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The deep layers of the superior colliculus

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1. Introduction

Converging lines of evidence derived from anatomical, electrophysiological and lesion data indicate that the deep layers of the superior colliculus (SC) are a critical component of the neural circuitry controlling saccadic eye movements (see Schiller (1984) and Sparks (1986) for recent reviews). This chapter summarizes the supporting evidence, emphasizing data obtained from the monkey and the cat, the subjects most commonly used in electrophysiological, anatomical and behavioral experiments. The contributions of the superficial layers of the SC to the generation of saccadic eye movements are reviewed in chapter 9.

2. Anatomical organization of deep SC

2.1. General organization

The mammalian SC consists of seven cyto- and myeloarchitecturally distinct layers (Viktorov, 1968; Kanaseki and Sprague, 1974; Norita, 1980, Laemle, 1981a,b): the zonal layer or stratum zonale (SZ), the superficial grey layer or stratum griseum superficiale (SGS), the optic layer or stratum opticum (SO), the intermediate grey layer or stratum griseum intermediale (SGI), the intermediate white layer or stratum album intermediale (SAI), the deep grey layer or stratum griseum profundum (SGP), and the deep white layer or stratum album profun-

dum (SAP). These layers are grouped into two functionally and connectionally different units, the superficial (SZ, SGS, SO) and deep compartments (SGI, SAI, SGP, SAP), on the basis of anatomical and behavioral data (Casagrande et al., 1972; Edwards et al., 1979; Edwards, 1980; Graham, 1977; Harting et al., 1973).

As discussed in chapter 9 of this volume, the superficial collicular layers are exclusively visual in terms of function and connections. In contrast, the deep compartment of the SC is, by virtue of anatomical connections with multiple sensory and motor systems and the physiological characteristics of its neuronal population, uniquely suited for a central role in sensorimotor integration.

2.2. Connections of deep collicular layers

This section briefly summarizes the pattern of afferent and efferent connections of the deep collicular layers. More extensive descriptions can be obtained from several recent reviews (Huerta and Harting, 1982c, 1984; Büttner-Ennever, 1988).

2.2.1. Afferents

The deep layers are recipients of anatomical projections from cortical and subcortical regions subserving both sensory and motor functions. The major sources of these inputs are summarized in Fig. 1. The actual signals being conveyed to the SC from these sources are, for the most part, unknown.

AFFERENTS

DESCENDING

1. Cerebral cortex
Extrastriate visual cortex (occipital)
Multimodal association cortex (parietal)
Auditory association cortex (temporal)
Somatosensory association cortex (postcentral)
Premotor, motor, and oculomotor cortex (precentral)
Prefrontal association cortex (frontal)
2. Diencephalon
Hypothalamus
Zona incerta
Fields of Forel
Thalamic nuclei: reticular
ventral medial
ventral lateral geniculate
3. Mesencephalon
Nucleus of the posterior commissure
Mesencephalic reticular formation
Cuneiform nucleus
Periaqueductal grey
Contralateral SC
Superficial SC (?)

ASCENDING

1. Diencephalon
Thalamic nuclei: suprageniculate
medial geniculate
medial dorsal
ventral anterior
lateral posterior
intralaminar
Zona incerta
Fields of Forel
2. Mesencephalon
Rostral interstitial nucleus of the MLF
Nucleus of the posterior commissure
Mesencephalic reticular formation
Cuneiform nucleus
Interstitial nucleus of Cajal
Supraoculomotor zone
Edinger-Westphal nucleus
Periaqueductal grey
Contralateral SC

DEEP SUPERIOR COLLICULUS

ASCENDING

1. Mesencephalon
Substantia nigra
Inferior colliculus
Ventral nucleus of the lateral lemniscus
Locus coeruleus
Dorsal raphe nucleus
2. Pons
Dorsomedial periolivary nucleus
Nucleus of the trapezoid body
3. Medulla
Vestibular complex
Perihypoglossal complex (prepositus, intercalatus)
Dorsal column nuclei
Spinal trigeminal nucleus
4. Spinal cord dorsal horn (L. IV)
5. Deep cerebellar nuclei

DESCENDING

I. Contralateral (predorsal bundle or tectospinal tract)

1. Pons
Dorsolateral pontine grey
Nucleus reticularis tegmenti pontis
Nucleus reticularis pontis caudalis
Nucleus reticularis pontis oralis
Paramedian pontine reticular formation
Abducens nucleus and area ventral and lateral to it
2. Medulla
Medial accessory nucleus of inferior olive
Vestibular nuclei (medial and descending)
Perihypoglossal complex (prepositus, intercalatus)
Supraspinal nucleus
Spinal trigeminal nucleus
3. Cervical spinal cord (ventral horn)

II. Ipsilateral (tectopontine–bulbar tract)

1. Mesencephalon
Parabigeminal nucleus (?)
Perilemniscal Zone
Inferior Colliculus (external capsule)
Mesencephalic reticular formation
Cuneiform nucleus
2. Pons
Dorsal lateral pontine grey
Nucleus reticularis tegmenti pontis
Nucleus reticularis pontis caudalis
Nucleus reticularis pontis oralis
Paramedian pontine reticular formation

Fig. 1. Summary of the major afferent and efferent connections of the deeper layers of the superior colliculus.

Nonetheless, based upon the density of the anatomical projections, the most significant sources of collicular afferents are summarized below.

In cats, projections from auditory cortical areas terminate primarily in the deepest grey layer (SGP) in the caudal part of the SC (Edwards et al., 1979). These projections originate in the suprasylvian fringe areas and the posterior ectosylvian area (Garey et al., 1968; Paula-Barbosa and Sousa-Pinto, 1973; Kawamura et al., 1974). The terminations of these cortical projections overlap the terminal distribution of the ascending auditory brain stem neurons (Garey et al., 1968). A projection from auditory association cortex to the deep SC has been demonstrated also in the monkey (Moore and Goldberg, 1963).

The neurons of origin of ascending auditory projections are located in brainstem relay nuclei: the external and pericentral nuclei of the inferior colliculus, the ventral nucleus of the lateral lemniscus, the dorsomedial periolivary nucleus, and the nuclei of the trapezoid body (Garey et al., 1968; Edwards et al., 1979). A projection from the inferior colliculus to the deep SC has been described in monkeys (Barnes et al., 1943; Whitlock and Nauta, 1956; Moore and Goldberg, 1966).

The major sources of ascending somatosensory input to the deep SC are the dorsal column nuclei (Edwards et al., 1979; Wiberg and Blomqvist, 1984; Bull and Berkley, 1984), the spinal trigeminal nucleus (Edwards et al., 1979; Huerta et al., 1981; McHaffie et al., 1986a), and lamina IV of the spinal cord dorsal horn (Edwards et al., 1979; Wiberg and Blomqvist, 1984; see also Clemo and Stein, 1986, for further references).

Descending somatosensory cortical projections arise in area SIV deep within the anterior ectosylvian sulcus (Clemo and Stein, 1982, 1983, 1986; Stein et al., 1983; Illing and Graybiel, 1986) and in area SV within the rostal suprasylvian sulcus (Clemo and Stein 1982, 1984; Huerta and Harting, 1984; Stein et al., 1983).

There is disagreement concerning the existence of a direct retinal projection to the deep collicular layers. Although a sparse retinal input to the deep

SC of the cat was suggested on the basis of electrophysiological (Berson and McIlwain, 1982) and anatomical data (Beckstead and Frankfurter, 1983), these findings are not in agreement with the results of earlier autoradiographic studies (Graybiel, 1975; Harting and Guillery, 1976) or more recent experiments using the retrograde transport of WGA-HRP (Hartwich-Young, unpublished observation).

In cats, the deep collicular compartment receives extensive projections from extrastriate visual cortical association areas. For example, the medial and lateral banks of the posterior, middle and anterior suprasylvian gyrus, as well as the ectosylvian visual area (EVA), project heavily upon the deep SC (Kawamura et al., 1974; Tortelly et al., 1980; Baleydier et al., 1983; Berson and McIlwain, 1983; Hartwich-Young et al., 1983a,b; Stein et al., 1983; Ogasawara et al., 1984; Segal and Beckstead, 1984; Berson, 1985). Moderately heavy inputs to the intermediate, but not the deep, layers of the SC arise from three additional cortical areas containing visually responsive neurons: the splenial visual area, the cingulate cortex (Hollander, 1974; Hartwich-Young et al., 1983a,b), and parietal cortical area 7 (Garey et al., 1968; Kawamura et al., 1974; Hartwich-Young et al., 1983a,b).

In monkeys, a prominent input to the deep collicular layers from the posterior parietal cortex (specifically, the inferior bank of the intraparietal sulcus) has been demonstrated by Kuypers and Lawrence (1967), Petras (1971) and Lynch et al. (1985). The inferior parietal lobule contains visually responsive neurons and appears to play an important role in visual attention, visuomotor discrimination and oculomotor control (see chapter 8 of this volume).

A subcortical source of visual input to the deeper layers of the SC is the ventral lateral geniculate nucleus (vLGN). This projection has been demonstrated in cats (Edwards et al., 1974; Graybiel, 1974; Grofova et al., 1978; Edwards et al., 1979; Hada et al., 1986) and rats (Brauer and Schober, 1982). The vLGN in thought to play a role in visuomotor integration because of its reciprocal connec-

tions with the pretectum and the SC (Edwards et al., 1974; Graybiel, 1974) and because some of its neurons discharge in association with head rotation (Magnin and Putkonen, 1978) and saccadic eye movements (Büttner and Fuchs, 1973).

In addition to sensory inputs, the deep layers of the SC also receive projections from cortical and subcortical areas considered to have motor functions. Extensive inputs from the frontal eye fields (FEF) to the intermediate and deep collicular layers are well documented in cats (Garey et al., 1968; Guitton and Mandl, 1974, 1976; Konno, 1979; Tortelly et al., 1980; Catsman-Berrevoets and Kuypers, 1981; Segal'et al., 1983; Olson and Farrell, 1985; Hartwich-Young and Weber, 1986), squirrel monkeys and owl monkeys (Huerta et al., 1986), and macaque monkeys (Astruc, 1971; Kunzle et al., 1976; Kunzle and Akert, 1977; Leichnetz et al., 1981; Stanton et al., 1982; Fries, 1984, 1985; Komatsu and Suzuki, 1985; Huerta et al., 1986). Also, indirect projections from the FEF reach the deep SC via the basal ganglia (Kunzle and Akert, 1977; Updyke, 1986). The FEF contain visually responsive neurons as well as neurons that discharge in association with saccadic eye movements (see chapter 7 of this volume). The oculomotor portion of the supplementary motor cortex or 'supplementary eye field' contains neurons discharging in association with saccadic eye movements (Schlag and Schlag-Rey, 1985, 1987) and projects heavily upon the SC (Kunzle, 1978; Leichnetz et al., 1981; Fries, 1984; but see Fries, 1985), as does a possibly analogous frontal cortical oculomotor area in cats (Hartwich-Young and Weber, 1986).

In macaque monkeys, the prefrontal association cortex, an area thought to be involved in tasks requiring precise spatial orientation (Goldman and Rosvold, 1970; Goldman et al., 1971), projects extensively upon the deep compartment of the SC (Goldman and Nauta, 1976; Fries, 1985). Additional prefrontal corticotectal projections arise in both motor (Fries, 1985) and premotor cortex (Kuypers and Lawrence, 1967; Hartmann-von Monakow et al., 1979; Fries, 1985). A corticotectal projection from similar areas of prefrontal agranu-

lar cortex has also been observed in cats (Stein et al., 1983; Hartwich-Young and Weber, 1986).

Inputs to the deeper layers of the SC from subcortical structures known to have neuronal activity related to saccadic eye movements include: (a) the central mesencephalic reticular formation of macaque monkeys (Cohen and Büttner-Ennever, 1984), an area containing cells with activity related to the horizontal component of eye movements (Cohen et al., 1985; Waitzman, 1982); (b) the substantia nigra, pars reticulata (SNpr; Hopkins and Niessen, 1976; Jayaraman et al., 1977; Grofova et al., 1978; Graybiel, 1978a; Edwards et al., 1979; Beckstead et al., 1981; Beckstead, 1983; Warton et al., 1983; May and Hall, 1984, 1986; Illing and Graybiel, 1985; Karabelas and Moschovakis, 1985; Hashikawa et al., 1986), which contains visually responsive neurons as well as neurons discharging in association with saccadic eye movements (Hikosaka and Wurtz, 1985b); (c) the deep nuclei of the cerebellum (Angaut, 1969; Batton et al., 1977; Edwards et al., 1979; Kawamura et al., 1982); (d) the nucleus prepositus hypoglossi (McCrea and Baker, 1985; Stechison et al., 1985); and (e) the reticular nucleus of the thalamus (Grofova et al., 1978; Parent and Steriade, 1984).

Several other subcortical structures presumably involved in sensorimotor transformations project to the deep collicular layers in cats: the nucleus of the posterior commissure (Grofova et al., 1978; Edwards et al., 1979; Huerta and Harting, 1982a); the locus coeruleus and dorsal raphe (Edwards et al., 1979); the nucleus intercalatus (Stechison et al., 1985); the mesencephalic reticular formation (Grofova et al., 1978; Edwards et al., 1979); the cuneiform nucleus (Edwards, 1975); the hypothalamus and zona incerta (Grofova et al., 1978; Edwards et al., 1979; Rieck et al., 1986); Forel's field and the periaqueductal grey (Grofova et al., 1978); and the ventral medial nucleus of the thalamus (Jimenez-Castellanos and Reinoso-Suarez, 1985).

Communication between corresponding as well as noncorresponding regions of the two superior colliculi of the cat occurs predominantly in the deep collicular compartment (Edwards, 1977; Graham,

1977; Magalhaes-Castro et al., 1978; Edwards et al., 1979; Behan, 1985; Moschovakis and Karabelas, 1985). Additionally, the tectal commissure contains decussating fibers from nontectal sources (Edwards, 1977). A small commissural projection is also present in the monkey (Harting, 1977; Karabelas et al., 1986; Moschovakis et al., 1986).

