

THE UNIVERSITY OF CALGARY

A 2-DEOXY-D- $[^{14}\text{C}]$ GLUCOSE EXAMINATION OF THE VISUALLY DECORTICATE
RAT SUPERIOR COLLICULUS

by

Perry Bryan Glimpel

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PERRY BRYAN GLIMPEL, 1988

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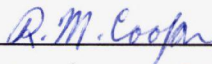
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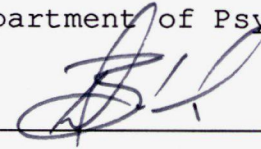
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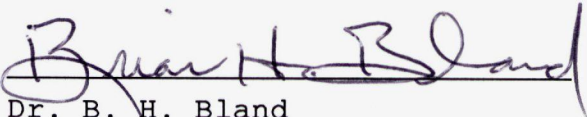
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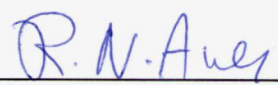
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ABSTRACT

The 2-deoxy-D-[^{14}C]glucose (2-DG) technique was used to assess glucose consumption in the superior colliculus (SC) of the visually decorticate rat under several visual conditions. Experiment I supported previous work indicating that SC consumption is reduced following a cortical ablation and also revealed that temporarily depressed cortex lying outside of the lesion area may add to the reduction, particularly in the deeper layers of the SC. In addition, Experiment I, which involved several groups tested in darkness at different postoperative intervals, demonstrated that there was considerable recovery from the initial reduction in SC glucose uptake. Experiment II was similar except that the animals were tested only at short (48 h) and long (30 day) postoperative intervals and during exposure to moving gratings and diffuse light. Apart from the alteration in baseline activity which had been observed in the rats tested in darkness, however, Experiment II showed nothing more than that the gratings and diffuse light had their normal effects of elevating and decreasing SC glucose uptake, respectively. Experiment III, the purpose of which was to determine whether the recovery following a visual cortex (VC) ablation involves increased metabolic control by retinal ganglion fibers, indicated that the recovery does not involve an increased dependence on retinal afferents.

The depression occurring in the SC after VC ablation is consistent with the position proposed by some investigators that cortex has a general facilitatory influence on SC excitability. The failure, however, to find a change in the way in which gratings and diffuse light affect SC glucose uptake also raised the possibility that the uptake of 2-DG reflects primarily the activity of afferent nerve terminals, not the activity of units intrinsic to the SC. Experiment IV provided a test of this possibility by first severing the

tectal commissural pathway, thus eliminating putative reciprocal inhibitory pathways connecting the two colliculi, and then by making a unilateral VC lesion 1.5 months later. The intertectal asymmetry in glucose uptake in these rats was less than in rats without the commissural section, suggesting that in fact the 2-DG procedure assesses the activity of tectal units as well as incoming activity.

The study most convincingly suggests that retinal and cortical afferent pathways contribute independently to SC glucose utilization as measured by the 2-DG technique. It is also consistent with the position that the nature of cortico-tectal control is broadly facilitatory and that tecto-tectal interactions are inhibitory.

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Chapter 1

Overview

Using a modification of the 2-deoxy-D-[^{14}C]glucose (2-DG) technique developed by Sokoloff and his collaborators (Kennedy et al., 1975), several studies have shown that the superior colliculus (SC) alters its metabolic activity in response to a variety of visual stimulation conditions. For example, when rats are exposed to patterned visual stimuli or moving gratings, the metabolic activity of the SC increases (McIntosh and Cooper, 1988; Rooney and Cooper, 1988), and when rats are exposed to diffuse light stimuli, the metabolic activity of the SC decreases (Rooney and Cooper, 1988). In addition, the metabolic activity of the SC also changes following optic nerve section (Cooper and Thurlow, 1985; Kennedy et al., 1975) and unilateral VC ablation even in the absence of visual stimulation (Thurlow and Cooper, 1985).

