areas, serving to send messages through the thalamus from one cortical area to another (Fig. 1B). More important, for understanding the messages that reach higher cortical areas, layer 5 corticothalamic axons, like many ascending axons to thalamus, are also branches of axons going to motor or premotor centers in the brain stem (Bourassa and Deschênes 1995; Bourassa et al. 1995; Guillery et al. 2001; Rockland 1998; and see figure). That is, these corticothalamic axons send copies of motor instructions to the thalamus for transmission to other cortical areas.

Where one or a few axons are traced from visual or somatosensory cortex to their terminal sites in the thalamus one sees that the layer 6 axons (not shown in the figure) never extend beyond the thalamus, whereas layer 5 axons also have branches that continue caudally to the tectum or pons (Bourassa and Deschênes 1995; Bourassa et al. 1995; Rockland 1998). For visual areas 17 and 18 of the cat, each corticothalamic axon with terminals in the pulvinar also sends a branch to the midbrain. Further, no axons go to the midbrain without first sending a branch to the pulvinar (Guillery et al. 2001). Details of branching patterns of corticothalamic projections for many cortical areas still remain to be defined.

Layer 5 corticothalamic axons represent the drivers to thalamic nuclei whose driver input had for long been undefined.
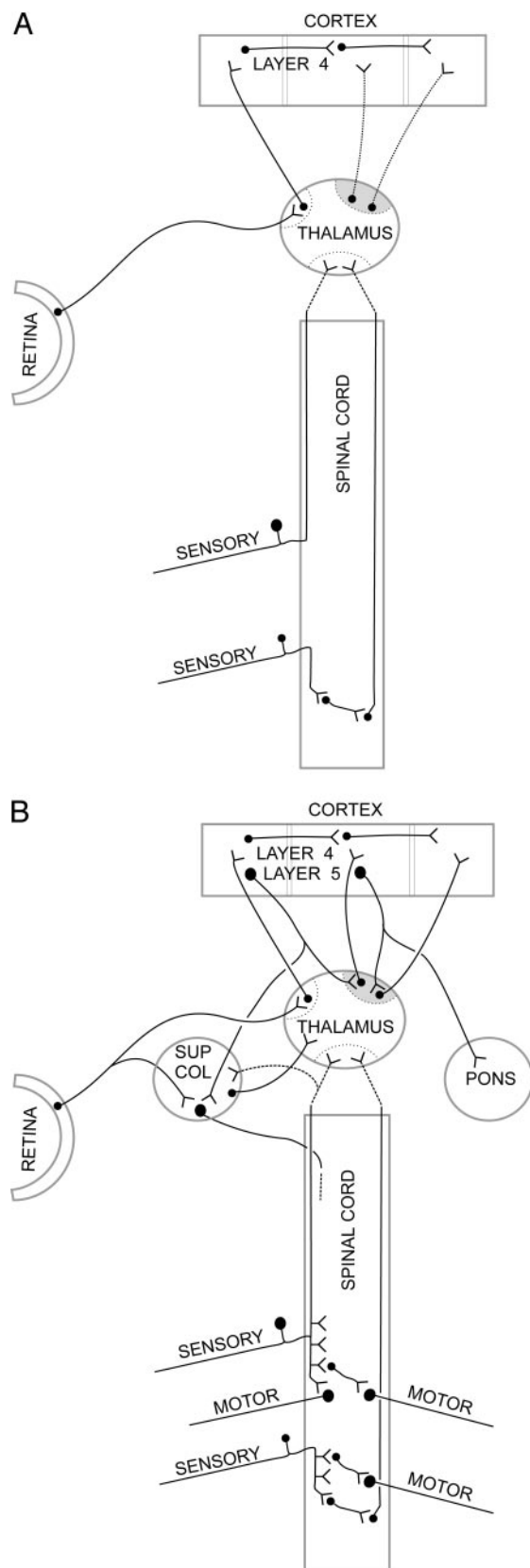
FIG. 1. Schematic representation of visual and somatosensory pathways relayed through the thalamus to the cortex. A: basic textbook schema of afferents that go from retina and spinal cord to thalamus and are then relayed from thalamus to cortex. The thalamic relay nuclei for these two pathways (lateral geniculate and ventral posterior nuclei) are outlined by a curved interrupted line. For simplicity the thalamocortical relay for the somatosensory pathways is not shown. It would resemble the visual relay in going to primary cortical area at the left for further transfer of messages to other cortical areas further to the right. Only the first stages of transfer through cortical areas are shown. Thalamocortical axons going to higher cortical areas on the right, arising from higher-order thalamic relays (shaded segment of thalamus), are shown as interrupted lines in A; generally these play no role in current analyses of perceptual processing (see text). B: some further connections discussed in text. They include motor branches of incoming sensory axons that terminate in the spinal cord and superior colliculus and also include *trans*-thalamic corticocortical pathways (see text). These arise from cortical layer 5 cells for relay through thalamus to other cortical areas and also have motor branches going to brain stem centers like the superior colliculus or the pons.

Specifically, for the pulvinar of the cat (Bender 1983; Chalupa 1991) and the posterior nucleus of the rat (Diamond et al. 1992) they provide the characteristic thalamic receptive field properties. Each higher-order thalamic nucleus that receives driver afferents from the cortex in turn relays the message to other (higher-order) cortical areas. The pulvinar sends its axons to many different visual cortical areas (Abramson and Chalupa 1985), and each of these cortical areas must be seen as receiving, from the thalamus, copies of messages from "lower" cortical areas that have already been sent to brain stem motor or premotor centers. That is, these layer 5 cortical cells send one branch to brain stem centers for action and another through the thalamus to higher cortical areas for perception.

THE SOMATOSENSORY PATHWAYS

Once the branching pattern of corticothalamic afferents is recognized as providing thalamic inputs that are copies of motor instructions, it becomes of interest to look at the branching patterns of other thalamic afferents. For this, the relevant branching occurs in axons that terminate in prethalamic as well as thalamic relays. For the somatosensory pathway, dorsal root axons enter the spinal cord and branch, with an ascending branch as well as local, spinal branches, and often a descending branch as well (Fig. 1B) (Brown et al. 1977; Brown and Fyffe 1981; Cajal 1911; Lu and Willis 1999). The common occurrence of such branching has to be seen in the light of evidence (Lu and Willis 1999) that false negative observations on branching are readily produced by anatomical and physiological methods. In spite of this difficulty, it is evident that both the dorsal column system and the anterolateral pathway are carrying messages to the thalamus that have already had an opportunity to act at spinal levels. Some messages, like those in the anterolateral pathway, act with a synaptic relay involved, and others, in the dorsal columns, act through branching of the incoming dorsal root axon.