2.2.2. Efferents

The outputs of the deep collicular layers, summarized in Fig. 1, may be grouped into two main categories: (1) an ascending pathway to the thalamus through which the SC may participate in complex feedback loops involving the basal ganglia and numerous areas of 'extraprimary' sensory and motor cortex; and (2) descending pathways which convey collicular motor commands to motor and premotor nuclei in the brainstem and spinal cord.

Huerta et al. (1986) made the interesting observation that most of the subcortical targets of the deep SC also receive inputs from the FEF (some of them are reciprocal) and the posterior parietal cortex. Furthermore, many of these tectorecipient regions are, themselves, interconnected and have extensive projections to other brainstem nuclei involved in oculomotor control (see Huerta et al., 1986, for details).

The main target of ascending deep collicular projections (primarily from the intermediate grey layer) is the suprageniculate nucleus (Graham, 1977; Takada et al., 1985; Hicks et al., 1986; Norita and Katoh, 1986; Updyke, 1986). This thalamic nucleus, in turn, sends fibers to the insular cortex (Graybiel and Berson, 1981) which is known to contain neurons that are both visually and acoustically responsive (Loe and Benevento, 1969), as well as to visually responsive regions of the caudate and putamen (Updyke, 1986). Likewise, the medial geniculate (Takada et al., 1985) and the lateral posterior (Harting et al., 1980; Updyke, 1986) nuclei of the thalamus receive inputs from the intermediate grey collicular layer and project to the caudate and putamen (Takada et al., 1985). Additional thalamic nuclei receiving deep collicular inputs are the mediodorsal nucleus (Harting et al., 1980; Velayos

and Reinoso-Suarez, 1982; Russchen et al., 1987), the ventral anterior nucleus (Harting et al., 1980), the ventromedial nucleus (Jimenez-Castellanos and Reinoso-Suarez, 1985), and several intralaminar thalamic nuclei (Harting et al., 1980; Graham and Berman, 1981; Velayos and Reinoso-Suarez, 1982; Kaufman and Rosenquist, 1985; Yamasaki et al., 1986). The fields of Forel and the zona incerta are two subthalamic targets of the deep SC (Graham, 1977).

Ascending axons of deep collicular neurons also terminate within the rostral interstitial nucleus of the medial longitudinal fasciculus, a structure which plays an important role in the generation of vertical saccadic eye movements (Büttner et al., 1977; Büttner-Ennever and Büttner, 1978), the nucleus of the posterior commissure, the interstitial nucleus of Cajal, the periaqueductal grey, the supraoculomotor zone and the Edinger-Westphal nucleus (Harting et al., 1980).

Collicular control over orienting movements of the eyes, head and pinnae is exerted through the descending pathways to motor and premotor areas in the brainstem and spinal cord which leave the deep layers through two major pathways: the contralaterally directed predorsal bundle or tectospinal tract and the ipsilateral tectopontine-tectobulbar tract.

The contralaterally projecting fibers of the tectospinal tract arise primarily from neurons located in the intermediate grey layer, cross in the dorsal tegmental decussation, and terminate within nuclei of the pontine and medullary reticular formation and the spinal cord (Harting et al., 1973; Graham, 1977; Harting, 1977; Kawamura and Hashikawa, 1978; Weber et al., 1979; Holcombe and Hall, 1981; Huerta and Harting, 1982c, 1984; May and Hall, 1984, 1986). Most of the targets of the tectospinal fibers have been shown to be involved in oculomotor control (Harting, 1977; Huerta and Harting, 1982b,c). For example, the majority of neurons within the nucleus reticularis tegmenti pontis (NRTP) of macaque monkeys burst or pause in association with saccadic eye movements of particular directions and amplitudes (Keller and Cran-

dall, 1981), much like deep collicular neurons (see section 4). Neurons projecting within the predorsal bundle also terminate in the nucleus reticularis pontis oralis, which corresponds, in part, to the paramedian pontine reticular formation (Harting, 1977; Huerta and Harting, 1982b,c; Schnyder et al., 1985). This area of the brain stem is instrumental in the generation of horizontal saccades (Raphan and Cohen, 1978). Inputs of predorsal bundle cells have also been reported to an area ventral and medial to the abducens nucleus, as well as to the abducens nucleus itself (Harting, 1977; Edwards and Henkel, 1978; Grantyn and Grantyn, 1982; Grantyn and Berthoz, 1985; Langer et al., 1986). Through their terminations within the medial accessory nucleus of the inferior olivary complex (Frankfurter et al., 1976; Graham, 1977; Kawamura and Hashikawa, 1978; Weber et al., 1978; Saint-Cyr and Courville, 1982, Saint-Cyr, 1987), contralaterally projecting deep collicular neurons gain access to the climbing fiber system and to visually responsive neurons in cerebellar lobules VI, VII and VIII in the posterior vermis (Graham, 1977; Weber and Harting, 1978; Weber et al, 1978; Jeneskog, 1981, 1983). This tec-to-olivo-cerebellar pathway has been suggested to include fibers also from acoustically and somesthetically responsive SGI neurons and to be critically involved in the cerebellar control of head and eye movements (Weber et al., 1978; Saint-Cyr and Courville, 1982). The nucleus prepositus hypoglossi not only projects to the deep SC but also receives inputs from deep collicular neurons and has efferent and afferent connections with numerous structures involved in movements of the head and eyes (Stechison et al., 1985; McCrea and Baker, 1985). Finally, descending crossed projections from the deep SC also terminate in the medial and descending vestibular nuclei, the nucleus intercalatus (Stechison et al., 1985) and the spinal trigeminal nucleus (Huerta and Harting, 1984).

In the monkey, only a few scattered axons of the predorsal bundle continue into the spinal cord (Harting, 1977). In the cat, however, deep collicular neurons also send numerous fibers to areas involved in the control of head movements; i.e., to the supraspinal nucleus (which then projects bilaterally to laminae VIII and IX of the first five cervical spinal cord segments) and to laminae VI-VIII of the first five cervical segments of the spinal cord (Kawamura and Hashikawa, 1978; Weber et al., 1979; Grantyn and Grantyn, 1982; Huerta and Harting, 1982b,c).

Ipsilaterally directed fibers of deep collicular neurons have been reported to project ventrolaterally to terminate on visually responsive neurons within the parabigeminal nucleus (Harting et al., 1973) and the dorsal lateral pontine grey (Kawamura and Brodal, 1973; Graham, 1977; Harting, 1977), as well as on oculomotor neurons within the mesencephalic reticular formation (Harting, 1977; Cohen and Büttner-Ennever, 1984). In cats, the paralemniscal region of the lateral pontine tegmentum, an area involved in movements of the pinnae, also receives ipsilateral inputs from the deep collicular layers (Henkel, 1981; Henkel and Edwards, 1978). Further targets of the ipsilateral descending pathway are the rostral pontine reticular formation, the dorsolateral wing of NRTP, and the nucleus reticularis pontis oralis or NRPO (Graham, 1977; Grantyn and Grantyn, 1982; Harting, 1977). The NRPO, in turn, has projections to the spinal cord and is thus thought to function in the mediation of head movements (Harting, 1977).

2.2.3. Relationship between deep and superficial SC

On the basis of Golgi studies (Cajal, 1911; Viktorov, 1968; Norita, 1980) and connectional data (Harting et al., 1973; Kanaseki and Sprague, 1974; Kawamura et al., 1974; Sprague, 1975; Graham, 1977), it was traditionally assumed that the superficial layers had direct connections with the deep SC. This view was challenged by Edwards and colleagues (Edwards et al., 1979; Edwards, 1980), who argued that the superficial and deep collicular compartments exhibited distinct differences in terms of physiological and histological characteristics as well as anatomical connections. Furthermore, Edwards and colleagues did not find any evidence for direct connections between the two compartments

in their anterograde and retrograde tracer studies and Golgi material (Edwards, 1980). The debate over interlaminar intracollicular connections has recently been reopened, however, by the results of experiments using intracellular recording techniques followed by the filling of isolated neurons with horseradish peroxidase (HRP). For example, Mooney et al., (1984) and Rhoades et al. (1985) demonstrated that dendrites of deep collicular neurons (in the intermediate grey and white and the deep grey layers) of hamsters extended superficially into the optic and superficial grey layers, and that axons of superficial collicular neurons could, in some instances, be traced into deeper layers. Similar data were obtained in the cat (Moschovakis and Karabelas, 1985) and in the squirrel monkey (Highstein et al., 1986; Karabelas et al., 1986; Moschovakis et al., 1986; see section 3.1.3 for more details). In the work of Highstein, Karabelas and Moschovakis, dendrites as well as axons of HRP-filled neurons in the intermediate and deep collicular layers of the cat and squirrel monkey can be seen to extend into adjacent superficial and intermediate layers. Further evidence suggestive of interlaminar collicular communication was presented by the results of another recent experiment employing intracellular recording followed by injection of HRP (Rhoades et al., 1986). In this study of the structural and functional characteristics of commissural neurons in the SC of the hamster, two neurons that were responsive to both visual and tactile stimulation displayed extensive dendritic arborizations into the uppermost sublamina of the superficial grey layer, and their axons could be traced into the lowest portions of the deep grey layer. The axon of one of these bimodal cells, which was located in the superficial grey, collateralized extensively into the optic and intermediate grey layers. The general impression to be gained from illustrations of the filled neurons is that their dendritic processes appear to span the entire dorsal-ventral extent of the SC (Rhoades et al., 1986). In the most recent study by Rhoades and colleagues (1987), 7.7% of the HRP-filled tectospinal neurons located in the intermediate and deep collicular

layers of the hamster were visually responsive. All of these, as well as many nonvisual cells, had dendrites that extended into the overlying superficial layers.

In summary, recent anatomical evidence appears to support the traditional view of direct communication between the two collicular compartments. In contrast, electrophysiological evidence for a functional linkage between superficial and deeper layers is lacking (Mays and Sparks, 1980a). Thus, the question of synaptic interconnections between the superficial and deep collicular layers and the functional significance of observed anatomical linkages needs additional study (see Addendum p. 255).

2.3. Intrinsic organization of deep SC

2.3.1. Patches, puffs, clusters, modules
An additional pattern of organization is superimposed on the laminar arrangement of deep collicular neurons: the terminals of afferent neurons, the cells of origin of efferent pathways, and the distributions of specific neurotransmitters within the deep SC are segregated in discrete patches, clusters or modules located in specific sublaminae of the intermediate grey layer. For example, many of the corticotectal inputs to the intermediate grey layer from extrastriate visual areas (Clemo and Stein, 1983; Segal and Beckstead, 1984), somatosensory (Stein et al., 1983) and prefrontal cortex (Goldman and Nauta, 1976; Kunzle, 1978), and frontal eye fields (Kunzle et al., 1976; Kunzle and Akert, 1977; Leichnetz et al., 1981; Segal et al., 1983) terminate in patches that occupy specific regions within the dorsal-ventral as well as the medial-lateral extent of this lamina (Huerta and Harting, 1984).

Subcortical projections to the deeper SC are distributed in a similarly discontinuous manner. This is the case with the nigrotectal afferents (Graybiel, 1978a; Jayaraman et al., 1977; Beckstead et al., 1979; Hashikawa et al., 1986) and the trigeminotectal pathway (Huerta et al., 1981), both of which end in patches within the intermediate grey layer that tend to align in longitudinal bands. The terminal patches of the trigeminal axons are restricted to the

medial portion of the rostral SC (Huerta and Harting, 1984). Patchy inputs from the nucleus of the posterior commissure ramify immediately ventral to those from the substantia nigra and may interdigitate with the trigeminotectal terminals (Huerta and Harting, 1982a). The patches formed by hypothalamic afferent terminals, on the other hand, are arranged in one dorsal and one ventral tier (Rieck et al., 1986). Additional clustered afferents to the deep SC are: the inferior colliculus (Kudo and Niimi, 1980), the dorsal nucleus of the lateral lemniscus (Kudo, 1981), the deep cerebellar nuclei (Kawamura et al., 1982), the lateral cervical nucleus (Flink et al., 1983), the dorsal column nuclei and the spinal cord grey (Flink et al., 1983), and the nucleus prepositus hypoglossi (McCrea and Baker, 1985). Huerta and Harting (1982b) coined the term 'module' in describing the segregation of a set of specific afferent patches in a specific subdivision within the medial-lateral and dorsal-ventral extent of the intermediate grey layer.

The cell bodies of origin of deep collicular efferents are also clustered in patches within the intermediate grey layer and segregated within specific efferent modules. The clusters formed by tectospinal neurons, for example, have been shown to aggregate in a discrete module restricted predominantly to the ventral half of the intermediate grey layer (Weber et al., 1979; Huerta and Harting, 1982b,c). Furthermore, an efferent module may be tightly coupled to one or more particular afferent module(s) (Huerta and Harting, 1984). Such is the case for the trigeminotectal and tectotrigeminal modules (Huerta et al., 1981) and the hypothalamotectal and tectoolivary modules (Huerta and Harting, 1984).

The distribution of neurotransmitters and metabolic enzymes within the deep layers of the SC has also been shown to be arranged in patches or clusters that are organized independently of each other. Acetylcholinesterase (AChE) activity within the intermediate grey layer, for instance, occurs in such a discontinuous distribution (Graybiel, 1978b, 1979; Illing and Graybiel, 1985; Beninato and Spencer, 1986; McHaffie et al., 1986b; Wallace, 1986;

Wiener, 1986). Moreover, the clumps of AChE activity are concentrated within the caudal SC, as are those of the enkephalin-like immunoreactivity described by Graybiel et al. (1984) within the intermediate grey layer of the cat. Histochemical indices of hexokinase (Sandell, 1984), cytochrome oxidase (Wallace, 1986; Wiener, 1986) and phosphorylase (Wallace, 1986) activity demonstrate that these enzymes are arranged in clusters or patches within the deeper collicular layers.

In some cases, specific afferent modules have been shown to coincide and/or interdigitate with modules exhibiting specific neurochemical activity. For example, the afferent terminals of such eye movement-related structures as the frontal eye field and the substantia nigra were found to converge upon clusters of high AChE activity located in the intermediate grey layer (Illing and Graybiel, 1985). Interestingly, inputs of several sensory systems (i.e., visual and somatosensory association cortex and somatosensory nuclei in the caudal medulla) are reported to avoid and/or partly interdigitate with these AChE-rich, motor-recipient modules (Illing and Graybiel, 1986). Future research may reveal modular associations of as yet unidentified collicular neurotransmitters with patches of other afferents and/or efferents.