These findings suggested that a 2-DG study of the visually decorticated SC under several visual conditions might yield information regarding cortical-tectal interactions. Chapters 2-5 of this thesis describe the results of such a study. This study yielded information regarding not only cortical-tectal interactions but also information regarding the 2-DG technique itself. However, before moving on to Chapters 2-5, the relevant anatomy and physiology of the SC will be briefly reviewed in the next two sections of Chapter 1. The final section of Chapter 1 will be devoted to a discussion of the 2-DG technique.

Section 1: Anatomy of the Rat Superior Colliculus

The following section describes the anatomical connections of the rat SC, with particular emphasis on retino-tectal, cortico-tectal, and tecto-tectal projections.

Efferents from the Superior Colliculus. The superior colliculus (SC) of the rat is composed of eight layers or "strata." The superficial layers include the most

dorsal layer called the stratum zonale (SZ), the layer just ventral to the SZ called the stratum griseum superficiale (SGS), and the layer ventral to the SGS called the stratum opticum (SO). The stratum griseum intermediale (SGM) lies just ventral to the SO, and is the first of what are called the deep layers of the SC. In turn, the stratum album intermediale (SAI) lies just ventral to the SGM, the stratum griseum profundum (SGP) lies just ventral to the SAI, the stratum album profundum (SAP) lies ventral to the SGP, and the stratum griseum et stratum fibrosum periventricular lies ventral to the SAP.

The superficial and deep layers of the SC project directly to several subcortical nuclei. It has been demonstrated that the SC projects ipsilaterally to the lateral geniculate nucleus pars dorsalis (LGNd) (Mackay-Sim, Sefton, and Martin, 1983; Reese, 1984), the nucleus of the optic tract, the nucleus of the inferior brachium of the SC (Takahashi, 1985), and to a region surrounding much of the cortico-spinal nucleus of the pons (Waldron and Gwyn, 1969). From the various layers in the SC, there are also projections to the ipsilateral and contralateral lateral geniculate nucleus pars ventralis (LGNv) (Mackay-Sim et al., 1983; Pasquier and Villar, 1982; Perry, 1980; Swanson, Cowan, and Jones, 1974), nucleus suprageniculatus, posterior pretectal nucleus (Takahashi, 1985), and the lateral posterior nucleus (LPN) (Mason and Groos, 1981; Perry, 1980).

The evidence for an intercollicular pathway in the rat rests primarily on its existence in other species such as the cat, hamster, and pigeon. In the cat, the rostral portions of the superior colliculi project heavily to one another (Edwards, 1977; Maeda et al., 1979, as cited in Fish et al., 1982; Magalhaes-Castro, et al., 1978). Fish et al. examined the intercollicular connection in the hamster, and found that layers below the SO in the rostral portion of the

SC contain intertectal neurons that terminate in the corresponding region of the contralateral SC. Fish et al. also found evidence for a minor contralateral projection to SGS. Using electrophysiological techniques, Robert and Cuenod (1969a; 1969b) examined the intertectal commissures of the pigeon and concluded there is an inhibitory interaction between the two superior colliculi via this pathway. Sprague (1966) provided physiological (but not anatomical) evidence for the existence of intercollicular connections by demonstrating that cats suffering unilateral hemianopia after a contralateral posterior cortex removal showed recovery after the SC contralateral to the damaged cortex was destroyed. The hemianopia could also be reversed by sectioning the intertectal commissure. Goodale (1973) reported an electrophysiological correlate of this recovery effect in the rat. Sherman (1974, 1977) has replicated the "Sprague effect" in the cat. All this data is suggestive of an inhibitory intertectal connection in the rat.

Afferents to the Superior Colliculus. The major afferent system of the SC is the optic tract (Huber and Crosby, 1943). Swanson et al. (1974) found that retinal input was confined to the three superficial layers, the SZ, SGS, and SO. Beckstead and Frankfurter (1983) however, found evidence for a direct monosynaptic projection from the retina to the SGM of the SC. Although the projections to the SGS and SO appear to be more numerous, the projection to SGM extends throughout its full rostro-caudal extent, and is homogeneous mediolaterally, with only a slightly more dense projection to the medial portion of the SC. It is also quite clear that this projection is fully crossed in all layers of the SC, as Beckstead and Frankfurter found very few, if any, projection fibers in any layer of the ipsilateral rat SC.