For many years sensory losses, characteristic of Tabes dorsalis, were taught to medical students to help them understand the function of the dorsal columns. Romberg's sign, a loss of balance evident when such a patient stood straight with legs together and then closed the eyes, was interpreted in textbooks as a loss of the proprioceptive pathway in the dorsal columns (Brodal 1969; Nolte 1988). However, as Brodal pointed out later (1981), citing Vierck (1978) and Wall and Noordenboos (1977; see also Brinkman and Porter 1977), the lesion involves the dorsal roots and differs from a pure dorsal column lesion, which spares the local, spinal branches of dorsal roots. That is, the dorsal column lesion interrupts the branch that transmits copies of motor instructions through the thalamus to the cortex for perceptual processing, whereas in Tabes the branches for action and perception are both interrupted.

Views on the pathways that transmit information about limb position to the cortex have varied over the years and are relevant to understanding the distinctions between pathways for action and perception. Whereas Sherrington (1894) in describing the muscle afferents saw these as providing information about limb position, Mountcastle and Rose (1959) and Skoglund (1973) saw the perception of limb position as depending on joint receptors. They distinguished this from the information from spindle afferents, which they regarded as not reaching cortical levels and therefore playing no role in per-

ception. This was a conceptually important distinction, separating the pathway for perception from the pathway for action. Burgess and Clark (1969) and Burgess and Wei (1982) subsequently demonstrated that joint receptor responses were too limited to provide useful information about limb position, and Matthews (1977, 1982) showed that activity in muscle afferents could be perceived. Further, Matthews pointed out that artificial joint replacements did not lead to a loss of position sense: this once more united perception and action in a single, branched pathway coming from the muscle spindles; the false separation was reversed.

Before the medial lemniscus and the anterolateral pathways reach the thalamus several axons are given off to intermediate stations, including the brain stem reticular nuclei, inferior olive, hypothalamus, and superior colliculus (summarized in Guillery and Sherman 2002a; only the ones to the superior colliculus are shown in Fig. 1B). Some of these have been shown to be given off by branching axons, some may arise from distinct cells in the dorsal column or lateral cervical nuclei (Berkley 1975; Berkley et al. 1980; Bull and Berkley 1984; Feldman and Kruger 1980), and for some the evidence about branching is not clear. Textbooks often treat these as intermediate stops on the way to the thalamus, presenting them as a part of the pathway for perception. However, the connections to the inferior olive and the hypothalamus are as readily regarded as acting on premotor pathways,[2] not leading to the cortex but influencing cerebellar or autonomic (affective) components of motor reactions. The superior colliculus can also be seen as a motor or premotor center on evidence discussed in the next section.

These patterns of axonal branching show that messages passed from the thalamus to the somatosensory cortex carry more, and different, information than simply the "sensory" messages from peripheral receptors. No matter how one views the branching axons, in terms of which represents a "copy" of the other, the branch to the thalamus carries, in addition to the sensory information that has been the major or only focus for sensory physiologists, a considerable burden of information about instructions currently going to centers for action. For the ascending and the motor branches of the dorsal root axons we know that the incoming messages pass along both branches. It is possible that not every incoming impulse passes along both branches, and the postsynaptic action may well differ at the two terminal sites, depending on the nature of the receptors and on other local factors (e.g., Markham et al. 1998). However, one can expect there to be a relatively constant relationship between the messages delivered by the two branches. The message going through the thalamus to cortex will *represent* a concurrent motor instruction that will influence a motor act, directly or indirectly, positively or negatively, without need for any further outcome of the perceptual process, and quite possibly before the completion of the perceptual process. An issue that is largely unexplored concerns how the perceptual processes relate to these instructions for action. Are they best

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[2] Sperry (1952), writing about motor aspects of perceptual processing has said: "The core of the perceptual process in the higher centers is more premotor or better pre-premotor in nature, owing to the hierarchical plan of neural organization." The important point here is that the sensory pathways have actions that, although they may be far removed from a motor neuron, are not on any of the classical sensory pathways, and they must be evaluated in terms of their eventual motor actions.

regarded as completely independent, as is often done, or can more be learned about perceptual processing by studying this relationship more closely?

THE VISUAL PATHWAYS

The isolation of the mechanisms for perception from those for action in many contemporary studies of the visual system has received careful and critical review by Churchland et al. (1994). They look for models of visual processing that relate more closely to the continuous interactions between action and perception, and consider a number of psychophysical phenomena that do not fit readily into a theory of "Pure Vision." They report on anatomical connections that appear to argue against the pure theory, and consider the computational advantages of what they call "interactive vision," that is, visual perception that is not waiting for a cortical analysis of the visual scene *before* action.

Churchland et al. (1994), having summarized much of the relevant connectional anatomy, comment: "what is frustrating about this assembly of data, as with neuroanatomy generally, is that we do not really know what it all means."[3] This is a valid point about the material they summarize; many of the relevant pathways, corticocortical, corticothalamic, and descending corticofugal, are given no clearly assigned functions. Drivers need to be distinguished from modulators, not only in the thalamus, where this is generally possible (although still in need of much more detailed experimental verification), but also in the corticocortical pathways, where this is essentially unexplored. Comparably, descending pathways to the brain stem and cord are generally not defined in terms of motor actions. It is important to know not only whether a descending corticofugal pathway is a driver or a modulator, but it may prove even more important to know the branching patterns of the axons, which, as indicated above for the somatosensory pathways, are often undefined. Where a branching axon sends a branch to a thalamic relay for transfer to the cortex, knowledge about the actions of its other, motor or premotor branch may provide additional clues about the message going to the cortex.

For retinogeniculate axons, branches for action and perception are readily recognized. For rodents and rabbits, all retinogeniculate axons have branches that go to the midbrain tectum or pretectum (Chalupa and Thompson 1980; Jhaveri et al. 1991; Linden and Perry 1983; Vaney et al. 1981). There is no "pure," unbranched geniculocortical pathway exclusively for perceptual processing in cortex. In cats the evidence for branching in the large (Y) and the small (W) ganglion cells is clear (Fukuda and Stone 1974; Leventhal et al. 1985; Wässle and Illing 1980). Evidence for the intermediate (X cells) at one time indicated that these might send a direct, unbranched pathway to the lateral geniculate nucleus. However, observations of some X-cell axons with fine-caliber branches heading to the midbrain (Sur et al. 1987) and, later, of six out of six filled X-cell axons with fine branches going to the pretectum (Tamamaki et al. 1994) suggest that there may be no pure unbranched retinogeniculate pathway in cats. In monkeys the

evidence about the largest and the smallest retinal ganglion cells (magnocellular and koniocellular; see Casagrande and Norton 1991) again shows the majority, probably all, with branching axons going to lateral geniculate nucleus and midbrain. The evidence for the parvocellular cells was summarized earlier (Guillery and Sherman 2002a); although it is inconclusive. However, given the difficulty of demonstrating fine branches (see Lu and Willis 1999) and evidence for cats that the midbrain branches of X-cells are very fine, it is reasonable to conclude that for all species most, possibly all, retinogeniculate axons have midbrain branches.