The functional significance of the modular organization of deep tectal afferents, efferents, neurotransmitters and other biochemicals has as yet not been determined. It may be speculated, however, that the arrangement of specific classes of neurons with different functions and anatomical connections in clusters, patches, puffs, bands and discontinuous sheets could potentially multiply opportunities for interactions between any one afferent system and a number of different efferent modules. Indeed, this type of organization may actually be a necessity in view of the numerous afferents converging upon and efferents exiting from the deep SC, with specific afferent terminals destined to synapse on particular sets and subsets of neurons projecting to a variety of different target structures. Thus, the accommodation of such a large number of segregated information channels

within the constraints of the intermediate grey collicular layer may be considered as an example of extremely efficient management of space.

2.3.2. Neurotransmitters of the deep SC

The distinct differences between the superficial and deep collicular compartments revealed by examination of their histological characteristics and anatomical connections are evident also with respect to the differential distribution of neurotransmitters within the SC. For example, one of the most prominent collicular neurotransmitters, acetylcholine (ACh), is reported to be homogeneously distributed within the superficial layers, but occurs in patches or clusters within the deeper compartment (Graybiel, 1978b, 1979; Beninato and Spencer, 1986; Illing and Graybiel, 1985, 1986; McHaffie et al., 1986b; Wallace, 1986; Wiener, 1986), as described in the previous paragraph. The ACh is apparently not synthesized within the SC, but is thought to reach the SC via afferent inputs from two cholinergic cell groups (Ch5 and Ch6) in the caudal midbrain and rostal pons, the pedunculopontine tegmental and lateral dorsal tegmental nuclei (Beninato and Spencer, 1986; McHaffie et al., 1986b).

Gamma-aminobutyric acid (GABA), the second most prominent collicular neurotransmitter, is also differentially distributed within the superficial and deep divisions of the SC. This inhibitory neurotransmitter is found throughout the SC, but is more abundant in the superficial layers (Mize et al., 1982; Lu et al., 1985; Mize and Horner, 1985; Mize, 1986). GABA has recently been suggested to play a crucial role in the initiation of saccadic eye movements by deep collicular neurons (Hikosaka and Wurtz, 1985a). As is the case with ACh, the SC is thought to receive GABA from extrinsic sources, most notably the substantia nigra (Vincent et al., 1978). This assumption is substantiated by data showing dramatic alterations in the activity of deep collicular neurons as well as in saccadic eye movements following applications of GABA agonists and antagonists within the SN (Hikosaka and Wurtz, 1985b). Indeed, high levels of glutamic acid decarboxylase (GAD) immunoreactivity have recently

been found to be associated with nigrotectal terminals that contact the large intermediate collicular cells giving rise to the predorsal bundle (Lu et al., 1985). Although this finding lends further support to earlier data revealing the importance of the GABAergic nigrotectal projection, the deep SC has been suggested to receive GABA also from additional extrinsic sources, such as specific regions of the mesencephalic reticular formation (Araki et al., 1984), the ventral lateral geniculate nucleus, and possibly intrinsic collicular interneurons (Lu et al., 1985).

In addition to ACh and GABA, recent studies have also identified serotonin (5-HT) as a collicular neurotransmitter (Ueda et al., 1985; Morrison and Foote, 1986). Unfortunately, there is disagreement concerning the distribution of 5-HT within the two collicular compartments. Whereas Morrison and Foote (1986) discribe the intermediate layers of the monkey SC to be more densely innervated by 5-HT than the superficial division, Ueda and colleagues (1985) report the opposite to be the case in the rat, cat, hamster and monkey. The observations of the latter authors, however, are in agreement with earlier findings (Steinbusch, 1981; Steinbusch et al., 1978) as to the preponderance of 5-HT in the superficial collicular layers. The most likely source of the 5-HT present within the SC is the raphe nuclei, which are known to have a tectal projection (Edwards et al., 1979).

The paucity of information concerning the neurotransmitter systems of the SC, their origins, functional significance and interactions with extrinsic as well as intrinsic collicular afferents and efferents is obvious from this brief review. In view of the only quite recent advent of transmitter immunohistochemistry, however, it is also obvious that this potentially vast unknown territory has just begun to be explored.

2.4. Summary and conclusions

The pattern of afferent and efferent connections of the deep collicular layers is consistent with the hypothesis that the SC functions in transforming sig-

nals from several sensory and motor areas into motor commands for initiating and guiding orienting responses of the eyes, head and pinnae. The deep compartment of the SC receives inputs from neural structures involved in processing visual, auditory, somatosensory and motor information. Deep collicular outputs are to nuclei in the brain stem and spinal cord that have direct connections with the motor neurons innervating the muscles of the eyes, neck and pinnae.

3. Electrophysiological studies

In this section, we review the sensory and motor properties of deep collicular neurons. The sensory responses of neurons are considered for three reasons. (1) To the extent that the motor activity of collicular neurons depends upon prior activation of sensory cells, the responses of sensory cells provide an index of the range and types of stimuli capable of guiding saccadic movements. (2) The apparent retinotopic organization of visually responsive cells in the deeper layers is related to the question of the frame of reference in which sensory signals directing saccadic movements are encoded. And (3) views concerning the functional organization of the SC have been influenced significantly by the observation that visual, auditory and somatosensory maps are aligned in the deeper layers.

3.1. Motor functions

3.1.1. Microstimulation studies

3.1.1.1. Motor map for saccadic eye movements. Adamuk reported in 1870 that electrical stimulation of the SC produces conjugate eye movements (Adamuk, 1870), but a complete description of stimulation-induced eye movements was not available until a century later (Robinson, 1972). Collicular stimulation in alert rhesus monkeys evokes conjugate, contralateral saccades; it does not produce smooth pursuit, vergence or nystagmic movements. For suprathreshold currents, the latency of evoked saccades is approximately 20–30 ms.
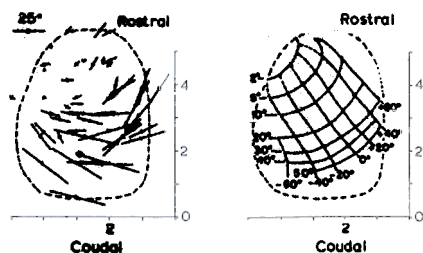

Fig. 2. Maps of the direction and amplitude of stimulation-induced saccades. A. Dorsal view of the left superior colliculus of a rhesus monkey. Arrows indicate the direction and amplitude of saccades produced by stimulation. B. Smoothed contours of the motor map of the superior colliculus. Isoamplitude lines (2° to 50°) run from medial to lateral and isodirection lines (−60° to +60°) run from anterior to posterior. (From Robinson, 1972.)

Threshold current varies as a function of electrode depth. Near the surface of the SC, thresholds are as high as 800 μA; but as the electrode is lowered, the threshold drops to approximately 200 μA and remains at this level for 1–1.5 mm until it abruptly falls to less than 20 μA (Robinson, 1972).

In monkeys, the direction and amplitude of saccades are a function of the site of stimulation in the SC. Within limits, the trajectory of the saccade is independent of stimulation parameters as well as the location of the eye in the orbit. An extensive map of the amplitude and direction of saccades evoked by stimulation of different points of the SC was developed by Robinson (see Fig. 2), who also noted the correspondence between the motor map and the overlying sensory map formed by the retinotopic projections to the superficial layers of the SC (Robinson, 1972). In a combined recording and stimulation study, Schiller and Stryker (1972) confirmed Robinson's microstimulation results and demonstrated, directly, an alignment between the visual and motor maps. These investigators mapped the receptive fields of visually responsive neurons and then stimulated at the same site. The stimulation-induced saccade moved the foveal projection to the region of the visual field corresponding to the neurons' receptive fields prior to stimulation.

Recent experiments (Sparks and Mays, 1983a) indicate that the current required to evoke saccades is greater if the animal is actively fixating a target and that, during fixation, stimulation-induced movements may have smaller amplitudes. Also, the direction and amplitude of saccades produced by collicular stimulation are altered if stimulation occurs shortly before an impending visually triggered saccade or if it immediately follows a saccade to a visual target. An effect of the original position of the eye in the orbit has also been noted (Goldberg and Segraves, 1986; Gerez and Sparks, unpublished observations).

3.1.1.2. Motor maps for eye and head movements. Results obtained from microstimulation studies in the SC of cats (Roucoux and Crommelinck, 1976; Crommelinck et al., 1977; Guitton et al., 1980; Harris, 1980; Roucoux et al., 1980; McIlwain, 1986) differ in several ways from results reported for monkeys. (1) The amplitude of the movements produced by collicular stimulation in cats is much more dependent upon the parameters of stimulation (current intensity, duration of stimulation train, etc.). (2) There is a pronounced influence of initial orbital position upon the direction and amplitude of the stimulation-induced movement. And (3) qualitatively different types of movements are produced in cats depending upon whether the stimulation site is located in the anterior two-thirds of the SC, the posterior one-third or the most caudal zone of the SC.

Stimulation of the anterior zone of the SC (lying beneath regions of the superficial layers representing the central 25 deg of the retina) in alert cats free to move their heads produces saccadic eye movements that may be accompanied by small, slow movements of the head (Roucoux et al., 1980). The amplitude of the stimulation-induced saccade depends upon the duration of the stimulus train, and the direction and amplitude of the movement depend upon the initial position of the eye. For example, stimulation of a collicular site that produces a purely horizontal saccade 10 deg in amplitude when the eye is near the center of the oculomotor range will produce a saccade with a downward component if the eye is elevated and an upward component if, prior to stimulation, the eye is rotated downward. Similarly, centrifugal stimulation-induced saccades are smaller than centripetal ones.

Stimulation of the posterior one-third of the SC in cats produces 'goal-directed' saccadic eye movements – saccades that bring the eyes to a particular position in the orbit. In cats with unrestricted head movements, the 'goal-directed' eye movements are accompanied by stimulation-induced, short-latency, high-velocity head movements. The combination of eye and head movements results in a high-velocity gaze shift that corresponds in direction and amplitude to the retinotopic map observed in the overlying superficial layers (Roucoux et al., 1980).

In cats, stimulation in the caudal collicular zone evokes head movements that bring the head axis to a particular location. It is hypothesized that this zone is involved in the initiation of orienting movements of the eyes, head and body (Roucoux et al., 1980).

Thus, in cats, stimulation data suggest that the SC is a part of a neural circuit involved in the coordination of orienting movements of the eyes, head and body toward the source of novel or biologically significant stimuli. The anterior zone controls small changes in gaze that are within the oculomotor range of the cat. The middle zone controls orienting movements of the eyes and head that direct gaze toward stimuli lying beyond the oculomotor range. And the posterior zone may be involved in shifts of gaze that require rotations of the entire body axis. A similar organization could be characteristic of the monkey SC, but is not obvious because of the large oculomotor range of the monkey. Contrary to previous reports (Stryker and Schiller, 1975), stimulation of the caudal SC in the monkey does produce combined eye and head movements (Goldberg and Segraves, 1986; Gerez and Sparks, unpublished observations).
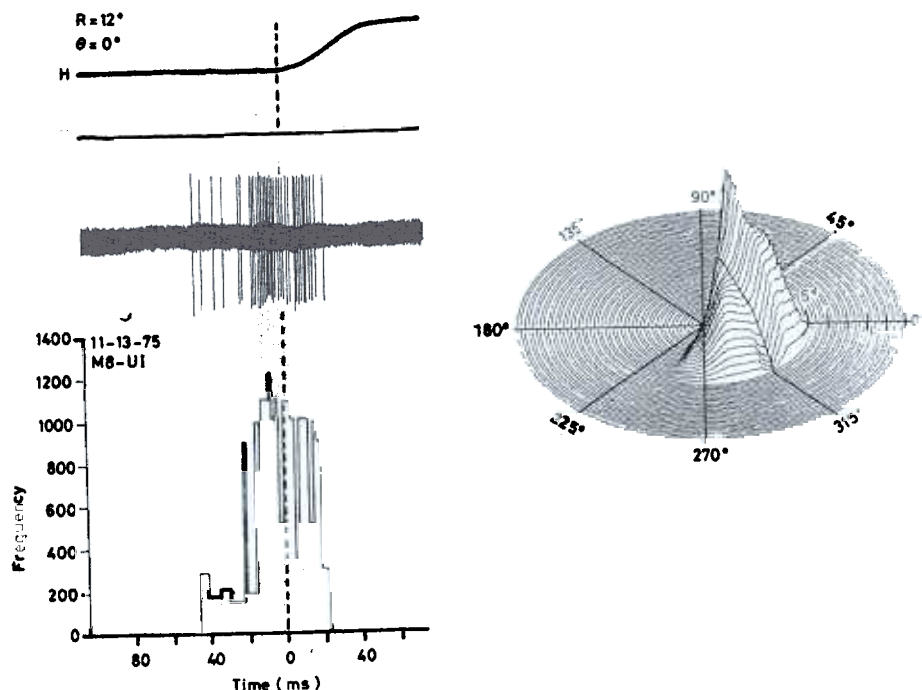
Fig. 3. Left. Discharge pattern recorded from a typical saccade-related burst neuron in the superior colliculus. H, horizontal eye position; V, vertical eye position. Middle tracing: spike discharge. Bottom graph: instantaneous spike frequency as a function of time. The dotted line represents the onset of the eye movement. Right. Three-dimensional representation of the number of spikes as a function of the angle and amplitude of eye movements. The maximal burst (48 spikes) preceded small, right saccades with a downward component (1° in amplitude at an angle of 320°). Movements within the movement field but less than or greater than 1° in amplitude were preceded by a less vigorous response. Similarly, if the angle of movement deviated from 320°, fewer spikes were observed. (From Sparks and Jay, 1986.)

3.1.2. Chronic unit recordings.

3.1.2.1. Cells with saccade-related activity.
Wurtz and Goldberg (1971) first described neurons in the SC of monkeys that discharge before saccadic eye movements. Their basic finding is now well known: neurons in the intermediate and deeper layers of the SC discharge before saccadic eye movements, and each cell displaying saccade-related activity has a movement field; i.e., the neuron discharges before saccades of certain directions and amplitudes, regardless of the initial position of the eye in the orbit.