The SC also receives projections from the ipsilateral LGNv (Legg, 1979; Ribak and Peters, 1975; Swanson et al.,

1974), the ipsilateral and contralateral parabigeminal nucleus (Pasquier and Tremazzini, 1979; Stevenson and Lund, 1982a; Stevenson and Lund, 1982b), the locus coeruleus and dorsal raphe nucleus (Stevenson and Lund, 1980; Watanabe and Kawana, 1976), and the substantia nigra pars reticulata (Beckstead, Domesick, and Nauta, 1979; Hopkins and Niessen, 1976; Pasquier and Tremazzini, 1979; Wright and Arbuthnott, 1981).

Although there is no evidence that the SC sends projections directly to visual cortex (VC), there is ample evidence that the SC receives projections directly from VC. Von Monakow (1889, as cited in Nauta and Bucher, 1954) found that part of the occipitotectal projection of the rat originates in the striate area of VC. Nauta and Bucher (1954) outlined the route taken by cortical projections in reaching the SC. They found that fibers from area 17 enter the external sagittal stratum of the medullary substance. From there, fibers run rostromedially in a broad band that gradually shifts to the internal sagittal stratum. The band then enters the caudal limb of the internal capsule, curving medially in front of the stria terminalis and hippocampal flexure. Then the projections bend caudally, to continue in the lateral quarter of the cerebral peduncle. Whereas a few of these fibers continue caudally to the pons, the majority of the fibers exit the peduncle to innervate the thalamus, subthalamus, pretectal region, and the SC. These fibers enter the lateral geniculate nuclei (LGN) ventrally, either via the optic tract or by traversing the structures between the LGN and the cerebral peduncle. Some of these fibers terminate in the LGNv and the dorsomedial part of the LGNd. Some continue through the LGN to enter the LPN from the lateral side. Fibers in the optic tract continue dorsally in the zonal fiber layer of the geniculate, which becomes the brachium of the SC (BSC). Some of these fibers enter the LPN from the dorsal surface. Many fibers entering the

LPN merely pass through it, destined for the pretectum and the SC, whereas some actually terminate in the LPN, especially the ventrolateral quarter of the LPN. Most of the fibers that enter the pretectum are destined for the SC although some terminate in the pretectum. The fibers enter the pretectum either superficially through the BSC or more deeply through the LPN or even more deeply, through the lateral and caudal aspects of the ventral thalamic nucleus, or through the substance of the ventral thalamic nucleus. The caudal pretectum becomes the SO and SGM of the SC. The SO is also innervated by fibers from the brachium of the SC. The SZ, SGS, SO and SGM are innervated by fibers from striate cortex which terminate mainly in the lateral two-thirds of the SC (Takahashi, 1985). The occipitofugal fibers also terminate in the optic tract and pretectal nucleus profundum.

Goodman and Horel (1966) and Lund (1966) agree with Nauta and Bucher's description of the descending pathways. Olavarria and Van Sluyters (1982) also showed that several separate retinotopic regions of extrastriate cortex (18 and 18a) project to the SC. Area 18 (extrastriate) and area 4 (motor cortex) project to SGM, whereas area 18a projects to the SGS and SO of the SC. Furthermore, Cadusseau and Roger (1985) found evidence that indicated a conspicuous projection to the SC's deeper layers (but above SGP) from somatosensory cortex, and more weakly from auditory cortex.

This brief survey of the literature indicates that the SC is anatomically connected with several other CNS structures. It is clear that the SC receives projections from VC but does not project directly to VC. Therefore, it should be possible to carry out a 2-DG examination of the effects of VC ablation on SC metabolic activity without having to give consideration to the possible effects of retrograde degeneration on the SC. The next section of Chapter 1 emphasizes physiological studies which deal with

the function of cortico-tectal projections.

Section 2: Physiology of the Superior Colliculus

Although evidence for occipito-tectal projections existed before the turn of the century (Von Monakow, 1889; as cited in Nauta and Bucher, 1954), it appears that no comprehensive attempts were made to investigate the nature of cortical-tectal interactions before the 1960's. This was presumably because prior to the 1960's researchers lacked a convenient technique for the investigation of cortical-tectal interactions. However, with the adoption of electrophysiological unit recording techniques, investigations of cortical-tectal interaction began to coalesce in the late 1960's.