The branch of the optic tract to the midbrain was earlier treated as an alternative route to the cortex (Diamond 1973; Schneider 1966; Sprague 1972) and thus as possibly another pathway for perception. This is because there are axons going from the superior colliculus to the pulvinar (Mathers 1971; Partlow et al. 1977), and the pulvinar sends its axons to several higher visual cortical areas (Abramson and Chalupa 1985). Two issues relate to this view of the midbrain as a visual relay to the cortex. One is that, whether or not there is a tecto-pulvino-cortical pathway, there is no doubt that the superior colliculus and the pretectal nuclei are motor centers concerned with head and eye movements. Even though the retinotectal axons go to the superficial layers of the colliculus, not to the deep layers more closely involved in motor control mechanisms themselves, the retinotectal axons must still be seen to provide access to tectal computations that produce head and eye movements. The second, more critical point concerns the nature of the messages going from the midbrain to the pulvinar. Are these drivers or modulators? In terms of their synaptic relationships and fine structural appearance in the pulvinar, reports vary (Mathers 1971; Partlow et al. 1977; Robson and Hall 1977). Perhaps most tellingly, pulvinar cells lose their characteristic receptive field properties after the visual cortex is silenced but not after tectal silencing (Bender 1983; Chalupa et al. 1972; Chalupa 1991), indicating that the tectum does not provide a significant driver input to pulvinar for perceptual processing.

Taking the visual system as a specific example, several stages are encountered from retina to higher cortical areas, where thalamic afferents can send one branch to the thalamus for transmission to cortex and one to motor or premotor centers of the brain stem. The visual message goes from the retina through the geniculocortical pathway to area 17 for early stages of perceptual processing, and along the retinotectal branches to the superficial layers of the superior colliculus for premotor action. From area 17, in turn, layer 5 axons go the pulvinar and also send a branch to the superficial layers of the superior colliculus (Guillery et al. 2002; Harting et al. 1992). Evidence that the axons coming from area 17 to the colliculus can affect a motor or premotor action comes from Schiller and Tehovnik (2001) and Tehovnik et al. (2002), who showed that microstimulation in area 17 of a monkey can affect the target choice of a saccadic eye movement. Thresholds for the evocation of saccades were lowest for the deep layers of the cortex, suggesting that the layer 5 corticofugal axons, which send branches to the thalamus and superior colliculus (see above), were being stimulated. The layer 6 axons are less likely to act on the saccade because they do not go beyond the thalamus, and are modulators in the thalamus.

The pulvinar itself sends axons to several different higher

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[3] It is worth pointing out that interpreting evidence from psychophysical studies or from computer models in terms of what they mean for the neural circuitry underlying particular perceptual processes is equally frustrating. The ways in which these different approaches to perception can be interrelated are but poorly defined as yet.

cortical areas, many of which, in turn, have layer 5 projections back to the thalamus (Abramson and Chalupa 1985). They also send axons to the superior colliculus, some to the superficial layers, but many to the deeper layers, nearer to the motor output (see Harting et al. 1992). That is, the outputs of these higher cortical areas, again, go to the cortex for perceptual processing and to the brain stem for action, although at present it is not known whether these two pathways represent branches of single axons or are two independent outputs. Currently there is no evidence about the branching patterns of these cortico-thalamic axons.

The problem that arises is to define exactly how visual perception and eye movements relate to each other, and to the pathways considered above. The rapid searching movements that occur when a new scene is examined (Yarbus 1967) are clearly relevant to perception, but most of the corticotectal axons from many different cortical areas (Harting et al. 1992) cannot yet be related to the production of these, or other, eye movements. Nor, at present, is it known how corticofugal messages to the tectum for action relate to messages passed through the thalamus to the cortex for perception. More information about the anatomy of the pathways is needed, but in addition, at each stage of corticothalamocortical processing the relationship of the motor instructions to the messages that contribute to the perceptual process needs to be understood.

An example is provided by the recent demonstration (Moore and Armstrong 2003) that changes in the visual responses of neurons in the cortical area V4 of monkeys can be produced by subthreshold stimulation of the frontal eye fields. Here, sub-threshold motor instructions for saccade production, possibly carried in corticotectal axons to the deep layers of the colliculus (Harting et al. 1992), produce a change in a "sensory" response in the cerebral cortex. Moore and Armstrong (2003) postulate "a common network for the control of visual and oculomotor selection." The possibility that this involves corticotectal (motor) axons that have branches going through a thalamic relay to the visual (sensory) cortex, merits exploration.

For the visual pathways, as for the somatosensory pathways, there is limited evidence about the losses produced by damage to one or another of the branches of axons afferent to the thalamus. Lesions of the superior colliculus in cats or tree shrews produce deficits in directed movements in response to visual stimuli (Diamond 1973; Sprague 1972). In primates Mishkin et al. (1983) briefly reported for rhesus monkeys (but with no details and no citation) that "complete bilateral destruction of the superior colliculus" had no effect on the performance of a visual "landmark task." Earlier, for monkeys Pasik et al. (1966) had reported essentially no changes after collicular lesions, whereas Anderson and Symes (1969) reported mild changes (see also Schiller, 1972). Dumont et al. (1974) reported briefly that bilateral lesions of the superior colliculus in monkeys produced abnormalities of eye movements, but found no evidence for loss of brightness, color, or pattern discrimination. Heywood and Ratcliff (1975) reported mild oculomotor abnormalities in humans after lesions of the superior colliculus. Pierrot-Deseilligny et al. (1991) described a patient with a lesion in the superior and inferior colliculi with abnormal saccades, and diplopia, but no other visual losses. Comparably Girkin et al. (1998) reported on a patient with a lesion in the brachium of the superior colliculus who had diplopia and pupillary defects, but no other visual sensory losses.

These are brief reports with little detail. It may prove important to explore the perceptual capacities more fully. Visual perceptions depend on extensive exploratory eye movements. On the basis of current evidence it appears that lesions of the midbrain branches of cortico- and retinogeniculate axons affect mechanisms of action, leaving those concerned with perception essentially intact.