Three distinct types of cells with saccade-related activity have been identified: (a) saccade-related burst neurons (SRBNs); (b) visuomotor cells, and (c) visually triggered movement cells.

(a) *Saccade-related burst neurons.* The burst profile of an SRBN is illustrated in Fig. 3. Some of these cells generate only a high-frequency burst beginning 18-20 ms before saccade onset. The discharge of other SRBNs is characterized by a prelude of low-
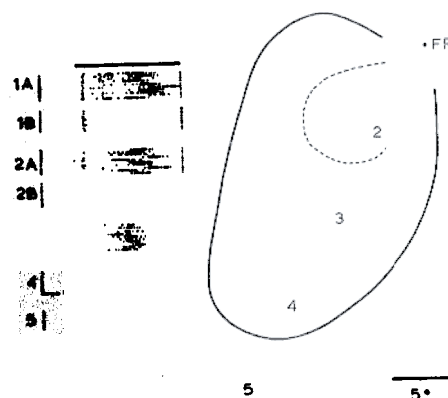

Fig. 4. Visuomotor cell with a visual receptive field (dashed outline) smaller than its movement field (solid outline). The response of the cell preceding the eye movement at points 1-5 is shown in the dot patterns on the left. For points 1 and 2, which are in both the visual receptive field and the movement field, the cell discharge is shown when an eye movement was made in response to the spot of light (1A, 2A) and when the spot of light appeared in the absence of an eye movement (1B, 2B). From Wurtz and Goldberg (1972a).
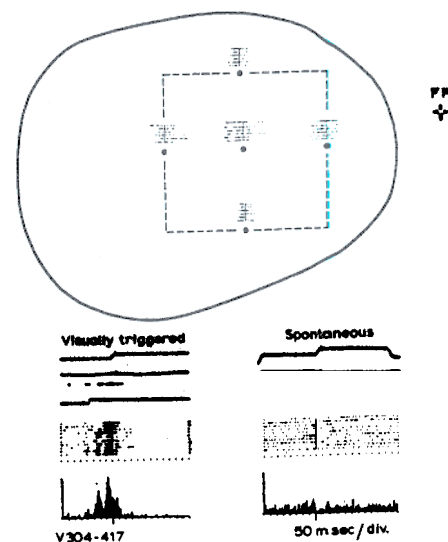

Fig. 5. Response properties of a visually triggered movement cell. The movement field of the cell is enclosed by the solid line. Spontaneous movements falling within the dashed line were selected for comparison with saccades made to the visual targets represented by the solid dots. Below, activity associated with saccades to the central target are shown in the left column (visually triggered). Activity associated with spontaneous saccades having comparable directions and amplitudes is shown in the right column (spontaneous). From Mohler and Wurtz (1976).

frequency activity followed by a relatively discrete burst of spike activity. The duration of the prelude of activity is variable from trial to trial, and the onset of the low-frequency activity is not tightly coupled to target onset or to saccade onset. In general, the prelude component of the saccade-related discharge resembles the activity of quasi-visual cells (see below) and this low-frequency activity may serve to hold in spatial register information concerning the direction and amplitude of an impending saccade.

(b) *Visuomotor cells.* Many visually responsive neurons in the deep SC also discharge before saccadic eye movements (Wurtz and Goldberg,

3.1.1.3. Other motor maps.
In cats and rats, stimulation of the deeper layers of the SC evokes movements of the pinnae and vibrissae (McHaffie and Stein, 1982; Schaeffer and Schneider, 1968; Stein and Clamann, 1981; Syka and Radil-Weiss, 1971). The lowest thresholds for producing pinna movements are obtained in the intermediate layers. In general, the pinna movements produced by SC stimulation are reported to correlate well with evoked eye movements. Stimulation-induced movements are directed contralaterally. Stimulation me-

dially produces movements with strong upward components; stimulation laterally elicits movements with downward components. Relatively small movements are evoked by stimulation of the anterior SC, while stimulation caudally produces larger movements (Stein and Clamann, 1981). Collicular stimulation also elicits movements of the vibrissae. These movements have not been studied systematically, but a topographical representation may be present in cats (Stein and Clamann, 1981).

1972a). When a saccade occurs in response to the visual stimulus, a biphasic pattern of activity is observed (Fig. 4). A visual response occurs approximately 40-50 ms after stimulus onset and is followed by a burst of activity preceding the saccadic eye movement (Wurtz and Goldberg, 1972a). Neurons that fire in response to visual stimuli as well as before eye movements have overlapping, but not necessarily co-extensive, movement and receptive fields (Wurtz and Goldberg, 1972a).

(c) *Visually triggered movement cells.* Mohler and Wurtz (1976) were the first to describe visually triggered movement cells (VTMs). VTMs both have a visual receptive field and produce a saccade-related discharge when saccades are made to a visual target. These cells are silent during similar spontaneous saccades in the dark or light (Fig. 5). Mays and Sparks (1980a) confirmed the observations of Mohler and Wurtz (1976) and found visually dependent cells that had no visual response, indicating that the property of visual dependence is not restricted to cells with visual receptive fields. They also noted that even a brief appearance of a direct-saccade target was sufficient to enable a visually dependent cell to fire. Thus, VTMs do not require that a visual stimulus be present at the initiation of a saccade; it is necessary only that the target has recently appeared in an area of the visual field that corresponds to the movement field of the cell.

3.1.2.2. Movement fields.

The vigor of the saccade-related discharge varies for saccades within the movement field (Sparks et al., 1976). Movements to the center of the movement field are preceded by a vigorous discharge, but movements deviating from this optimal direction and amplitude are accompanied by less vigorous responses (Fig. 3). The movement fields of collicular neurons are also characterized by a temporal gradient. The interval between the onset of the spike discharge and the onset of a saccade is greater for movements to targets near the center of the movement field than for movements to the periphery of the field (Sparks et al., 1976; Sparks and Mays, 1980). Moreover, the size of the movement field is a function of the

amplitude of the optimal movement. Neurons discharging before small saccades have small and sharply tuned fields, while neurons discharging before large saccades have large movement fields, and tuning is relatively coarse.

Cells in the deeper layers are organized topographically according to their movement fields (Schiller and Koerner, 1971; Wurtz and Goldberg, 1972a; Sparks et al., 1976). Neurons discharging before small saccades are located anteriorly, and neurons firing before large saccades are found posteriorly. Cells near the midline of the SC discharge before movements with upward components and cells located laterally fire maximally before movements with downward components. In general, Robinson's (1972) motor map (Fig. 2) derived from microstimulation studies is an accurate description of the organization of neurons with saccade-related discharges within the SC.

3.1.2.3. Coupling of neuronal activity and saccade occurrence.

If the SC participates in the initiation of saccades, then it should be possible to isolate a subpopulation of collicular neurons in which the onset of spike activity is tightly coupled to saccade onset. Sparks (1978) found that SRBNs meet this criterion. If the duration of a visual target is varied so that the stimulus sometimes elicits a saccade and sometimes fails to do so, the occurrence of the spike burst is almost perfectly correlated with saccade occurrence (Sparks, 1978). For SRBNs, there is a clear distinction between the most vigorous neuronal activity occurring in the absence of a saccade and the least vigorous activity accompanying appropriate saccades. However, the tight coupling between neural activity and saccade occurrence or saccade onset is not characteristic of all collicular neurons displaying saccade-related activity (Mohler and Wurtz, 1976; Mays and Sparks, 1980a).

3.1.2.4. Coding of saccade metrics.

How is information about the metrics (direction, amplitude, velocity) of a saccade encoded by collicular neurons? Although the vigor of discharge of a particular sac-

cade-related burst cell varies for different movements within the movement field, information concerning saccade direction and amplitude is not contained within the discharge of a single cell (Sparks and Mays, 1980). As illustrated in Fig. 6, except for the maximal discharge preceding saccades to the center of the movement field, the discharge of collicular neurons is ambiguous with respect to saccade direction and amplitude. Identical discharges may precede many saccades having different directions and amplitudes. Note, for example, the similarity of the burst profiles in B, F, 2 and 6 (Fig. 6), although these bursts preceded saccades with large differences in direction and amplitude. Moreover, the discharges of different saccade-related burst units, some of which discharge max-
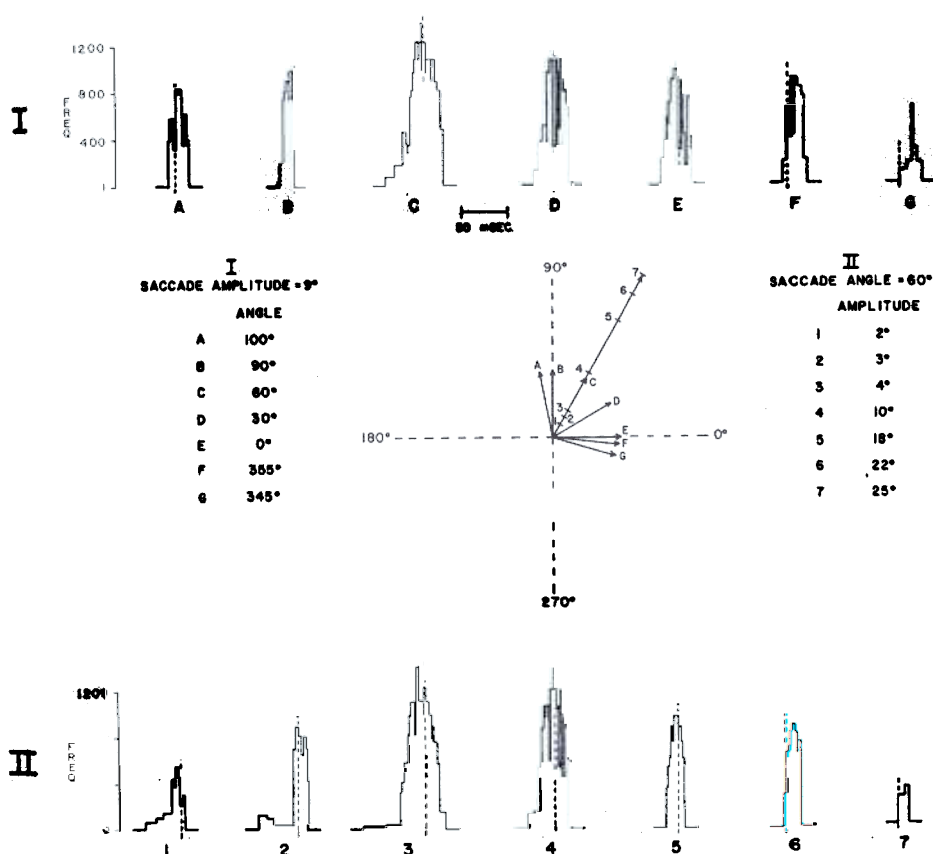

Fig. 6. Variations in the configuration and timing of the discharge of a typical saccade-related burst neuron. I. Instantaneous spike frequency records for seven saccades of the optimal amplitude (9°) but differing in direction. The dotted line represents saccade onset. II. Instantaneous spike frequency records for seven saccades of the optimal direction (theta = 60°) but differing in amplitude. See text for additional details. From Sparks and Mays (1980).

imally to small saccades, and some of which discharge maximally to large saccades, are indistinguishable (Sparks and Mays, 1980). Thus, the SC does not generate specific rates of firing for saccades of different directions and amplitudes. It is the location of the active population of neurons in the SC, not their frequency of firing, that specifies saccade direction and amplitude.

Preliminary data indicate that the frequency of firing of SRBNs in rhesus monkeys may encode vectorial velocity (Rohrer et al., 1987). While the velocity of saccades is reduced after collicular ablations (Wurtz and Goldberg, 1972b; Schiller et al., 1980) or reversible deactivation of collicular neurons (Hikosaka and Wurtz, 1985a), we were unable in our earlier experiments (Sparks and Mays, 1980) to find a relationship between the discharge of SRBNs and saccadic velocity. This was probably due to the small range in saccadic velocity observed when movements of the same direction and amplitude are made to continuously present visual targets. In recent experiments in which monkeys were required to look to the position of a remembered target (Rohrer et al., 1987) or look to the location of auditory targets (Jay and Sparks, 1987a,b), we observed that saccades to remembered targets and saccades to auditory targets were reduced in velocity. Because of these variations in velocity, we were able to observe a relationship between the average firing rate during saccade-related bursts and saccadic velocity. A relationship between instantaneous firing frequency and saccadic velocity has already been described in cats (see below, Berthoz et al., 1986). These findings are consistent with the suggestion of van Gisbergen and colleagues (van Gisbergen et al., 1985) that, for oblique saccades, a signal of the velocity of the composite movement (vectorial velocity) is computed first and subsequently decomposed into separate velocity signals for the horizontal and vertical components (see section 5). Preliminary data in both cats and monkeys suggest that a signal of vectorial velocity may be present at the level of the SC.

In summary, three conclusions can be reached concerning the saccade-related motor signals found in the SC. First, the activity of collicular neurons encodes the desired change in eye position, not a movement to a particular orbital position. Secondly, saccade direction and amplitude are encoded anatomically. It is the location of the active neurons within the topographical map of movement fields, not their frequency of firing, that specifies the trajectory of a saccade. Thirdly, saccadic velocity may be encoded by the frequency of firing of the active population.

3.1.3. Destination of collicular signals
While the motor properties of collicular neurons have been studied extensively (see above), little is known about the destination of collicular signals or their contribution to the processing that occurs in other brainstem oculomotor nuclei. Raybourn and Keller (1977) studied collicular pathways to the paramedian pontine reticular formation, an area containing the neural network controlling horizontal saccadic eye movements. They examined the response of functionally identified pontine cells to electrical stimulation of the SC and found evidence for mono- and disynaptic connections between collicular cells and two types of pontine cell. On the basis of this study, it was not possible to identify the functional classes of collicular neurons projecting to the pontine reticular formation. However, Keller (1979) also reported that 10 of 10 SRBNs recorded in the SC were antidromically activated by stimulation of the region of the paramedian pontine reticular formation containing pause units. Only 1 of 11 other collicular neurons with saccade-related discharges, but lacking the high-frequency burst, was antidromically activated by paramedian pontine reticular formation stimulation. Thus, the axons of SRBNs probably comprise a major efferent pathway from the SC to subsequent pre-oculomotor neurons, particularly those within the paramedian pontine reticular formation.