Wickelgren and Sterling (1967; 1969a; 1969b; see also Sterling and Wickelgren, 1969) were the first to provide evidence for a specific involvement of occipito-tectal projections in the operation of the SC using the electrophysiological unit recording technique. They studied the receptive-fields of single units in the SC of intact and visually decorticate cats. In intact cats they found that the majority of the receptive-fields of units located in the two most superficial lamina of the SC lay in the contralateral half of the visual field and that the size of a receptive-field ranged from a few degrees near the area centralis to 20° or more in the periphery. Although the contralateral eye was dominant for driving these units, the majority could be binocularly driven. Wickelgren and Sterling also observed that the SC units of intact cats responded best to moving stimuli and poorly to changes in background illumination or to stimuli turned on or off. Most units showed a preference for lines and edges of a particular orientation, and over half showed a preference for movement in a particular direction. Of those that responded best to movement in one direction, 87% preferred movement from the center of gaze toward the contralateral

visual field. In contrast, in cats in which VC had been ablated one to three weeks previously, units in the SC demonstrated no directional or orientational preference and responded briskly to the onset or offset of stationary light spots. Furthermore, binocularly driven cells were absent. Wickelgren and Sterling concluded that orientational and directional preferences as well as binocularity of cat SC units are dependent upon an intact cortico-tectal pathway.

In agreement with their 1967 research, Wickelgren and Sterling (1969a) again reported that there was little or no evidence of directional selectivity in tectal units at 1-4 weeks after cortical ablations or during cortical cooling. Furthermore, spatial summation could be induced in the denervated units, whereas this phenomenon did not occur in intact cats. Wickelgren and Sterling (1969a) also compared the effects of removing just area 17 and the effects of removing just areas 18 and 19 and found no indication that removal of either area was more effective at producing the above results.

Rosenquist and Palmer (1971) also observed a decrease in the percentage of directionally selective units (from 75% to 12%) and a decrease in the proportion of binocularly driven units (from 80% to 17%) in cats where area 17 of cortex had been removed either acutely (1 h to 3 days recovery period) or chronically (26-41 day recovery, and one of 16 months). However, unlike Wickelgren and Sterling (1967;1969a), Rosenquist and Palmer found no decrease in directional selectivity or binocularity after ablation of areas 18 and 19 of VC. Therefore, Rosenquist and Palmer concluded, the directional selectivity and binocularity of SC units are dependent upon the integrity of area 17. Rosenquist and Palmer's study supports Wickelgren and Sterling's claim of a reduction in directional selectivity and binocularity following ablation of VC, but disagrees with Wickelgren and Sterling on the cortical areas that are responsible for the

effect.

Palmer and Rosenquist (1974) provided information that supported the idea that cortico-tectal projections might confer directional selectivity and binocularity to SC receptive-fields. They antidromically stimulated cells in striate cortex of cats by electrically stimulating the SC and then plotted the receptive-fields of the striate cortex units. The units were located in layer V of VC and had complex, large receptive-fields, that were orientation selective, largely directionally selective, and were usually driven equally efficiently by both eyes. One unit, found to reside in area 18, did not differ from the other cortico-tectal units. Therefore, Palmer and Rosenquist's results support the hypothesis that VC may be responsible for some of the receptive-field properties of units in the SC, but suggests that some of these units may reside outside of area 17, thereby raising the question once again of which cortical areas are necessary for conferring receptive-field properties on the SC.

Berman and Cynader (1972) also produced results favoring Wickelgren and Sterling's (1969a) interpretation of the influence of cortex over the SC. They compared the response properties of SC units in Siamese and normal cats and found them to be very similar, although in the Siamese cat the tectal surface that is devoted to the ipsilateral half-field is nearly twice the size of that of normal cats, and in Siamese cats 80% of the units are monocular whereas in the normal cat most units are binocular. In addition, Berman and Cynader reported that visual cortex ablation almost entirely removed directional selectivity in both breeds of cat, and that the visual cortex ablation made the tectal units more responsive to flashing spots. The ablation of VC in normal cats changed the ocular dominance distribution in favor of the contralateral eye, but had no effect on ocular dominance in the Siamese cat. This study substantiates the

findings of Wickelgren and Sterling (1967; 1969a) by demonstrating a loss of directional selectivity in two breeds of cat as a result of VC ablation.