Lesions in the visual cortex (area 17) in primates produce blindness (Holmes and Lister 1916; Polyak 1957; Walsh and Hoyt 1957), showing again that visual perception depends on the geniculate branches, not on the midbrain branches. The phenomenon called "blindsight" (Weiskrantz 1986), which allows a patient to respond with some degree of discrimination to a stimulus presented in the blind visual field, again demonstrates this separation of action from perception. Details of pathways underlying the action component of blindsight remain unexplored, although pathways through pulvinar or amygdaloid nuclei have been proposed (e.g., Hamm et al. 2003; Weiskrantz 2003). If the pulvinar were involved, it would probably not be a driver pathway transmitting receptive field properties to the cortical areas, given that these cortical areas are concerned with perceptual processing. It would more likely involve tectothalamic modulators that alter the response properties of pulvinar cells, with some visuotopic (localizing) organization. However, since "blindsight" is demonstrable after a hemidecortication (Perenin and Jeannerod, 1978) it seems more probable that subcortical mechanisms are involved. They are capable of the topographical sophistication needed to account for the responses recorded in blindsight. Frogs can catch flies, a cat without visual cortex can turn accurately to a visual stimulus, and even a spinal dog can accurately scratch a local stimulus on the flank.

OTHER BRANCHED AFFERENTS TO THE THALAMUS

Although, as indicated above, evidence about branching axons is difficult to obtain, there are observations, summarized by Guillery and Sherman (2002a), that many afferents serving as drivers to one or another thalamic nucleus have branches that innervate lower brain stem centers. The evidence for the auditory pathways is weakest, perhaps because the branching has been of no interest, or possibly because lower levels of the auditory system are less closely linked to motor actions. There is good evidence that cerebellothalamic and mamillothalamic axons both have brain stem branches (Cajal 1911; and see Guillery and Sherman 2002). From the evidence available currently it is possible to entertain the hypothesis that *all* driver axons to the thalamus, ascending and cortical, have motor or premotor brain stem branches. The hypothesis is worth testing not only because it suggests an interesting new generalization about the organization of the thalamus, but also because, provided more reliable methods can be developed for demonstrating branches, then, if the hypothesis can be proved wrong, an important functional question will arise: how do the branched pathways differ functionally from the unbranched pathways?

INTERACTIONS BETWEEN ACTION AND PERCEPTION

Although the idea that perceptual processing involves more than the passive transmittal of messages from receptors to cerebral cortex is not new, it merits a new focus that relates to the anatomy summarized above. Helmholtz (Warren and Warren 1968) wrote:

"The correspondence, therefore between the external world and the perceptions of sight rests, either in whole or in part, on the same foundation as all our knowledge of the actual world—on *experience,* and on constant *verification* of its accuracy by experiments which we perform with every movement of our body" (stress in the original).

and,

"[N]o perceptions obtained by the senses are merely sensations impressed on our nervous systems. *A peculiar intellectual activity* is required to pass from a nervous sensation to the conception of an external object which the sensation has aroused" (stress added).

Sperry (1952) has stated:

"An analysis of our current thinking will show that it tends to suffer generally from a failure to view activities in their proper relation, or even in any relation, to motor behavior. The remedy lies in further insight into the relationship between the sensori-associative functions of the brain on the one hand and its motor activity on the other."

The brain stem branches of afferents to the thalamus provide an important anatomical clue for reevaluating perceptual processing in accord with the views of Helmholtz; they may provide the "remedy" sought by Sperry. These branches show that few if any messages transmitted to the cerebral cortex do not *concurrently* influence the motor apparatus, in some way or another, directly or indirectly, to increase or decrease a motor response. The relationship between Sperry's "sensori-associative" functions and motor activity can be sought in the motor links of thalamic afferents. The search need not be limited, as in Sperry's proposed "remedy," to links of higher cortical areas. The motor links are there for primary ascending afferents to the thalamus. For these, the motor message must accompany, and generally precede, perceptual processing in cortex. That is, the anatomy shows that, where this branching occurs, the sensory input will inevitably initiate both action and perception. The motor message is a *necessary* accompaniment of the perceptual process.

There is a serious question about the messages that are passed along any of these branching thalamic afferents. Are they to be seen as a mechanism producing motor effects, or as sensory messages? Because the axons branch, the answer for the experimentalist must be "both" when the whole live organism is considered. However, it will inevitably be seen as a sensory mechanism where an animal is anesthetized, perhaps paralyzed as well. This is an important limitation for many early studies of perceptual processing in cortical cells. The role of a particular pattern of neural activity in perceptual processing has been based on the fact that the neural activity occurred in the cortex, and that there was a conceivable link between this and known perceptual processes. There could be no direct evidence linking the neural activity to particular perceptual processes, or more importantly for the present discussion, to motor actions. It is of interest to compare studies of cortex in cats or monkeys (e.g., Hubel and Wiesel 1977) with those on the tectum of frogs (Maturana et al. 1960), where considerations about perception were never in the forefront. Rather, for the frog (and for the investigators) the important issue, in relation to tectal activity recorded, was the likely motor reaction to a visual stimulus: if it is large, retreat; if it is small, eat it.

Studies of visual processing in the cerebral cortex of cats and monkeys, which dominate much contemporary thinking about perceptual processing, start at visual area V1 (area 17), progressing through simple, and complex cells, and then continuing through several hierarchical stages of cortical processing, with specializations for color, movement, and with putative "where" and "what" pathways (e.g., Kandel et al. 2000). This type of analysis of sensory circuitry has deep roots in studies of anesthetized preparations and still relies to a significant extent on such studies. Recent studies using fMRI or recordings from awake animals are beginning to change the picture, but the interpretations of the cortical records (e.g., Luppino et al. 2001; Nakamura et al. 2001; Rizzolatti and Luppino 2001; Sereno et al. 2002; Tolias et al. 2001) are still commonly expressed in terms of a relatively passive chain of messages transferred from one cortical area to another, toward a motor cortical "outlet," with no attention paid to thalamic inputs that any one of the cortical areas receives, or to any of the outputs that each of the cortical areas sends to lower motor centers.

To explore how sensory mechanisms relate to motor outputs, consider an organism that develops a new set of sensors. It can be a primitive organism first developing light- or sound-sensitive receptors, or a higher mammal, conceptually human, developing new sensors, such as mystacial vibrissae, an echolocating system, or electro-receptors for use, perhaps, in aquatic recreations. When these receptors first appear they will be of no use, except insofar as they lead to motor responses. It is not likely that they could lead to perceptual functions until after some motor reactions had been produced. These motor reactions in themselves are likely to produce further, positive or negative, experiences, although these experiences will be of limited use unless they are stored in memory. This record of the sensory–motor experience can then provide the first trace of what can later form the basis of perceptual processes, after more experiences of similar stimuli and various motor responses. In terms of the acquisition of new sensory mechanisms, sensory machinery that connects to higher levels of processing, without first connecting to the motor pathways will bring to those higher levels a puzzling set of messages that can be given empirical sense only by reference first to lower-level motor, exploratory mechanisms.