Moschovakis and colleagues (1986; see Addendum) recorded in the SC of alert squirrel monkeys while monitoring their spontaneous eye movements. Subsequent to recording, HRP was injected into several functionally classified neurons with saccade-related activity, thus permitting their morphological identification. One class, vectorial long-lead burst neurons, have functional properties that are quite similar, if not identical, to SRBNs described in the rhesus monkey. Vectorial long-lead burst neurons display little spontaneous activity, have movement fields, and generate high-frequency bursts of activity beginning about 20 ms before saccade onset. The cell bodies of recovered HRP-filled vectorial long-lead burst neurons are located in the stratum opticum, are ovoid in shape, and have soma sizes ranging from 265 to 468 μm^2. The main axons of these cells cross the midline in the dorsal tegmental decussation and join the predorsal bundle. Additionally, thin recurrent collaterals ramify in both the deeper and the superficial layers of the SC near the parent soma. Other axon collaterals enter the tectal commissure, terminating in the contralateral tectum. Also, axonal branches run rostrally towards the ipsilateral parafascicular nucleus of the thalamus and the zona incerta and ramify within the interstitial nucleus of Cajal. Still other axonal branches project heavily to the ipsilateral mesencephalic reticular formation.

Munoz and Guitton (1985, 1986) identified tecto-reticulo-spinal neurons (TRSNs) in the SC of alert behaving cats by antidromic activation via stimulating electrodes in the ventromedial funiculus of the spinal cord at C1 levels or by stimulation of the predorsal bundle, immediately rostral to the abducens nucleus. These neurons are characterized by the total absence of a spontaneous firing rate; they are visually responsive, having large visual receptive fields, and generate a sustained discharge that seems to encode gaze motor error (the amplitude and direction of the difference between the current gaze position and the location of the visual target). TRSNs also emit a high-frequency burst of spikes before visually triggered gaze shifts made in the head-fixed or head-free condition. These presaccadic bursts are weak or absent when gaze shifts are made to the remembered position of visual targets, and they are absent during spontaneously generated gaze shifts.

Berthoz, Grantyn and Droulez (1986) recorded, intracellularly, from axons of TRSNs impaled with microelectrodes in the region just rostral to the abducens nucleus. The TRSNs were identified electrophysiologically by direct orthodromic responses to stimulation of the contralateral SC and by antidromic invasion following stimulation of the anterior funiculus in the C1 or C2 spinal segments. They confirmed many of the findings of Munoz and Guitton (1985, 1986) but added the important observation that some TRSNs generate presaccadic bursts with instantaneous frequency profiles closely correlated with the profile of saccadic eye velocity.

3.2. Sensory responses

Studies in anesthetized and/or paralysed subjects have delineated the sensory attributes to which collicular neurons are sensitive, while recordings obtained from alert, behaving subjects indicate that many cells responsive to sensory stimuli also discharge before saccadic eye movements.

3.2.1. Responses to visual stimuli

3.2.1.1. Acute experiments. Compared to neurons in the geniculo-striate system, cells in both superficial and deep collicular layers have large receptive fields. The receptive fields of deep collicular neurons are larger than those of superficial cells and, within the deep layers, receptive field size increases with increasing depth (McIlwain, 1975). The general consensus of studies conducted in both cats (McIlwain and Buser, 1968; Sterling and Wickelgren, 1969; Berman and Cynader, 1972; Stein and Arigbede, 1972a; Gordon, 1973; Berman and Cynader, 1975) and monkeys (Humphrey, 1968; Cynader and Berman, 1972; Goldberg and Wurtz, 1972a; Marrocco and Li, 1977) is that despite the distinct histological, anatomical and physiological differences between the superficial and deep divisions of the SC, the response properties of visually responsive deep collicular neurons are remarkably similar to those of visual neurons in the superficial layers. Both superficial and deep cells respond best to moving stimuli, are directionally selective, have

transient or unstable responses, and habituate rapidly to repetitive stimuli (habituation is more common and more pronounced in neurons within the deeper layers). Furthermore, the response properties of visually sensitive neurons in the deep colliculus of cats and monkeys exhibit only a few minor differences; the most notable difference is that directionally selective cells are more prevalent in cats (67%) than in monkeys (5%) (Cynader and Berman, 1972). Two types of visual neuron that are sensitive to relative motion have been identified recently by Mandl (1985) in the intermediate grey collicular layer of cats. One of these may encode position in depth; the other could encode velocity information about patterns moving with respect to each other.

In monkeys, the activity of corticotectal cells in area 17 is relayed primarily to neurons in the deep layers of the SC (Schiller et al., 1974). Cortical cooling does not affect the responsiveness of cells in superficial layers but reduces or eliminates responses of cells in the deep layers.

3.2.1.2. Chronic unit studies. With the major exceptions noted below, when neurons in the deeper layers are studied in alert animals, the functional properties of visually responsive cells are similar to those described in acute experiments.

(i) *Visuomotor cells.* Many visually responsive neurons in the deep colliculus also discharge before saccadic eye movements (Wurtz and Goldberg, 1972a) (see above), but the functional role of visuomotor cells is unknown. These cells display visual responses even when saccades are not made to the stimulus producing the sensory response, and saccade-related bursts are observed in the absence of a visual response (Wurtz and Goldberg, 1972a; Mays and Sparks, 1980a). Thus, without additional information, recipients of the output of visuomotor cells would be unable to determine the source (visual or motor) of the input.

(ii) *Quasi-visual cells.* In acute experiments, the receptive fields of visually responsive cells in deep SC are in register with those of overlying superficial neurons receiving topographically mapped inputs directly from the retina (Sprague et al., 1968; Gordon, 1973). Based upon these findings, it is reasonable to assume that visual responses of cells in the deeper layers also depend upon stimulation of specific regions of the retina. However, Mays and Sparks (1980a) found that the activity of some visually responsive neurons in the intermediate and deeper layers (quasi-visual or QV cells) does not depend upon activation of a particular retinal region. Their experiments were guided by models of the saccadic system (Robinson, 1975; Zee et al., 1976) implying that there are at least three neural representations of a visual target to which a saccade is made: (1) a representation of retinal error; i.e., the distance and direction of the target image from the fovea; (2) a representation of the location of the target in a head or body frame of reference; and (3) a representation of saccadic motor error; i.e., the difference between current and desired eye position. The response properties of hypothetical neurons encoding the position of a target in these three different ways and the test conditions permitting the identification of these neurons are outlined in Fig. 7. Neurons in the superficial layers of the SC of monkeys encode retinal error. Other cells in the deeper layers encode motor error. A representation of target location in head or body coordinates has not been found in the SC of monkeys.

Mays and Sparks (1980a) found that visually responsive neurons in the superficial layers of the SC were activated only when a particular region of the retina was stimulated. When plotted in the coordinates of the tangent screen, the location of the receptive field shifted with each change in gaze (see Fig. 7). Thus, retinal error is represented by the site of neuronal activity within the retinotopic map observed in the superficial layers of the SC.

When using tasks similar to those described in Fig. 7, Mays and Sparks (1980a) found that QV neurons are visually responsive, but appear to signal motor error instead of retinal error – i.e., QV cells discharge whenever a saccade with a particular direction and amplitude is appropriate, regardless of whether the movement becomes appropriate because of the onset of a visual stimulus or because of
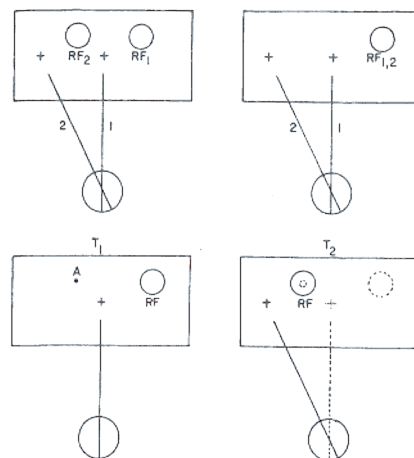

Fig. 7. Response properties of three types of hypothetical neuron. Top left. The activity of neurons signaling retinal error is dependent upon excitation of receptors in a particular region of the retina. Therefore, the receptive field moves with each change in gaze (fixation 1 to fixation 2). However, the distinction between neurons encoding retinal error and those signaling motor error depends upon a critical test, described below. Top right. Neurons representing a saccade target in a head or body frame of reference would respond to targets in a specific region of the visual environment, regardless of the position of the eye in the orbit. The plot of the receptive field of such a neuron while the animal was fixating point 1 would be the same as the plot of the receptive field when the animal was fixating point 2. Thus, these neurons are responsive to stimuli occupying a particular region of visual space, regardless of the retinal locus of the target image. Note that the spatial properties of these neurons would not be detected in an acute recording study or in a chronic recording experiment in which the receptive field was plotted with a single fixation point. Bottom. Hypothetical neurons coding a saccadic motor error signal would alter their discharge rate when there is a certain difference between current and desired eye position. This motor error could be produced either by the appearance of a visual target located a certain distance and direction from the fixation point or by a change in eye position after the visual target has disappeared. On the left, the response field of a hypothetical motor error neuron is represented as a circle (RF). With fixation straight ahead, the neuron discharges in response to saccade targets presented in the circular response field. The neuron discharges not because a particular region of the retina was activated, but because, after the appearance of the saccade target, the difference between current and desired eye position requires a

an eye movement occurring after the disappearance of the target. The discharge of a QV cell is illustrated in Fig. 8. On trials in which a direct saccade was made in response to a single visual stimulus (0–A trials), the onset of the discharge was tightly coupled to target onset, not saccade onset, and the cell appeared to have a receptive field in the lower left quadrant of the visual field (Fig. 8C). On double-saccade trials, after fixation of the center target 0 for a variable period, the offset of the fixation target was followed by a brief presentation of target B. The duration of target B was less than the reaction time of the monkey, and thus target B was extinguished before a saccade occurred. The monkey learned that on trials with a brief presentation of target B, reward was contingent upon a saccade to B (0–B) and a second saccade (B–0) back to the position of the fixation target. QV cells also gave a vigorous discharge on double-saccade trials in which the target was flashed in the right visual field, the field opposite to the cell's apparent receptive field. However, after the eyes had reached position B, the cell began to discharge and continued to do so until after the saccade back to position 0. This increase in discharge frequency was neither associated with the appearance of target B nor tightly coupled to the onset of the 0–B saccade (Fig. 8B). Note that computation of the trajectory of the B–0 saccade must be based upon both retinal information and information about the change in eye position that occurred as a result of the 0–B saccade.

The hypothesis that the activity of QV cells encodes saccadic motor error was tested in a separate

saccade with a particular trajectory. Note that if this is the only test applied, the discharge of the cell appears simply to reflect retinal error. A saccade target presented at position A outside the response field will not activate the neuron as long as fixation of the center point is maintained. Suppose, however, after target A disappears, gaze is shifted to a new fixation point but a saccade to the remembered location of target A is still required (right). Because the difference between current and desired eye position is in the response field of the neuron, a change in discharge rate will signal this new motor error. This signal is created, not by the appearance of a new target, but by a change in eye position occurring after the original target disappeared. (From Sparks and Mays, 1983b.)
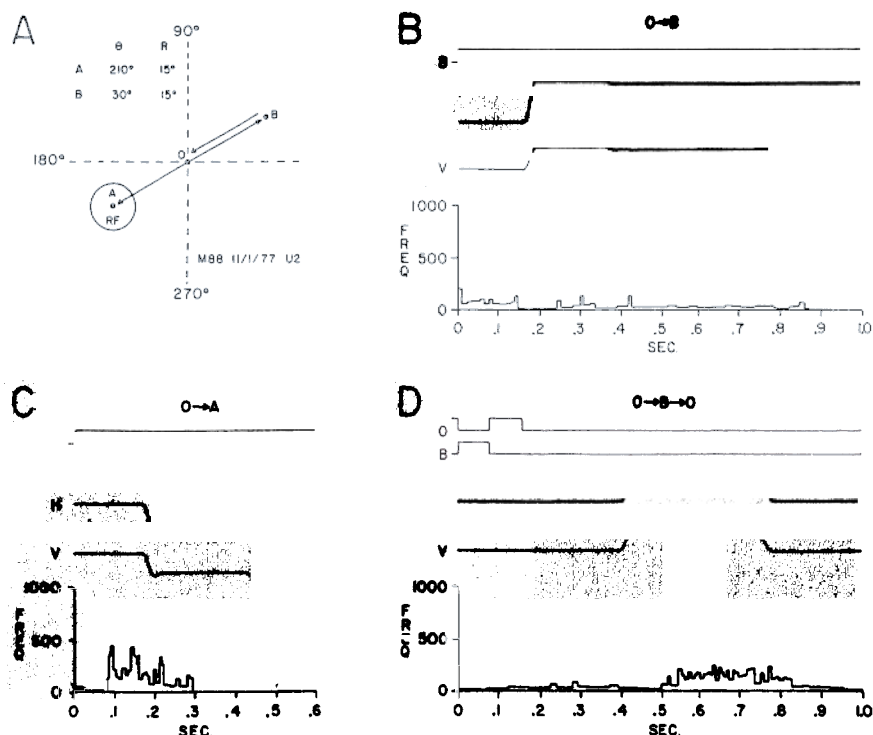
Fig. 8. Discharge pattern of a QV cell. (a) Trajectories of the saccades occurring on single (0–A) and double (0–B and B–0) saccade trials. (b) Lack of neuronal response on a control trial (0–B saccade). B, onset of target B; H, horizontal eye position; V, vertical eye position; bottom trace, instantaneous spike frequency of the QV cell during this trial. (c) Typical response of a QV cell on single-saccade trials. A vigorous discharge, tightly coupled to target A onset, is observed. Typically, the increase in spike frequency continues until after the 0–A saccade. (d) Typical response of a QV cell on double-saccade trials. No observable alteration in discharge rate is related to the onset of targets B or 0, but after the eyes have reached position B, an increase in discharge frequency begins and continues until after the return (B–0) saccade. (From Sparks and Mays, 1983a.)

experiment (Sparks and Porter, 1983) by recording from QV cells during trials in which the monkey compensated for perturbations in eye position produced by microstimulation of the SC (Mays and Sparks, 1980b). The hypothesis was confirmed by the finding that QV cells increased their discharge rate whenever there was a certain difference between current and desired eye position regardless of whether this motor error was produced by the sudden appearance of a visual target or by a stimula-tion-induced change in eye position after target off-set. These experiments demonstrate that the neural map of visual space formed by QV cell activity is a dynamic one. If a target is displaced, or if the eyes move after a brief target has disappeared, the site of QV cell activity shifts to a location that represents the trajectory of the movement required to look to the target rather than the location of the stimulus in retinal, head or body coordinates.