Berman and Cynader (1975) also examined the response properties of units in the superficial layers of the cat SC after unilateral visual decortication (including areas 17, 18, and 19) that supported, for the most part, the claims made by Wickelgren and Sterling (1969a). They recorded from the ipsilateral SC 3 - 225 days after the ablation. Three types of SC units were distinguished on the basis of their visual receptive-field properties. One group of cells (5%) demonstrated concentrically arranged "on" and "off" regions. These units were binocular and would often respond to the onset or offset of diffuse illumination and to strobe flashes. The response latency of these units was between 30 - 50 msec. The second group of cells (12%) had extremely weak surrounds and possessed the capacity to respond to stimuli presented at high frequencies. These units also responded to moving stimuli over an extremely broad range of velocities although they were not directionally selective. The response latency of these units was between 28 - 40 msec. The third group of SC cells (83%) demonstrated a tighter velocity tuning (responded optimally to a more limited range of stimulus velocities) and had suppressive surrounds. These units were not directionally selective and the responsivity of these units to visual stimuli was unreliable. Diffuse strobe flashes had minimal effect on the responses of SC units in intact cats. Therefore, it appears that diffuse strobe flashes are effective only in the decorticated SC. Berman and Cynader noted the presence of binocularly driven units following VC ablation, and in this respect their study conflicts with those of Wickelgren and Sterling (1967;1969a). However, Berman and Cynader did not report the presence of directionally selective units following VC ablation, and in this regard their study is

supportive of Wickelgren and Sterling.

Rhoades and Chalupa (1976) examined the response properties of SC units in the golden hamster for indications of directional selectivity. They reported that 58% of the units were directionally selective. Chalupa and Rhoades (1977), using a statistical criterion, reported that 60.6% of the visually responsive units demonstrated significant directional selectivity. Following acute, unilateral ablations of VC, only 27.5% of the units demonstrated significant directional selectivity. The effect of VC ablation on directional selectivity was confined to the superficial layers. Therefore, Chalupa and Rhoades (1977), largely in agreement with Wickelgren and Sterling's (1969a) findings for the cat SC, concluded that the directional selectivity of many units in the superficial layers of the hamster SC are cortically mediated.

Graham, Berman, and Murphy (1982) examined the effects of unilateral VC ablations on the receptive-field properties of units in the rabbit SC. The rabbits were allowed to recover from the ablation for three days to 3.5 months. Graham et al. reported that following the ablation, a smaller proportion of units in the upper and lower SGS demonstrated habituation and a larger proportion responded well to stationary stimuli. In addition, in the SGS and SGM, a smaller proportion of directionally selective units was found following visual decortication. Graham, Berman and Murphy's study supports Wickelgren and Sterling's (1967; 1969a) claim that VC ablation affects directional selectivity in the SC, and in addition suggests that the effect is not limited to the superficial layers of the SC as Chalupa and Rhoades' (1977) study suggests.

Although there have been several electrophysiological unit recording studies that have supported the findings of Wickelgren and Sterling (1969a), there have also been several unit recording studies that have failed to find that

eliminating VC has an effect on directional selectivity in the SC (Hoffmann and Straschill, 1971; Marchiafava and Pepeu, 1966; Maslund, Chow, and Stewart, 1971; Rizzolatti, Tradardi and Camarda, 1970).

Marchiafava and Pepeu (1966) reported that complete acute ablation of neocortex had no effect on the response properties of SC units in the cat. Marchiafava and Pepeu found evidence for two types of units in the intact cat SC, one type responded to small angular movements of stimuli ($6-12^{\circ}$) while the second type responded to large angular movements ($30-45^{\circ}$). Most of these units were stimulated by visual input through the contralateral eye. Direction and speed of movement of the stimulus were important to units that were movement sensitive. Complete acute ablation of the neocortex had no effect on the response properties of the SC units. Cortex was not viewed by Marchiafava and Pepeu as being responsible for any of the response properties of single units within the SC.