A more direct approach to the acquisition of new sensors can be based on the experience of providing a prosthesis to individuals who lack a particular sense. In a probably unrepeatable study, Button and Putman (1962) implanted into the occipital cortex of a blind subject wires attached to a light-controlled stimulator. They report that "with a few moments' practice, she learned to point the photocell at a light in the room." Bach-y-Rita (2003) has written about blind subjects provided with a TV camera that delivered information about the visual scene to skin receptors, indicating that the subjects' ability to appreciate the visual scene depended on their ability to control the camera, including zooming, aperture, and focus. "*After sufficient training* (stress added), our subjects reported experiencing the image in space, instead of on the skin. They learn to make

perceptual judgments, using visual means of analysis." It is not clear from accounts I have seen what perceptual abilities can be developed in the complete absence of any motor control of the sensor. This information is not of obvious interest for developing or using a prosthesis but it may prove of considerable interest for understanding the development of new perceptual capacities.

Helmholtz (Warren and Warren 1968) addressed the appearance of *new* sensory systems by considering an infant, developing a perceptual apparatus. He wrote of the infant exploring objects by handling them, putting them into its mouth, regarding them from different angles, to make judgments about the causes of the sensations: "It is only by voluntarily bringing our organs of sense in various relations to the objects that we learn to be sure as to our judgments of the causes of our sensations."

Here the importance of the motor exploration confirms the above discussion, but the "voluntary" nature of the exploration merits separate consideration. Helmholtz stresses the importance of the exploration of the sensory environment that allows us, through motor actions, to make judgments about our environment, that is, to establish perceptual structures. He wrote:

"If we ask whether there exists some common characteristic distinguishable by direct sensation through which each perception related to objects in space is characterized for us, then we actually find such a characteristic in the circumstance that bodily movement places us in different spatial positions relative to the perceived objects, and in doing so also changes the impressions which these objects make on us. The impulse to movement, however, which we give through the innervation of our motor nerves, is something which can be perceived directly. We feel we are doing something when we give such an impulse. But what it is we are doing we do not know directly."

For the last statement it is worth comparing the first with the second half. In the first half the movement might represent an involuntary act, perhaps even the action of a motor branch of a sensory axon, but then he makes clear that this is not his intention; he has the observer as initiating the movement, even though there is some mystery about the basis of that initiation; *and he ascribes a perceptual experience to the motor act.*

Two points arise clearly from what Helmholtz has written. One is that our perceptions depend on and are in part generated by our movements. The other is that the observer makes these movements (voluntarily) *in order* to explore the environment. The second point is quite explicit when he says:

"Finally, the tests we employ by voluntary movements of the body are of the greatest importance in strengthening our conviction of the correctness of the perceptions of our senses."

This is as extreme as he gets; it is easy to sense the history of a life devoted to testing the correctness of the perceptions of the senses, although that is not how most people operate most of the time. We do not feel a need to test the correctness of the perceptions of our senses. Our daily lives, which consist predominantly of motor reactions to changing sensory inputs, provide us with a store of corollary discharges, each associated with a particular sensory event and passed, as such, to the next, higher cortical level as yet another corollary discharge.

In general, impulses generated in sensory nerves can be said to vary the conditions under which the "structure" of the sensory environment is perceived. That is, these impulses *produce* the movements that vary the conditions. One can ask: who actually is in control? Are we initiators of the movements,

as Helmholtz suggests, or does the environment *initiate* the movements, which then allow us to develop our perceptual categories? Which of our movements are a direct response to sensory stimuli bombarding us continuously; which are "voluntary," "exploratory" movements that we have initiated *to explore the environment*; and how much of the circuitry may actually be concerned with the suppression of movements that might otherwise be produced by the incoming messages?

The anatomy is clear about an early involvement of motor connections in perceptual mechanisms. Where these connections are branches of axons that also serve perception, the mechanisms are not "voluntary," they are parts of the machinery committed to particular motor outputs. This applies to the incoming (e.g., retinofugal or dorsal column) axons and also applies to corticothalamic axons from cortical layer 5 that pass copies of motor instructions to higher cortical areas.

Although the anatomy shows close links between pathways for perception and action, this does not imply that perception cannot occur without action. There may be sensory systems that pass straight to the cortex, without any lower motor connections. Once, in the course of evolution, a sensory system is established with close links to motor systems, then it could, perhaps, develop direct connections into a previously established "perceptual" center that has no prethalamic links into motor systems. This would fit closely to a model of "Pure Sensation," parallel to the system of "Pure Vision" (Churchland et al. 1994). It would be a pathway where cortical analysis of perceptual structures could be independent of movement. In principle this seems feasible and could be studied experimentally. However, it has been shown that with current techniques, negative evidence about axonal branching cannot be interpreted as evidence for the absence of branching. The possibility that there are pathways, perhaps the parvocellular part of the visual pathway in primates (see above), or parts of the auditory pathway (for listening to Bach), that go straight to the cortex with no subcortical branches, may prove hard to demonstrate until methods of studying fine axonal branches are more sensitive.

A telling dissociation of action and perception is seen in the "locked-in" syndrome (Allain et al. 1998; Plum and Posner 1966), since patients demonstrate a virtual absence of movement but a good survival of perceptual functions. However, in these patients the perceptual skills were established at a time when the motor actions produced by the nonthalamic branches were still effective, and action and perception could be related. After the brain stem (or other) injury the action of the motor branches is no longer effective, but many of the sensory messages passed to the thalamus are likely to be unchanged and can be interpreted in terms of past experience. That is, in these patients, the ascending afferents carry copies of messages to motor cells (e.g., ascending branches from spindle afferents), but are carrying messages that cannot be obeyed. Nonetheless, these copies will be transmitted to the cortex through the thalamus. Similarly, afferents that send copies of messages to premotor (or pre-premotor) centers are sending copies of messages that can still play a significant role in central processing even if there can be no final motor outcome. The corticothalamic axons will be intact and will be sending copies of "intended" motor instruction from one cortical area to another; these are messages that were previously used in perceptual processing in higher cortical areas, and can still be used.

Transthalamic messages from cortex will represent intended movements in a way that the direct corticocortical messages probably would not. The higher-order circuits can then be seen to represent a complex of instructional messages that relate to perceptual processing even when the final execution of the motor instructions is no longer possible.

GENERAL CONCLUSIONS

The citation at the beginning of this review refers to a sense where the interaction of action and perception is striking. I have argued that the anatomy of sensory pathways provides strong evidence for close interactions of this nature in many other sensory systems, possibly all that traverse the thalamus. Not only is there evidence of interactions in many ascending pathways to the thalamus, but in addition there is the interaction that must occur whenever a corticocortical pathway linking one sensory cortical area to another relays in the thalamus and sends a descending branch to the brain stem or beyond.