Subsequently, cells with similar properties were

observed in the SC of cats. Munoz and Guitton (1985, 1986) reported that tecto-reticulo-spinal neurons (TRSNs) in the SC of alert behaving cats generate a sustained discharge encoding gaze motor error (the difference between the current gaze position and the location of the visual target). This discharge seems to be related to gaze error and not to the individual components of gaze error (eye motor error or head motor error).

3.2.2. Responses to auditory stimuli

3.2.2.1. Acute experiments. Early reports of acoustically sensitive neurons in the deep SC were based on incidental observations made while investigating the physiological characteristics of visual neurons in experiments with anesthetized and/or paralyzed subjects. Complex sounds, such as hisses, whistles, finger snaps or jangling of keys, were found to effectively activate neurons in the deep SC of mice (Drager and Hubel, 1975a,b, 1976), hamsters (Chalupa and Rhoades, 1977), cats (Gordon, 1973; Stein, 1978; Stein and Arigbede, 1972a; Wickelgren, 1971) and Cebus monkeys (Updyke, 1974). In squirrel monkeys, specific sounds were particularly effective in activating deep collicular auditory neurons (Allon and Wollberg, 1978). Like visual collicular cells, auditory neurons in the deep SC also habituate to repetitively presented stimuli; i.e., response probability decreases with stimulus repetition (Hirsch et al., 1985).

Perhaps the most important finding to emerge from these early studies was the suggestion of a topographical map of auditory space within the deep collicular compartment (Chalupa and Rhoades, 1977; Drager and Hubel, 1975a,b; Gordon, 1973; Harris et al., 1980; Tiao and Blakemore, 1976; Wickelgren, 1971). Gordon (1973), for instance, recorded from deep collicular neurons in paralysed cats that responded to both visual and auditory stimuli. In some cells the visual and auditory receptive fields were aligned. In cases where the auditory receptive fields were large and poorly defined, there was a correspondence between the locations of the medial edges of both receptive

fields. For purely acoustically responsive neurons, the medial edge of the auditory receptive field was aligned with the medial edge of the visual field of adjacent neurons. A topographic map of auditory space was thus inferred by referring the location of auditory receptive fields to the location of visual receptive fields known to be topographically organized (Chalupa and Rhoades, 1977; Drager and Hubel, 1975a,b; Gordon, 1973; Harris et al., 1980; Tiao and Blakemore, 1976; Wickelgren, 1971).

Knudsen's (1982) discovery of a map of auditory space in the optic tectum of owls was the catalyst for investigators to reexamine the auditory responsiveness of collicular neurons in cats using precisely controlled acoustic stimuli. These studies revealed a topographical organization of acoustically responsive neurons organized according to their responses to interaural intensity differences (Irvine and Wise, 1983; Hirsch et al., 1985; Wise and Irvine, 1985; Yin et al., 1985) or, when a moveable speaker was used, according to the 'best area' (Middlebrooks and Knudsen, 1984). In the experiments of Middlebrooks and Knudsen (1984), all auditory units exhibited spatial tuning in the form of a peak response to a limited range of stimulus locations. The area in which acoustic stimuli evoked responses greater than 75% of maximum was defined as the 'best area' and the 'best areas' of cells varied systematically with their locations in the SC, forming a map of auditory space that coincided with the map of the visual field. A similar topographical organization of auditory space was observed in the SC of guinea pigs (King and Palmer, 1983).

3.2.2.2. Chronic unit recording experiments. Jay and Sparks (1984, 1987b) obtained evidence that the auditory map in the SC of monkeys is dynamic and organized in motor, rather than sensory, coordinates. Their experiments were based upon the observation that, from the perspective of guiding saccadic eye movements, the task of sensory systems is to specify the change in eye position required to look to a target, not the location of the target in head, body or retinal coordinates. Consid-

er the example of a monkey with the head fixed and positioned 'straight ahead' but with gaze directed 24° to the left of center. When an auditory stimulus is presented 10° to the right of center, interaural cues will be used to localize the target in head coordinates ('target is 10° right'). But, since the eyes are directed 24° left of center, looking to the target requires a 34° rightward saccade and neurons in caudal regions of the left SC must be activated to produce this movement. If an auditory target is presented in the same location on another occasion while gaze is directed 24° to the right of center, cells in the right SC must be activated to produce the 14° leftward saccade required to look to the stimulus. Thus, according to Jay and Sparks, initiation of an appropriate saccade by activating particular subsets of collicular neurons requires that auditory signals be translated into signals of saccadic motor error.

In the experiments of Jay and Sparks (1984, 1987a,b), monkeys trained to look to either visual or auditory targets in a completely darkened room were placed with their heads fixed in the center of a semicircular track. Movement of a speaker (with a light-emitting diode attached) along the track and rotation of the track allowed targets to be presented at most locations on an imaginary sphere surrounding the animal. Three fixation lights separated by 24° were placed along the horizontal meridian. At the beginning of each trial, one of the three fixation lights was randomly activated. After a variable interval, an auditory (broad-band noise burst) or visual target was presented and the animal was required to look to the target location in order to receive a liquid reward. A delayed saccade task was used to separate, temporally, sensory and motor activity. Receptive fields of sound-sensitive cells in the SC of alert monkeys were plotted while varying the direction of visual fixation. If the receptive fields of auditory neurons in the SC are organized in head-centered coordinates, the direction of fixation would have no effect. But if, as hypothesized, the response of auditory neurons is organized in motor error coordinates, then the response should depend upon both speaker position and fixation direction.

For every sound-sensitive cell encountered in the SC, the position of the eyes in the orbit had a distinct effect upon the response to an auditory stimulus (Jay and Sparks, 1987b). The discharge of acoustically responsive neurons was not determined solely by the position of the auditory stimulus in space, but depended upon the position of the eyes in the orbit relative to target position. Thus, the map of auditory space found in the monkey SC is not a static representation. With each movement of the eyes in the orbit, the population of neurons responsive to an auditory stimulus in a particular spatial location changes to a new collicular site, a site representing the new saccadic motor error signal.

3.2.3. Somatosensory responses
Since little is known about the sensory guidance of saccades by somatosensory stimuli, the responsiveness of deep collicular neurons to these stimuli is not reviewed here (see Stein, 1984; Sparks, 1986, for recent reviews).

3.2.4. Multimodal neurons; alignment of visual, auditory and somatosensory maps
Many sensory neurons in the intermediate and deep grey collicular layers are multimodal; that is, they respond to visual, somatosensory and/or auditory stimuli. Bimodal and trimodal deep collicular neurons have been described in monkeys (Cynader and Berman, 1972; Jay and Sparks, 1987b; Updyke, 1974), cats (Jassik-Gerschenfeld, 1965; Straschill and Hoffmann, 1969; Wickelgren, 1971; Stein and Arigbede, 1972b; Gordon, 1973; Abrahams and Rose, 1975; Stein et al., 1975, 1976; Stein, 1984; Meredith and Stein, 1983, 1985, 1986a,b; Munoz and Guitton, 1986), guinea pigs (King and Palmer, 1985), hamsters (Chalupa and Rhoades, 1977; Mooney et al., 1984; Rhoades et al., 1985, 1986) and mice (Drager and Hubel, 1975a,b). The responses of multimodal neurons to a stimulus of one modality can be modified by the simultaneous occurrence of stimuli from a different modality. Studies examining these multimodal interactions are reviewed elsewhere (Sparks and Nelson, 1987; Sparks, 1986).

Topographic alignment of visual, somatosensory and/or auditory receptive fields within the SC has been observed in a number of animals, such as barn owls (Knudsen, 1982), iguanas (Gaither and Stein, 1979; Stein and Gaither, 1981), mice (Drager and Hubel, 1975a,b), hamsters (Tiao and Blakemore, 1976; Chalupa and Rhoades, 1977; Finlay et al., 1978), guinea pigs (Palmer and King, 1982; King and Palmer, 1983, 1985), cats (Gordon, 1973; Stein et al., 1976; Harris et al., 1980; Clemo and Stein, 1984; Munoz and Guitton, 1986) and monkeys (Updyke, 1974; Wurtz and Albano, 1980). For example, in acute recordings from the SC of mice, the receptive fields of superficial visual cells seem to have a constant topographic relationship with underlying somatosensory receptive fields, especially those involving the whiskers (Drager and Hubel, 1975a,b, 1976). It appears that a large portion of the visual field of mice is crossed by whiskers. Whenever visual receptive fields of superficial cells were located in regions crossed by whiskers, somatosensory responses of neurons encountered in the same electrode penetration were elicited only from stimulation of whiskers or immediately adjacent fur, but never by stimulating more distant areas of the body. It was consequently assumed that inputs from sensory modalities other than vision were topographically organized to be in spatial alignment with the visual map.

While considerable effort has been devoted to demonstrating an alignment of auditory, somatosensory and visual maps in the SC, the functional significance of the observed correspondence remains obscure (see Sparks, 1986; Sparks and Nelson, 1987). The observed correspondence between sensory maps in the SC of anesthetized and/or paralysed subjects is curious because the spatial location of a stimulus is encoded differently for each of these sensory systems. The neural code for the location of a visual stimulus is based upon information about the locus of retinal stimulation and the position of the eyes in the orbits. In contrast, the location of sound sources is encoded using head-centered cues such as interaural differences in the timing and intensity of incoming sound waves. Tactile stimuli are localized in a third, body-centered, reference system. The apparent alignment of auditory, visual and somatosensory maps in the SC implies that these sensory signals have been translated into a common coordinate system, but this hypothesis cannot be tested in the anesthetized animal (Poppel, 1973) because, under these conditions, the axes of the head-centered auditory system, the retinotopic visual system and body-centered somatosensory system are aligned. Thus, this observation could be an epiphenomenon resulting from the fortuitous alignment of retinal and head coordinates occurring when, in acute experiments, the head and eyes are in the primary position.

Nonetheless, researchers assume that the alignment of the sensory maps observed in the deep division of the SC is functionally significant. A common assumption is that the deep division of the SC contains a topographical map of sensory space such that a point in the space surrounding the animal is represented by neurons residing at a particular location in the SC. It is assumed, further, that sensory signals from different modalities originating from the same point in space activate a common pool of collicular neurons located within this representation. The activation of these sensory neurons, in turn, is hypothesized to initiate motor responses resulting in orienting movements toward the source of the stimuli. These hypotheses have not yet been formalized into a model of collicular function, and many of the assumptions remain implicit and untested. If the sensory maps are static, what is the basis of the correspondence between sensory maps? One possibility, supported by the experiments of Mays and Sparks (1980a) and Jay and Sparks (1984, 1987b), is that the maps of sensory space observed in the deep division of the SC are dynamic and that sensory signals are encoded in motor, rather than sensory, coordinates. According to this view, the sensory maps are dynamic and the receptive fields of collicular neurons shift with relative movements of the eyes, head and body. A dynamic mapping of sensory space is required because of constraints imposed by the organization of the motor map.

3.2.5. Arousal/attention effects

The responsiveness of deep collicular neurons depends greatly on the state of arousal, alertness or attention of monkeys (Marrocco and Li, 1977) and cats (Grantyn and Berthoz, 1985; Munoz and Guitton, 1985, 1986). For example, while studying stimulus interactions in the deep SC of cats, Munoz and Guitton (1986) observed that the responses of collicular neurons to visual, auditory and tactile stimuli were dramatically reduced while cats were fixating food targets. Similarly, the visuomotor activity of tectoreticulospinal neurons within the intermediate grey collicular layer increased significantly when cats were anticipating the appearance of a food target (Munoz and Guitton, 1985). Increases in the discharge frequency of tectoreticulospinal neurons were reported to occur also when novel, interesting objects were presented to cats (Grantyn and Berthoz, 1985).

Thus, information not only about events in the external environment, but also about the internal state of the animal (i.e., limbic and/or visceral signals) can either attenuate or exacerbate collicular responses to pure sensory stimuli that would otherwise occur in the absence of these internal signals. There is ample evidence demonstrating the possible anatomical substrate for this limbic and/or visceral input to the deep SC. Such projections have been shown to originate in limbic and paralimbic cortical areas; i.e., the splenial visual area and cingulate cortex (Hollander, 1974; Hartwich-Young et al., 1983a,b), as well as in the hypothalamus (Grofova et al., 1978; Edwards et al., 1979; Huerta and Harting, 1984; Rieck et al., 1986). Furthermore, the hypothalamic afferents to the intermediate grey collicular layer are known to be tightly coupled with tectoolivary (and possibly tectospinal) efferent modules in the intermediate grey collicular layer (Huerta and Harting, 1984). On the basis of these findings, it was suggested that hypothalamic inputs to the deep collicular multimodal efferent neurons could effectively alter the responses of these neurons to pure sensory stimulation in order to appropriately pair orienting behaviors with the existing emotional and visceral status of an animal (Rieck et

al., 1986).

An attentional component of the collicular orienting response could be derived from the tectal projections of such cortical areas as the FEF and the parietal cortex. Both of these areas have been shown to play important roles in attentive behaviors (Mountcastle et al., 1975; Lynch et al., 1977; Goldberg and Bruce, 1985). Additionally, response enhancement in association with selective attention has also been demonstrated in superficial collicular neurons (Goldberg and Wurtz, 1972b; Wurtz and Mohler, 1976), and some of the effects of attention on multisensory interactions of deep collicular neurons may originate in the superficial layers.

4. Lesion studies

4.1. Lesions of the SC

On the basis of the anatomical and electrophysiological evidence reviewed above, it may be assumed that the SC is of crucial importance for the control of saccadic eye movements. Despite its undisputed importance, however, the SC does not appear to be absolutely essential for the occurrence of saccadic eye movements. This fact was suggested by the results of lesion studies (Bernheimer, 1899) conducted approximately three decades after Adamuk's (1870) discovery that electrical stimulation of the SC produced conjugate eye movements. Bernheimer (1899) found that unilateral as well as bilateral collicular lesions did not seem to impair either normal or stimulation-induced eye movements in monkeys. Similar findings were reported by Ferrier and Turner (1901), who declared the results difficult to understand 'if the anterior bodies are the centres for co-ordinating visual impressions with the movements of the eyeballs.'