Rizzolatti, Tradardi, and Camarda's (1970) findings are similar to those of Marchiafava and Pepeu (1966). Rizzolatti, Tradardi, and Camarda (1970) removed cortical areas 17, 18, and 19, and the medial half of the suprasylvian gyrus unilaterally in cats and recorded from the SC three to five days following the ablation. In the superficial layers (SGS and SO) of the SC ipsilateral to the cortical ablation, approximately 30.3% were directionally selective, 24.2% demonstrated modest directional selectivity, and approximately 45.5% were not directionally selective. In addition, 30.8% were monocular, preferring the contralateral eye, 69.2% were binocular (46.1% of the binocular units preferred the contralateral eye). In the deeper layers of the SC (SGM and SGP), 85.7% of the SC units were directionally selective, 7.15% had slight directional selectivity, and 7.15% had no directionally selective characteristics. This is comparable to the ratio of

directionally selective and non-directionally selective units found in the deep layers of intact cats. Furthermore, in the deep layers, 84.6% of the units were binocular (30.8% of these preferring the contralateral eye). Although the proportion of directionally selective units in the superficial layers of the SC were lower than the proportion usually reported in intact cats, Rizzolatti et al. concluded that the role of the cortico-collicular pathway is not simply to establish directional selectivity and binocularity in the SC, because these properties remain in the SC in the absence of VC.

Hoffmann and Straschill (1971) also examined the influence of cortico-tectal inputs in the cat. First, they electrically stimulated visual cortex and reported that 87% of the tectal units recorded from were influenced by this stimulation. Hoffmann and Straschill found no correlation between type and latency of the tectal reactions to cortical shock and the presence or absence of directional selectivity. Second, Hoffmann and Straschill assessed such tectal unit characteristics as directional selectivity, spontaneous activity, adaptation, and responsiveness to stationary stimuli in visually decorticate and intact cats, and found no difference between decorticate and intact cats. Finally, Hoffmann and Straschill reported that during cooling of VC, the response characteristics of directionally selective units of the SC to visual stimuli remained unaltered. Hoffmann and Straschill concluded from their results that movement and direction selectivity in the cat SC are not dependent upon input from areas 17, 18, or 19.

Masland, Chow, and Stewart (1971) examined the receptive-field characteristics of neurons in the SC of the rabbit. The rabbit's retina contains ganglion cells with both concentrically organized fields and complex receptive-field properties like directional, orientational, and local contour selectivity. One might expect that some

of these properties might be exhibited by neurons to which these ganglion cells project, such as neurons in the LGNd, LGNv, and SC. Masland et al. found SC cells with concentrically organized receptive-fields, uniform fields, movement selective fields, directionally selective fields, and hypercomplex fields. Masland et al. also described SC units with "indefinite fields," units that showed inhibition of spontaneous activity in the presence of diffuse light. Units with reliable responses and well defined receptive-fields were found almost entirely in the superficial layers of the SC (SZ, SGS, and SO), while units in the deeper layers were more likely to demonstrate rapid adaptation, indistinct fields, and responses to nonvisual stimuli. Masland et al. also studied the influence of VC on the receptive-fields of the SC in the rabbit by examining SC unit responses in rabbits that had VC ablated at least four months previous to the unit recordings. They reported no difference in SC receptive-field properties as a result of VC ablation, and concluded that the receptive-field properties of collicular cells in the rabbit are not dependent on input from neurons of the VC.

The studies of Marchiafava and Pepeu (1966), Rizzolatti et al. (1970), Hoffmann and Straschill (1971), and Maslund et al. (1971) represent some studies that have failed to replicate Wickelgren and Sterling's (1967; 1969a) results, thereby undermining the idea that cortico-tectal projections primarily confer directionally selective and binocular receptive field properties to SC units. Also undermining this idea is the fact that most studies report that not all directionally selective (Berman and Cynader, 1975; Chalupa and Rhoades, 1977; Graham, Berman, and Murphy, 1982; Rosenquist and Palmer, 1971) and binocular (Berman and Cynader, 1975; Rosenquist and Palmer, 1971) receptive fields in the SC are lost following VC ablation. This suggests that cortex is not crucial for conferring these properties

on SC. Units in the SC may have these receptive field properties conferred upon them from sources other than the VC, or the organization intrinsic to the SC may itself be responsible for these properties.