The pathways considered here provide the cortex with an ongoing record of motor instructions. That record provides the input for perceptual processing. It can be regarded as providing the machinery of perceptual processing. Sperry (1952) wrote: "In so far as an organism perceives a given object, it is prepared to respond with reference to it," which suggests the model of an incoming sensory train discharging its perceptual load for the initiation of a motor response; yet he continues: "That the preparation for response *is* (his italics) the perception is suggested by further considerations." This view of perception as the preparation for response can be seen in terms of the anatomy, which shows perceptual processing as built up from the ongoing motor instructions.

For Helmholtz (Warren and Warren 1968) our perceptions are a "symbol" for the source of the stimulation. They are not an "image," standing in some particular relation to an object; the symbol is arbitrary, comparable to writing, which is a symbol of words but not an image of words. Helmholtz wrote: "Thus even if our sensory perceptions in their quality are only symbols, whose special nature depends entirely on our organization, they must not be discarded as empty appearances; rather they are symbols for something, either existing or happening—and what is most important—they can represent the laws governing this event for us."

These symbols are created from the copies of motor and premotor (and pre-premotor) instructions from a great range of sources. Some come almost directly from the environment, for instance, pain fibers that innervate spinal reflex mechanisms and send ascending messages to the thalamus. Others come from higher cortical areas, representing thalamocortical circuits that are recording motor instructions that have already been sent out by other, lower cortical centers. Anatomy shows action and perception inexorably linked at all levels, from the peripheral input to the higher cortical areas.

Finally one should ask why all of these pathways go through the thalamus. This opens another chapter, a subject for another review. Briefly, as an end note, it is important to recognize that all of the copies of motor instructions that pass through the thalamus are there exposed to rich modulatory influences that come from the cortex, the thalamic reticular nucleus, and the brain stem. This modulation (see Guillery and Sherman 2002b; Sherman and Guillery 1996, 2001) represents an important function of the thalamic relay, allowing it to modulate transmission to the cortex in accord with current attentional needs. The modulation can be global or it can be highly localized and specific; it can allow for changing interactions between one circuit (or part of one circuit) and another in a complex pattern of interactions that are currently almost entirely unexplored. This characteristic action of the thalamic relay will be able to modify all of the messages passing through the thalamus for perceptual processing, but will leave the motor branches for action unaffected.

DISCLOSURES

REFERENCES

Abramson BP and Chalupa LM. The laminar distribution of cortical connections with the tecto- and cortico-recipient zones in the cat's lateral posterior nucleus. *Neuroscience* 15: 81–95, 1985.

Allain P, Joseph PA, Isambert JL, Le Gall D, and Emile J. Cognitive functions in chronic locked-in syndrome: a report of two cases. *Cortex* 34: 629–634, 1998.

Anderson KV, and Symmes D. The superior colliculus and higher visual functions in the monkey. *Brain Res* 13: 37–52, 1969.

Bach-y-Rita P. Late post-acute neurologic rehabilitation: neuroscience, engineering and clinical programs. *Arch Phys Med Rehab* In press.

Bender DB. Visual activation of neurons in the primate pulvinar depends on cortex but not colliculus. *Brain Res* 279: 258–261, 1983.

Berkley KJ. Different targets of different neurons in nucleus gracilis of the cat. *J Comp Neurol* 163: 285–303, 1975.

Berkley KJ, Blomquist A, Pelt A, and Fink R. Differences in the collateralization of neural projections from dorsal column nuclei and lateral cervical nucleus to the thalamus and tectum in the cat: an anatomical study using two different double labeling techniques. *Brain Res* 202: 273–290, 1980.

Born RT. Visual processing: parallel-er and parallel-er. *Curr Biol* 11: R566–R568, 2001.

Bourassa J and Deschênes M. Corticothalamic projections from the primary visual cortex in rats: a single fiber study using biocytin as an anterograde tracer. *Neuroscience* 66: 253–263, 1995.

Bourassa J, Pinault D, and Deschênes M. Corticothalamic projections from the cortical barrel field to the somatosensory thalamus in rats: a single-fiber study using biocytin as an anterograde tracer. *Eur J Neurosci* 7: 19–30, 1995.

Brinkman J and Porter J. Movement performance and afferent projections to the sensorimotor cortex in monkeys with dorsal column lesions. In: *Active Touch, the Mechansim of Recognition of Objects by Manipulation: A Multidisciplinary Approach,* edited by Gordon G. Oxford, UK: Pergamon Press, 1977, p. 119–137.

Brodal A. *Neurological Anatomy in Relation to Clinical Medicine* (2nd ed.). Oxford, UK: Oxford University Press, 1969, p. 108.

Brodal A. *Neurological Anatomy in Relation to Clinical Medicine* (3rd ed.). New York: Oxford University Press, 1981, p. 140.

Brown AG and Fyffe RE. Direct observations on the contacts made between IA afferent fibres and alpha motoneurons in the cat's lumbosacral spinal cord. *J Physiol* 313: 121–140, 1981.

Brown AG, Rose PK, and Snow PJ. The morphology of hair follicle afferent fibre collaterals in the spinal cord of the cat. *J Physiol* 272: 779–797, 1977.

Bull MS and Berkley KJ. Differences in the neurones that project from the dorsal column nuclei to the diencephalon, pretectum and tectum in the cat. *Somatosens Res* 1: 281–300, 1984.

Burgess PR and Clark FJ. Characteristics of knee joint receptors in the cat. *J Physiol* 203: 317–335, 1969.

Burgess PR and Wei JY. Signaling of kinesthetic information by peripheral sensory receptors. *Annu Rev Neurosci* 5: 171–187, 1982.

Button J and Putman T. Visual responses to cortical stimulation in the blind. *J Iowa State Med Soc* 52: 17–21, 1962.

Cajal S and Ramón Y. *Histologie du Système Nerveux De l'Homme et des Vertébrés,* translated by Azoulay L. Paris: Maloine, 1911.

Casagrande VA and Norton TT. Lateral geniculate nucleus: a review of its physiology and function. In: *Vision and Visual Dysfunction,* edited by Leventhal AG. London, UK: MacMillian Press, 1991, p. 41–84.

Chalupa LM. Visual function of the pulvinar. In: *The Neural Basis of Visual Function,* edited by Leventhal AG. Boca Raton, FL: CRC Press, 1991, p. 140–159.

Chalupa LM, Anchel H, and Lindsley DB. Visual input to the pulvinar via lateral geniculate, superior colliculus and visual cortex in the cat. *Exp Neurol* 36: 449–462, 1972.

Chalupa LM and Thompson I. Retinal ganglion cell projections to the superior colliculus of the hamster demonstrated by the horseradish peroxidase technique. *Neurosci Lett* 19: 13–19, 1980.