Notwithstanding these early findings, interpretation of anatomical data (Crosby and Henderson, 1948) and clinical reports of deficits in vertical eye movements resulting from midbrain damage (Cogan, 1964; Holmes, 1921) led to the persisting notion that the SC was involved in the control of vertical gaze and reflexive or automatic eye move-

ments. The contradiction between prevailing concepts of collicular function and actual lesion data gave Pasik and colleagues (1966) the impetus to conduct the first systematic study of collicular lesions via direct measurements of eye movements. The effects of unilateral and bilateral collicular lesions were studied in 12 macaque monkeys. The animals were given a general postoperative neurological examination and subjected to tests for spontaneous eye movements; pursuit of visual, auditory and somatosensory stimuli; optokinetic nystagmus and afternystagmus; vestibular nystagmus induced by irrigation of the canals; and oculocephalic reflexes. Eye movements associated with optokinetic and vestibular nystagmus were measured with electrooculograms. The conclusion reached from these experiments was that neither bilateral nor unilateral ablation of the SC had any permanent effects on any of the measures of oculomotor function examined, and that 'the superior colliculi in the monkey are dispensable structures for conjugate gaze, including ocular deviations in the vertical plane, no matter what type of eye movements are considered, namely, spontaneous, pursuit, fixation, optokinetic and vestibular nystagmus' (Pasik et al., 1966).

In contrast to these negative findings concerning the effects of collicular lesions on eye movements are reports of profound orientation deficits (i.e., contralateral sensory neglect or hemi-inattention) following collicular ablation in the monkey (Denny-Brown, 1962; Latto, 1977; Milner et al., 1978; Collin and Cowey, 1980; Albano et al., 1982), cat (Sprague and Meikle, 1965; Sprague, 1966; Flandrin and Jeannerod, 1981), tree shrew (Casagrande et al., 1972; Casagrande and Diamond, 1974; Raczkowski et al., 1976), rat (Goodale and Murison, 1975; Goodale et al., 1978) and hamster (Schneider, 1970; Mort et al., 1980). Contralateral neglect manifests itself in a tendency to ignore stimuli on the side contralateral to the lesion, and to orient toward ipsilateral stimuli, even though the animal is able to detect the stimuli and can orient toward them if necessary (Wurtz and Goldberg, 1972b; Schiller et al., 1980; Mohler and Wurtz,

1977; Albano and Wurtz, 1982). It must be noted that this orientation deficit was not observed following ablation of the superficial SC, but was shown to be associated exclusively with damage to the deep collicular compartment (Raczkowski et al., 1976). On the other hand, deficits in form and pattern discrimination and visual search (Anderson and Symmes, 1969; Sprague et al., 1970; Berlucchi et al., 1972; Casagrande and Diamond, 1974; Raszkowski et al., 1976; Tunkl and Berkley, 1977, 1985; Latto, 1978; Cardu et al., 1980; Kurtz et al., 1982) may be attributable to the involvement of the superficial SC in the lesion (Casagrande et al., 1972; Raczkowski et al., 1976). The differential effects of deep versus superficial collicular lesions are a further demonstration of the functional distinction between the two divisions of the SC, in addition to the anatomical and physiological differences reviewed in sections 2 and 3.

The discovery by Wurtz and Goldberg (1971) that neurons in the deeper layers of the SC discharge before saccadic eye movements stimulated renewed interest in the effects of collicular lesions on eye movement parameters. In a follow-up experiment, Wurtz and Goldberg (1972b) made focal lesions in specific collicular areas in which they had recorded from neurons that discharged before saccades with particular amplitudes and directions. These restricted lesions increased the latency of visually triggered saccades in the movement fields of the lesioned neurons by 100–200 ms without affecting eye movements to visual targets in other regions of the visual field. The velocity and accuracy of saccades were apparently not impaired, and the latency deficits disappeared after 1–7 weeks. The basic findings of these experiments were subsequently replicated in numerous experiments studying the effects of chronic collicular lesions on the oculomotor behavior of monkeys. The deficits observed include: increases in saccadic latency and decreases in amplitude (Mohler and Wurtz, 1977; Schiller et al., 1979, 1980; Kurtz and Butter, 1980; Albano and Wurtz, 1982; Keating et al., 1986); reductions in the frequency and accuracy of saccades (Cardu et al., 1975; Mohler and Wurtz, 1977; But-

ter, 1979; Schiller et al., 1980; Kurtz and Butter, 1980; Albano and Wurtz, 1982; Albano et al., 1982); and reduced saccadic velocity (Schiller et al., 1980; Kurtz and Butter, 1980). Further, colliculectomized monkeys were found to be reluctant to make large eye movements and exhibited deficits in fixating eccentric targets (Keating, 1974; Latto 1977; Butter et al., 1978; Kurtz and Butter, 1980; Albano and Wurtz, 1982; Albano et al., 1982; Kurtz et al., 1982; Keating et al., 1986). Another frequently reported abnormality in monkeys and tree shrews with collicular ablations is a 'vacant stare' or 'fixed gaze' (Denny-Brown, 1962; Anderson and Symmes, 1969; Casagrande et al., 1972; Casagrande and Diamond, 1974; Keating, 1974; Cardu et al., 1975; MacKinnon et al., 1976; Raczkowski et al., 1976; Butter, 1979; Kurtz and Butter, 1980; Lawler and Cowey, 1986). It has been suggested, however, that several of the deficits resulting from chronic collicular lesions may be attributable to damage of oculomotor structures adjacent to the SC, such as the pretectum and thalamus. For example, Albano and Wurtz (1982) proposed that the deficit in saccadic accuracy interpreted by them as 'an inability to match accurately the position of the eye to visual targets' was most likely due to damage to the pretectum and posterior-medial thalamus. Further, they hypothesized that 'nuclei in the pretectum and posterior-medial thalamus may be the critical structures in producing this deficit, possibly because of their interconnections with the superior colliculi and frontal eye fields' (Albano and Wurtz, 1982). Indeed, eye position deficits and decreases in ocular range similar to those described by Albano and Wurtz (1982) were also found by Keating et al. (1986) to result from lesions of the SC and pretectum/thalamus, one of which was restricted entirely to the pretectum and thalamus. However, Keating et al. (1986) reported that lesions limited to the SC were associated with eye position deficits along the horizontal axis, while pretectal/diencephalic pathology was related to eye position deficits along the vertical axis. Another oculomotor deficit, a 'vacant stare' or 'fixed gaze', has likewise been described as a consequence of lesions limited to the SC (Keating,

1974; Schiller et al., 1980; Kurtz and Butter, 1980) as well as of lesions restricted to the pretectum and/or posterior thalamus (Lawler and Cowey, 1986). The latter authors interpreted this deficit as diplopia due to faulty vergence (misalignment of the visual axes) and compared their findings to previous reports of diplopia and impaired stereopsis resulting from tectal and pretectal damage (Lawler, 1981; Cowey et al., 1984). Unfortunately, the pretectal and thalamic lesions of Lawler and Cowey (1986) were combined with lesions of the FEF, and thus it cannot be said definitively which of the lesions is responsible for the vergence abnormalities. Similarly inconclusive is the evidence concerning the anatomical correlate for the deficits in looking to eccentric targets, as this abnormality has been observed following collicular ablation including the pretectum/posterior-medial thalamus (Albano and Wurtz, 1982) as well as lesions limited to the SC (Butter et al., 1978; Keating, 1974; Kurtz and Butter, 1980; Kurtz et al., 1982). However, the question of whether damage to the SC or the pretectum/thalamus or to both is responsible for deficits in looking to peripheral targets cannot be answered until a definitive study has been conducted in which lesions are restricted entirely to pretectal and/or thalamic structures. In the latest attempt at this type of experiment (Keating et al., 1986), a pretectal/thalamic lesion not involving the SC was placed in only one of 10 monkeys.

It is obvious from this brief review that some of the evidence derived from chronic collicular lesion studies is inconclusive, if not confusing, and that this technique has considerable drawbacks. The most serious of these problems is that it is difficult to limit the extent and location of a chronic collicular lesion precisely; that lesions intended to be unilateral are often partially bilateral, and intended bilateral lesions usually are only partially so; and that chronic collicular lesions frequently involve adjacent oculomotor areas. Furthermore, ablation of the SC inevitably disrupts afferent and efferent connections with sensory and motor systems (e.g., projections from the FEF; ascending collicular projections to thalamic nuclei, which in turn connect

the SC with neocortical areas and the basal ganglia; and descending projections to premotor and motor areas in the brainstem and spinal cord). It is only logical that the number, types and severity of deficits will differ with the number, types and extent of different oculomotor structures involved in a collicular lesion. Another problem associated with the chronic collicular lesion studies reviewed above is that different testing paradigms were used to assess the effects of these lesions on the behavior of animals. For example, most behavioral testing procedures involve arm, hand and finger movements in monkeys (Keating, 1974, 1976; Mohler and Wurtz, 1977; Butter et al., 1978; Schiller et al., 1980; Albano and Wurtz, 1982; Albano et al., 1982; Lawler and Cowey, 1986) or paw movements in cats (Vievard et al., 1986), in addition to employing different types of eye movement task. Localization of a visual target using eye movements (i.e., looking at the target) involves a different type of motor behavior and, thus, different neural circuits than does localization of a visual target using limb movements (i.e., reaching for the target, which includes looking at it). Obviously, it is difficult if not impossible to make generalizations about the effects of collicular lesions when each experiment uses a different measure of orientation and/or oculomotor behavior.

In view of the difficulties encountered in making chronic lesions, it is encouraging to note that more precise information concerning collicular function in oculomotor behavior can be obtained with the use of a new technique, the placement of reversible lesions. This technique permits the temporary inactivation of a specific set of collicular neurons following identification by recording and/or stimulation. In this manner, deficits in saccadic eye movement parameters can be assessed immediately following incapacitation, before compensation can occur, and without involving other oculomotor structures or major pathways. Using this new technique of reversible inactivation, Hikosaka and Wurtz (1983, 1985a) recently observed deficits in the latency, accuracy and velocity of visually triggered saccades following intracollicular injections

of muscimol (a GABA agonist). Latencies were increased by >300 ms, and saccades were grossly hypometric. The effects were restricted to the movement field of collicular neurons located in the area of the injection site. Similar findings were reported on the basis of more recent experiments in which reversible collicular lesions were made with injections of the local anesthetic lidocaine (Hikosaka and Wurtz, 1986). In these studies, the velocity and amplitude of saccades into the affected movement field were reduced, and saccadic latency was increased. Hikosaka and Wurtz (1983, 1985a, 1986) noted that the deficits in saccade metrics observed by them following reversible inactivation were more severe than the deficits reported to result from chronic collicular lesions. This effect is undoubtedly due to the fact that in chronic lesions, other oculomotor structures have time during the postoperative recovery period to take over the function(s) lost by ablation of the SC.

Thus, as is evident from the results of experiments with lesions restricted to the SC, this structure alone is not essential for the occurrence of saccadic eye movements. The major deficits observed are an increase in saccadic latency, a decrease in the frequency and the velocity of saccades, and a small reduction in saccadic accuracy, particularly for stimuli in the peripheral visual field. However, as demonstrated by the results of the most recent studies examining the effects of reversible focal lesions of the deep SC, this structure appears to be crucial for the accurate computation of saccade direction, amplitude and velocity.

4.2. Effects of combined cortical and collicular lesions

The effects of lesions of the striate cortex or the SC or combined cortical and collicular lesions on the detection of visual stimuli and the accuracy of saccades were examined by Mohler and Wurtz (1977). Immediately after focal lesions of the striate cortex, monkeys were no longer able to detect the onset of a visual stimulus in the region of the visual field represented by the lesioned area, or to make saccades

to targets in the area of the scotoma. If the targets were made brighter, however, monkeys with striate cortex lesions did detect and make saccades of normal latency and accuracy to stimuli in the affected area. On the other hand, animals with lesions of the SC alone exhibited no deficits on the detection task. Concurring with the results of earlier studies (Wurtz and Goldberg, 1972b), however, increased latencies and small deficits in accuracy were observed during saccade trials. In contrast to the relatively minor deficits incurred by either striate cortex or SC lesions alone, combined cortical and collicular lesions resulted in blindness in the portion of the visual field represented by the joint lesions. Moreover, the performance of the monkeys on either the detection or the saccade task did not improve during 15 weeks of postoperative testing. Mohler and Wurtz (1977) concluded that visual detection and visually guided saccadic eye movements can be mediated either by the striate cortex or the SC. Furthermore, the functional integrity of either of the two is not only sufficient but necessary, because combined lesions of both structures result in permanent deficits in the ability to detect and to make saccadic eye movements to visual targets.

The effects of lesions of the frontal eye fields (FEF) and the SC, as well as combined lesions of both structures, on saccadic eye movements and fixation patterns were investigated by Schiller et al. (1979, 1980). In these experiments, monkeys were trained to reach for and remove pieces of apple arranged in various positions on a board while eye position and saccades were measured. Unlesioned animals looked to the locations of the apple pieces during the task. Unilateral and bilateral lesions of the FEF resulted in relatively minor temporary deficits in eye movements, whereas collicular ablation reduced the frequency and velocity of saccades and the accuracy of fixation. Combined lesions of the FEF and SC, on the other hand, produced severe and relatively permanent deficits. For example, the monkeys with double lesions were virtually unable to make visually triggered saccades; the range of the residual eye movements was drastically reduced, as were the frequency and velocity of saccades and the

fixation accuracy; and little recovery was observed over time. However, the failure to look at the apple pieces during performance of the task was apparently not attributable to a deficit in general attention or motivation because the animals still reached for and removed the apple bits. Schiller and colleagues noted, however, that the monkeys with combined lesions retained the ability to make a few saccades confined to a small area around the primary position, but these residual movements were thought to be due to incomplete lesions.