Michael's (1972a;1972b) research suggests that, at least in the ground squirrel, it is the retino-tectal afferents that are responsible for conferring directionally selective receptive fields on the SC. Michael described the visual receptive fields and the functional organization of single units in the SC of the ground squirrel. The ground squirrel has an all-cone retina, and Michael (1972a) claims that of the three types of optic nerve fibers, contrast sensitive (53%), directionally selective (23%), and opponent-color (24%), only the directionally selective units project to the SC. Michael (1972a) claims that within the SC of the ground squirrel there are two types of units: 1) Directionally selective (64%) and 2) Hypercomplex (36%) units.

The directionally selective units can only be driven from the contralateral eye, and their receptive-fields are rectangular in shape. Each directionally selective unit has an antagonistic surround. Spatial summation along the long axis of the spatial field is a characteristic of these units. The units prefer movement in a direction perpendicular to the long axis of the receptive-field. Motion of the stimulus in a direction opposite the preferred direction does not elicit a change in the background rate of spontaneous activity. Michael (1972b) suggested that the directionally selective units of the SC derive their characteristics from the convergence of afferents from several directionally selective ganglion fibers with the same direction of preferred motion.

The hypercomplex units can only be driven from the contralateral eye and only respond to moving stimuli. These units respond optimally to a specifically oriented light or dark bar of a limited length. The central activating region

is flanked on either end by antagonistic suppressive surrounds. The hypercomplex cells are excited by light bars (44%), dark bars (22%), or by edges (29%), whereas a few are excited equally well by light or dark bars (5%). These units have very low rates of spontaneous activity. They respond to movement in a direction perpendicular to the long axis of the receptive-field, and although some demonstrate a directional preference, occasionally both directions perpendicular to the long axis are equally effective. Michael (1972b) suggested that the properties of hypercomplex SC units are conferred upon them by the convergence of at least three complex cortical fibers.

According to Michael's (1972b) hypothesis, at least three complex cortical cells with the same receptive-field sizes and shapes, the same field-axis orientation, and the same stimulus requirements, such as preferred direction of motion, converge on the hypercomplex SC unit. The cortical cells receptive-fields must lie adjacent to one another along a straight line. The cortical afferents will be inhibitory for the antagonistic flanks and excitatory for the central activating region. In support of his hypothesis Michael (1972b) reported that both chronic visual decortication and temporary visual decortication (induced by cortical cooling) results in abolition of responses to visual stimuli by hypercomplex SC units, whereas directionally selective units are unaffected. Michael (1972b) also reported that the SC is organized into vertical columns, and that each unit within these columns has the same directional selectivity and axis orientation. Directionally selective units are located primarily in the superficial layers, and the hypercomplex cells are located primarily in the deeper layers.

Therefore, while not finding evidence for changes in directional selectivity as a result of visual decortication, Michael (1972) does argue that visual decortication results

in the abolition of hypercomplex unit responses in the ground squirrel SC. This suggests that cortical-tectal interactions may determine what stimuli are appropriate for activating certain SC cells, but that directional selectivity and binocularity are not necessarily the only properties that cortex confers upon the SC. Supporting this idea are reports that directionally selective units are rare in the monkey and rat SC (Cynader and Berman, 1972; Humphrey, 1967; 1968), although cortico-tectal projections are known to exist in both species.

Humphrey (1967; 1968) found no evidence for directionally selective units in the intact rat or monkey. Humphrey reported that SC units in the SGS and SO layers of the intact rat form two functionally distinct groups. In the SGS layer, units had circular fields 2° - 15° across that responded with a continuous discharge to slowly moving (5-10 deg/sec) black or white spots. Furthermore, these units gave "on" and "off" responses over the whole field, a characteristic which Wickelgren and Sterling (1967) reported only in the SC of visually decorticate cats. Humphrey reported that in the SO layer, units had oval or irregular fields, 30° - 90° across, and that these fields tended to be patchy, suggesting that they may be conglomerates of smaller fields. Humphrey also reported that units in the SO layer either responded with a continuous discharge to slowly moving stimuli or with a discharge lasting only a few seconds to a stimulus which had entered the field and then stopped. Humphrey also states that there seemed to be a slight preference for dark spots over bright spots.