Churchland PS, Ramachandran VS, and Sejnowski TJ. A critique of pure vision. In: *Large-Scale Neuronal Theories of the Brain,* edited by Koch C and Davis JL. Boston, MA: MIT Press, 1994, p. 23–65.

Diamond IT. The evolution of the tectal-pulvinar system in mammals: structural and behavioral studies of the visual system. *Symp Zool Soc Lond* 33: 205–233, 1973.

Diamond ME, Armstrong-James M, Budway MJ, and Ebner FF. Somatic sensory responses in the rostral sector of the posterior group (POm) and in the ventral posterior medial nucleus (VPM) of the rat thalamus: dependence on the barrel field cortex. *J Comp Neurol* 319: 66–84, 1992.

Dumont M, Ptito M, Cardu B, and Lepore F. Collicular system as oculomotor coordination or visual perception centers. *Trans Am Neurol Assoc* 99: 23–27, 1974.

Feig S and Harting JK. Corticocortical communication via the thalamus: ultrastructural studies of corticothalamic projections from area 17 to the lateral posterior nucleus of the cat and inferior pulvinar nucleus of the owl monkey. *J Comp Neurol* 395: 281–295, 1998.

Feldman SG and Kruger L. An axonal transport study of the ascending projection of medial lemniscal neurons in the rat. *J Comp Neurol* 192: 427–454, 1980.

Fukuda Y and Stone J. Retinal distribution and central projections of Y-, X-, and W-cells of the cat's retina. *J Neurophysiol* 37: 749–772, 1974.

Geisert EE, Langsetmo A, and Spear PD. Influence of the cortico-geniculate pathway on response properties of cat lateral geniculate neurons. *Brain Res* 208: 409–415, 1981.

Gilbert CD and Kelly JP. The projections of cells in the different layers of the cat's visual cortex. *J Comp Neurol* 163: 81–105, 1975.

Girkin CA, Perry JD, and Miller NR. A relative afferent pupillary defect without any visual sensory deficit. *Arch Ophthalmol* 116: 1544–1545, 1998.

Grant G, Boivie J, and Silfvenius H. Course and termination of fibres from the nucleus Z of the medulla oblongata. An experimental light microscopical study in the cat. *Brain Res* 55: 55–70, 1973.

Guillery RW. Anatomical evidence concerning the role of the thalamus in corticocortical communication: a brief review. *J Anat* 187: 583–592, 1995.

Guillery RW, Feig SL, and Van Lieshout DP. Connections of higher order visual relays in the thalamus: a study of corticothalamic pathways in cats. *J Comp Neurol* 438: 66–85, 2001.

Guillery RW and Sherman SM. The thalamus as a monitor of motor outputs. *Phil Trans R Soc Lond B* 357: 1809–1821, 2002a.

Guillery RW and Sherman SM. Thalamic relay functions and their role in corticocortical communication: generalizations from the visual system. *Neuron* 33: 163–175, 2002b.

Hamm AO, Weike A, Schupp HT, Treig T, Dressel A, and Kessler C. Affective blindsight: intact fear conditioning to a visual cue in a cortically blind patient. *Brain* 126: 267–275, 2003.

Harting JK, Updyke BV, and Van Lieshout DP. Corticotectal projections in the cat: anterograde transport studies of twenty-five cortical areas. *J Comp Neurol* 324: 379–414, 1992.

Heywood S and Ratcliff G. Long term oculomotor consequences of unilateral colliculectomy in man. In: *Basic Mechanisms of Ocular Motility and Their Clinical Implication,* edited by Lennerstrand D, Bach Y Rita P. Oxford: Pergamon, p. 561–564.

Holmes G and Lister WT. Disturbances of vision from cerebral lesions with special reference to the cortical representation of the retina. *Brain* 39: 34–73, 1916.

Horsley V. The function of the so-called motor area of the brain. *Br Med J* 2: 125–132, 1909.

Hubel DH and Wiesel TN. Functional architecture of macaque monkey visual cortex. *Proc R Soc Lond B Biol Sci* 198: 1–59, 1977.

Jhaveri S, Edwards MA, and Schneider GE. Initial stages of retinofugal axon development in the hamster: evidence for two distinct modes of growth. *Exp Brain Res* 87: 371–382, 1991.

Johansson H and Silfvenius H. Input from ipsilateral proprio- and exteroceptive hind limb afferents to nucleus Z of the cat medulla oblongata. *J Physiol* 265: 371–393, 1977.

Kalil RE and Chase R. Corticofugal influence on activity of lateral geniculate neurons in the cat. *J Neurophysiol* 33: 459–474, 1970.

Kandel ER, Schwartz JH, and Jessel TM. *Principles of Neural Science* (4th ed.). New York: McGraw-Hill, 2000.

Leventhal AG, Rodieck RW, and Dreher B. Central projections of cat retinal ganglion cells. *J Comp Neurol* 237: 216–226, 1985.

Linden R and Perry VH. Massive retinotectal projection in rats. *Brain Res* 272: 145–149, 1983.

Lu GW and Willis WD. Branching and/or collateral projections of spinal dorsal horn neurons. *Brain Res Rev* 29: 50–82, 1999.

Luppino G, Calzavara R, Rozzi S, and Matelli M. Projections from the superior temporal sulcus to the agranular frontal cortex in the macaque. *Eur J Neurosci* 14: 1035–1040, 2001.

Markram H, Wang Y, and Tsodyks M. Differential signaling via the same axon of neocortical pyramidal neurons. *Proc Natl Acad Sci USA* 95: 5323–5328, 1998.

Mathers LH. Tectal projections to the posterior thalamus of the squirrel monkey. *Brain Res* 35: 295–298, 1971.

Matthews PB. Where does Sherrington's "muscular sense" originate? Muscles, joints, corollary discharges? *Annu Rev Neurosci* 5: 189–218, 1982.

Matthews PBC. Muscle afferents and kinesthesia. *Br Med Bull* 33: 137–142, 1977.

Maturana HR, Lettvin JY, and Pitts WH. Anatomy and physiology of vision in the frog (*Rana Pipiens*). *J Gen Physiol* 43: 129–175, 1960.

Mishkin M, Ungerleider LG, and Macko KA. Object vision and spatial vision: two cortical pathways. *Trends Neurosci* 6: 414–417, 1983.

Moore T and Armstrong KM. Selective gating of visual signals by microstimulation of frontal cortex. *Nature* 421: 370–373, 2003.

Nakamura H, Kuroda T, Wakita M, Kusunoki M, Kato A, Mikami A, Sakata H, and Itoh K. From three-dimensional space vision to prehensile hand movements: the lateral intraparietal area links the area V3A and the anterior intraparietal area in macaques. *J Neurosci* 21: 8174–8187, 2001.