4.3. Parallel circuits for the control of saccades

The results of the experiments involving cortical or collicular lesions described above suggest that neither the visual cortex, nor the FEF, nor the SC alone is necessary for the generation of visually triggered saccadic eye movements. These results also suggest that saccades to visual targets may be controlled by parallel pathways. This suggestion is given further credence by the results of a study in which both the FEF and the SC were stimulated simultaneously (Schiller et al., 1979); the resultant saccadic eye movements were found to be the weighted average of the saccades elicited with stimulation of either the FEF or the SC alone. Schiller and colleagues proposed that the averaging may possibly take place in the pons. This seems a very plausible suggestion in view of anatomical evidence showing projections of both the FEF and the SC to the saccade generator in the brainstem, the paramedian pontine reticular formation (Schnyder et al., 1985; Huerta et al., 1986).

The existence of parallel pathways in the control of visually triggered saccades is not surprising in view of the fact that, in a complex visual environment, the oculomotor system is capable of generating visually triggered saccades based on information about the size, shape, hue and other properties of visual targets (Sparks and Pollack, 1977). It is unlikely that exactly the same subset of visual and supranuclear oculomotor neurons is involved in each of these tasks. For the generation of visually evoked saccades, the oculomotor system draws on

the analytical ability of various visual 'channels' (depending on the contingencies of the current task) to compute the spatial coordinates of the target. The elimination of any one of these 'channels' by the ablation of a single neural structure is unlikely to incapacitate the system because most tasks can be solved with alternative strategies and other computational elements (Sparks and Pollack, 1977).

It is also highly unlikely that any one of these parallel pathways is completely redundant; however, the specific contributions of individual components of the parallel circuits have thus far not been determined. To date, the effects of lesions on oculomotor capabilities have been assessed via relatively limited behavioral tasks, such as looking to a single dot in an otherwise blank field. The accuracy of saccades requiring integration of signals from more than one modality has not yet been examined. Other questions as yet unanswered are how lesions of the SC affect the ability of animals to select one of several simultaneously presented stimuli, to make saccades to a remembered target, or to make predictive saccadic eye movements.

On the basis of the observations made following combined SC and striate cortex lesions and combined SC and FEF lesions, it would appear that the corticotectal oculomotor pathway is through the FEF. However, experiments investigating the effects of collicular ablation on eye movements induced by cortical stimulation do not support this conclusion. Following unilateral ablation of the SC, Schiller (1977) found that saccades could no longer be evoked by stimulation of ipsilateral visual cortex, whereas stimulation of contralateral visual cortex and either of the FEF still elicited normal eye movements. Keating et al. (1983) concurred with these results and found, additionally, that eye movements produced by electrical stimulation of prestriate cortex and the 'eye fields' of the inferior parietal cortex were also abolished by collicular lesions. Thus, if visual cortical areas have access to oculomotor circuitry through the FEF, the existence of this alternative pathway is not revealed by microstimulation. Clearly, very little is known at present about the exact anatomical circuitry under-

lying the various parallel routes available for the translation of visual signals into commands for saccadic eye movements.

4.4. Summary and conclusions

In view of repeated demonstrations that animals with collicular lesions can generate saccades to visual targets (see above), the question arises whether or not the SC contributes significantly to visually guided eye movements in the unlesioned animal. One of the more prominent and consistently observed consequences of collicular lesions is an increase in the latency of visually triggered saccades. This finding implies that the SC of the normal animal is involved in initiating saccades with normal latency. Other, longer-latency pathways apparently take over the function(s) of the SC in its absence. In this context, it is interesting to note that, while the latency of FEF stimulation to saccade onset is shorter than that of SC stimulation to saccade onset (Robinson, 1972), the visual activation of FEF neurons occurs with a longer latency than that of SC neurons (Wurtz et al., 1980). In addition to being involved in saccadic latency, the SC also plays a role of central importance in the accurate computation of saccade direction, amplitude and velocity, as shown by the results of the most recent studies using reversible focal lesions. Thus, the findings obtained from lesions restricted to the SC lend firm support to the hypothesis that the SC plays a crucial role in the generation of normal saccades. In the absence of the SC, other brain regions will eventually compensate for the behavioral deficits. But before this occurs, parallel pathways (involving such areas as the FEF and visual cortical areas) are unable to generate accurate saccades with short latencies. Presumably the parallel circuits require time and practice to compensate for the normal role of the SC in the control of visually triggered saccades (Hikosaka and Wurtz, 1983, 1985a, 1986).

5. Role of the SC in models of the saccadic system

5.1. Models of the saccadic system

Most current models of the saccadic system (Robinson, 1975; Zee et al., 1976) assume that visual targets for saccadic eye movements are localized in spatial (i.e., head or body), rather than retinocentric, coordinates. These models assume that (with the head stationary), a signal of retinal error (the distance and direction of the target image from the fovea) is combined with a signal of the position of the eyes in the orbit to produce a representation of target position with respect to the head. After a delay, a signal of the current eye position (derived from a copy of the motor command to move the eye) is subtracted from the signal of the target position in head coordinates, resulting in a signal of the distance and direction of the required eye movement (saccadic motor error). Neural circuits located in the brainstem are thought to perform the computations required to translate the saccadic motor error signal into commands appropriate for each of the extraocular muscles. Neurons located in the pontine and medullary reticular formation are thought to generate the signals responsible for the horizontal component of saccadic eye movements while neurons in the rostral midbrain are thought to generate the commands for the vertical components (see chapter 3 of this volume for further details).

The earliest model of the brainstem pulse/step generator was the local feedback scheme proposed by Robinson (1975). The model only considers horizontal saccades and is based upon the properties of cells found in the pontine reticular formation: medium-lead burst neurons (MLBs); omnipause neurons (OPNs); and tonic neurons (TNs). MLBs generate a high-frequency burst before ipsilateral saccades. Omnipause neurons (OPN) fire at a relatively constant rate during fixation and pause during saccades in all directions. It is assumed that OPNs exert a powerful inhibition upon MLB neurons, since electrical stimulation in the vicinity of OPNs prevents the occurrence of sac-

cadic eye movements. The arrival of a trigger signal that briefly inhibits pause cells would allow burst neurons to begin their high-frequency burst. TNs discharge at a frequency proportional to horizontal eye position and are thought to provide the step component of motoneuron firing. It is assumed that the firing of TNs represents the output of a neural integrator that converts the saccadic pulse into a step signal.

According to the model, there are two inputs to this brainstem circuit: a signal of the desired position of the eyes and a trigger signal. An important feature of the model is that the input which specifies the saccade metrics does so by providing a signal of final eye position in the orbit and not the required displacement of the eyes. Saccades are initiated by a trigger signal that briefly inhibits the OPNs, permitting the MLB neurons to discharge at a rate proportional to horizontal motor error (the difference between desired horizontal position and an internal estimate of current horizontal eye position). The pulse of activity generated by MLB neurons is transmitted directly to motoneurons and to a neural integrator (NI). The NI converts the pulse into a step of activity that is sent to motoneurons and used as the estimate of current horizontal position. Once activated, this circuit drives the eyes at a high velocity until the representation of current horizontal position matches the desired horizontal position signal. At that point, the eyes stop on target, and the pause cells are allowed to resume firing, thereby inactivating the saccadic generator until a new trigger signal arrives.

It has been hypothesized (Sparks, 1978) that saccade-related burst neurons (SRBNs) serve as a trigger input to the pontine pusle/step generator. SRBNs are characterized by low levels of spontaneous activity and a discrete high-frequency burst of activity before saccade onset (Sparks, 1978). Consistent with the features of the trigger signal, the high-frequency burst of these neurons is tightly linked to saccade onset and precedes saccade onset by an appropriate time, approximately 20 ms (Sparks, 1978); and their discharge signals saccade onset, not saccade direction, amplitude or dura-

tion. This suggestion is supported by Keller's (1979) observations that 10 of 10 saccade-related burst units recorded in the SC were antidromically activated by stimulation of the region of the paramedian pontine reticular formation containing pause units. Only 1 of 11 other collicular neurons with saccade-related discharges, but lacking the high frequency burst, was antidromically activated by paramedian pontine reticular formation stimulation.

5.2. Transformations of collicular signals required by models of the saccadic system

What transformations of collicular signals are required to interface the colliculus with the pulse/step generators? First, separate pulse/step generators exist for the control of the horizontal and vertical components of a saccade. But the activity of a single neuron in the SC may be related to both horizontal and vertical components of saccades. Thus, separate signals of horizontal motor error and vertical motor error must be extracted from the anatomical map of motor error found in the colliculus. Secondly, the separate signals of horizontal and vertical motor error must be coordinated in order to produce oblique saccades. Oblique saccades usually have straight (rather than curved) trajectories because the onsets of the horizontal and vertical pulses are synchronized and the durations of the horizontal and vertical displacements are approximately equal even if the amplitude of the horizontal displacement is twice that of the vertical displacement. This suggests (van Gisbergen et al., 1985) that a signal of the velocity of the combined movement (vectorial velocity) is computed (perhaps at the level of the SC; see above) and later decomposed into separate velocity signals for the horizontal and vertical components (component velocity). Thirdly, signals that compensate for the origin and endpoint of a saccadic eye movement may be needed to supplement the collicular signal. Saccades to visual targets compensate for the initial and final position of the eye in the orbit, and the cerebellum appears to be involved in the generation of signals that compensate for the position-depend-

ent viscous and elastic forces imposed on the eye (Ritchie, 1976). Apparently, these compensatory signals are not added when saccades are produced by collicular stimulation (Segraves and Goldberg, 1984; Gerez and Sparks, unpublished observations).

With respect to Robinson's model of the horizontal pulse/step generator, note that the input needed is a signal of the desired absolute horizontal position of the eye in the orbit. However, saccade-related activity in the SC specifies the change in eye position required for target acquisition. Robinson's model does not specify how the desired horizontal position signal is formed; but the formation of a signal corresponding to desired eye position requires additional processing. Collicular neurons generate commands for changes in eye position or desired displacement, rather than commands to move the eyes to a particular position in the orbit. Thus, the formation of a signal of desired horizontal position requires that the saccadic motor error signal found in the SC be decomposed into appropriate horizontal and vertical components and that an estimate of the current horizontal position be added to a signal of the desired horizontal displacement.

Modifications of Robinson's model have been proposed by several investigators (Becker and Jurgens, 1979; Keller, 1981; Hepp and Henn, 1982; Fuchs et al., 1985; Tweed and Vilis, 1985). In part, these modifications were attempts to design a more parsimonious model that does not require the addition of eye position signals to the displacement signals observed in the superior colliculus and frontal eye fields. Accordingly, a common characteristic of these alternative models is that MLB neurons are driven by a signal specifying the desired change in eye position rather than a signal of the desired absolute position of the eye in the orbit. With this modification, the motor error signals found in the frontal eye fields and SC need not be combined, again, with a signal of eye position to form a signal of desired eye position. A second neural integrator, reset after each saccade, is added to provide feedback about the change in horizontal position. The MLBs are driven by the difference in this signal and a signal of

the desired change in eye positon. The role of signals observed in the SC for these models is considered in more detail elsewhere in this volume (chapter 3).

6. Summary and conclusions

The evidence is compelling that the deep layers of the SC are involved in the translation of sensory signals into motor commands for the control of saccadic eye movements. The deep layers receive inputs from brain areas involved in the analysis of stimuli (visual, auditory and somatosensory) used to guide orienting movements. Patterns of activity recorded from collicular neurons are appropriate for the initiation and direction of saccades, and neurons carrying these signals are organized topographically, forming a map of motor (saccadic) space. Efferent projections from the deep layers are to brainstem nuclei having direct or indirect connections with motoneuron pools innervating extraocular muscles. Finally, reversible inactivation of neurons in the deep colliculus severely impairs the ability of animals to generate accurate saccades.

Major gaps in our knowledge of the anatomical and functional organization of the SC remain. The physiological signals conveyed to the SC over afferent pathways are, for the most part, unknown. The intrinsic organization of the SC is poorly understood; and the question of whether or not there is extensive communication between neurons in the superficial and deep divisions has not yet been resolved. Very little is known about the morphology, location or physiological response properties of the cells of origin of the major efferent pathways; and the neural circuits involved in decoding information about the direction, velocity and amplitude of saccades (contained in the spatial and temporal pattern of neural activity of collicular cells) are still unspecified.

In general, the contribution of the sensory responses of deep collicular neurons to the initiation of orienting movements is unknown. There is no experimental evidence that the activity of deep collicular neurons responsive to sensory stimuli is either necessary or sufficient for the generation of the motor signals observed in the SC, and patterns of connections within the SC specifically involved in the translation of sensory signals into motor commands have not been identified.

The alignment (in anesthetized or paralysed animals) of auditory, somatosensory and visual maps in the SC has influenced thinking about the process of sensorimotor integration. It is commonly assumed that the deep division of the SC contains topographical maps of sensory space – i.e., a point in the space surrounding the animal is represented by neurons residing at a particular location in the SC. It is assumed, further, that sensory signals from different modalities originating from the same point in space activate a common pool of collicular neurons located within this representation. The activation of these sensory neurons, in turn, is hypothesized to initiate motor responses resulting in orienting movements toward the source of the stimuli. These hypotheses have not yet been formalized into a model of collicular function and many of the assumptions remain implicit and untested.

An alternative view, the working hypothesis of the author's laboratory, is that sensory signals observed in the deep colliculus are organized in motor (not sensory) coordinates. The motor map is thought to be fixed. This demands a transformation of sensory signals into signals in motor coordinates – specifically, into signals specifying the change in eye position required to orient to the stimulus. Sensory-induced activity in the deep SC is viewed as a representation of the trajectory of the movement required to look to a target rather than a representation of the target's location in space. Thus, the sensory maps are dynamic and the receptive fields of collicular neurons are expected to shift with relative movements of the eyes, head and body. Many questions are raised by this hypothesis. For example, are dynamic maps of sensory space, found in the deeper layers of the monkey colliculus, also present in animals with more limited oculomotor ranges? and what is the anatomical and physiological basis of the dynamic mapping?

Finally, new and/or improved models of the role of the SC in the generation of saccadic command signals are needed as guides for future research.

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Addendum. Several important papers related to this issue have appeared since completion of the manuscript of this review: Mooney et al. (1988) J. Neurosci. 8, 1384–1399; Moschovakis et al. (1988) J. Neurophysiol. 60, 232–262 and 263–302.