Nolte J. *The Human Brain.* St. Louis, MO: CV Mosby, 1988.

Ojima H. Terminal morphology and distribution of corticothalamic fibers originating from layers 5 and 6 of cat primary auditory cortex. *Cereb Cortex* 4: 646–663, 1994.

Partlow GD, Colonnier M, and Szabo J. Thalamic projections of the superior colliculus in the rhesus monkey, *Macaca mulatta.* A light and electron microscopic study. *J Comp Neurol* 72: 285–318, 1977.

Pasik T, Pasik P and Bender MB. The superior colliculus and eye movements. An experimental study in the monkey. *Arch Neurol* 15: 420–436, 1966. **Perenin MT and Jeannerod M.** Visual functions within the hemianopic field following early cerebral hemidecortication in man: I Spatial localization. *Neuropsychologia* 16: 1–13.

Pierrot-Deseilligny C, Rosa A, Masmoudi K, Rivaud S, and Gaymard B. Saccade deficits after a unilateral lesion affecting the superior colliculus. *J Neurol Neurosurg Psychiatry* 54: 1106–1109, 1991.

Plum F and Posner JB. *The Diagnosis of Stupor and Coma.* Philadelphia, PA: FA Davies, 1966.

Polyak S. *The Vertebrate Visual System.* Chicago, IL: University of Chicago Press, 1957.

Rizzolatti G and Luppino G. The cortical motor system. *Neuron* 31: 889–901, 2001.

Robson JA and Hall WC. The organization of the pulvinar in the grey squirrel (*Sciurus carolinensis*). II. Synaptic organization and comparisons with the dorsal lateral geniculate nucleus. *J Comp Neurol* 173: 389–416, 1977.

Rockland KS. Convergence and branching patterns of round type 2 corticopulvinar axons. *J Comp Neurol* 390: 515–536, 1998.

Rose JE and Mouncastle VB. Touch and kinesthesis. In: *Handbook of Physiology. Neurophysiology.* Washington, DC: Am. Physiol. Soc., 1959, sect. 1, vol. 1, p. 387–429.

Rouiller EM and Welker E. A comparative analysis of the morphology of corticothalamic projections in mammals. *Brain Res Bull* 53: 727–741, 2000.

Schiller PH. Some functional characteristics of the superior colliculus of the rhesus monkey. *Bibl Ophthalmol* 82: 122–129, 1972.

Schiller PH and Tehovnik EJ. Look and see: how the brain moves your eyes about. *Prog Brain Res* 134: 127–142, 2001.

Schmielau F and Singer W. The role of visual cortex for binocular interactions in the cat lateral geniculate nucleus. *Brain Res* 120: 354–361, 1977.

Schneider GE. Two visual systems. *Science* 163: 895–902, 1969.

Sereno M, Trinath T, Augath M, and Logothetis NK. Three-dimensional shape representation in monkey cortex. *Neuron* 33: 635–652, 2002.

Sherman SM and Guillery RW. Functional organization of thalamocortical relays. *J Neurophysiol* 76: 1367–1395, 1996.

Sherman SM and Guillery RW. On the actions that one nerve cell can have on another: distinguishing "drivers" from "modulators." *Proc Natl Acad Sci USA* 95: 7121–7126, 1998.

Sherman SM and Guillery RW. *Exploring the Thalamus.* San Diego, CA: Academic Press, 2001.

Sherrington CS. On the anatomical constitution of nerves of skeletal muscles; with remarks on recurrent fibres in the ventral spinal root. *J Physiol* 17: 211–258, 1894.

Skoglund S. Joint receptors and kinesthesis. In: *Handbook of Sensory Physiology,* edited by Iggo A. Berlin: Springer-Verlag, 1973, vol. II, p. 111–136.

Sommer MA and Wurtz RH. A pathway in primate brain for internal monitoring of movements. *Science* 296: 1480–1482, 2002.

Sperry RW. Neurology and the mind–brain problem. *Am Scientist* 40: 291–312, 1952.

Sprague JM. The superior colliculus and pretectum in visual behavior [review]. *Invest Ophthalmol Visual Sci* 11: 473–482, 1972.

Sur M, Esguerra M, Garraghty PE, Kritzer MF, and Sherman SM. Morphology of physiologically identified retinogeniculate X- and Y-axons in the cat. *J Neurophysiol* 58: 1–32, 1987.

Tamamaki N, Uhlrich DJ, and Sherman SM. Morphology of physiologically identified X and Y axons in the cat's thalamus and midbrain as revealed by intra-axonal injection of biocytin. *J Comp Neurol* 354: 583–607, 1994.

Tehovnik EJ, Slocum WM, and Schiller PH. Differential effects of laminar stimulation of V1 cortex on target selection by macaque monkeys. *Eur J Neurosci* 16: 751–760, 2002.

Tolias AS, Smirnakis SM, Augath MA, Trinath T, and Logothetis NK. Motion processing in the macaque: revisited with functional magnetic resonance imaging. *J Neurosci* 21: 8594–8601, 2001.

Van Essen DC, Anderson CH, and Felleman DJ. Information processing in the primate visual system: an integrated systems perspective. *Science* 255: 419–423, 1992.

Vaney DI, Peichl L, Wässle H, and Illing RB. Almost all ganglion cells in the rabbit retina project to the superior colliculus. *Brain Res* 212: 447–453, 1981.

Vidnyánszky Z, Borostyánkoi Z, Gõrcs TJ, and Hámori J. Light and electron microscopic analysis of synaptic input from cortical area 17 to the lateral posterior nucleus in cats. *Exp Brain Res* 109: 63–70, 1996.

Vierck CJ Jr. Comparison of forelimb and hindlimb motor deficits following dorsal column section in monkeys. *Brain Res* 146: 279–294, 1978.

Wall PD and Noordenbos W. Sensory functions which remain in man after complete transection of dorsal columns. *Brain* 100: 641–653, 1977.

Walsh FB and Hoyt WF. *Clinical Neuroophthalmology.* Baltimore, MD: Williams & Wilkins; 1957, p. 77–84.

Warren RM and Warren RP. *Helmholtz on Perception: Its Physiology and Development.* New York: Wiley, 1968.

Wässle H and Illing RB. The retinal projection to the superior colliculus in the cat: a quantitative study with HRP. *J Comp Neurol* 190: 333–356, 1980.

Weiskrantz L. *Blindsight: A Case Study and Implications.* Oxford, UK: Clarendon Press, 1986.

Weiskrantz L. Mind—the gap, after 65 years: visual conditioning in cortical blindness. *Brain* 126: 265–266, 2003.

Yarbus AL. *Eye Movements and Vision.* New York: Plenum, 1967.