In the monkey SC, Humphrey (1968) reported that these collicular units were in many respects similar to the rat's collicular units, responding primarily to movement, not directionally selective, and with little spontaneous activity. There were also some important differences however. The monkey SC units did not divide functionally

into two functionally distinct groups. The increase in field size was more progressive than in the rat, without a clear division into small and large receptive-fields. All fields lay in the contralateral visual half-field but none of the large-field units demonstrated patchiness as in the rat. Furthermore, these units responded in regular discontinuous bursts to stimuli moving through the unit's receptive-field, whereas in the rat the response was continuous. Finally, Humphrey noted that in some units, repeated stimulation would result in increased spontaneous activity in units until it would mask stimulus-evoked responses. This occurred in units with rather large fields only.

Cynader and Berman (1972) examined the receptive-field organizations of units in the rhesus monkey and cat SC. They reported that in both species, the units in the superficial layers had homogenous activating regions flanked by inhibitory surrounds. In the superficial layers of both species, units responded best to movement, and were insensitive to details of stimulus shape or orientation. The major difference between the two species was the much greater prevalence of directionally selective units in the cat SC (67%) than in the monkey SC (5%).

The effects of visual decortication on SC receptive fields have also been examined in the rat (Humphrey, 1968) and monkey (Schiller, Stryker, Cynader, and Berman, 1974).

Humphrey (1968) examined the responses of units in the SC of visually decorticate rats (three bilateral, one unilateral and one in which bilateral spreading depression was induced) and found response properties no different than the response properties described for the intact rat. However, Humphrey suggested that before concluding that cortex has no influence on the response properties of collicular units, one should consider the possibility that even in the intact preparations the cortex was rendered not

functional due to spreading depression caused by passage of the electrode through cortex. Humphrey emphasized that this was mentioned as a caveat only, and not as a likely explanation.

Schiller, Stryker, Cynader and Berman (1974) examined the response properties of single units in the rhesus monkey SC after unilateral cortical ablation and during cortical cooling. The monkeys were permitted five to 223 days to recover from the unilateral cortical ablations. In both anaesthetized and alert animals, ablation or cooling of areas 17, 18, and 19 silenced units with visual receptive-fields in the ipsilateral SC ventral to dorsal SO. The units in SGS and dorsal SO were basically unaffected although there was some evidence that the receptive-fields of the superficial layer units were patchy following VC ablation. Recall that Humphrey (1967; 1968) reported patchy receptive fields in the SO of intact rats. Although one must be cautious about making generalizations across species, the report of patchy receptive fields in the monkey following visual decortication suggests that Humphrey may have produced a generalized cortical depression in the intact rats merely by passing the recording electrodes through cortex, and this suggests that the response properties of units in the intact rat SC may not have been accurately described. Schiller et al. reported that eye movement units in the deeper layers of the monkey SC, which discharge prior to saccades of specific size and direction (Schiller and Stryker, 1972), appeared to entirely lack visual receptive-fields as a result of the cortical ablation or cooling. These units still discharged prior to certain eye movements, however. In considering the nature of the cortical information reaching the SC, Schiller et al. considered the possibility that cells in VC with complex receptive-field properties converge on single units in the deep layers of the SC and therefore impart visual

receptive-field properties on the SC units. However, Schiller et al. also speculated that, in the monkey, VC may modulate the flow of visual information from the superficial down to the deeper layers. According to this model, deeper layer units would derive their visual response properties from the superficial SC units. Their results suggested that VC controls the flow of visual information to the deeper layers of the SC whether that information comes directly from VC or from the superficial layers of the SC.

Therefore, in the superficial layers of the rat and monkey SC, the effects of VC ablation appear to be negligible (Humphrey, 1968; Schiller et al., 1974). In the monkey, VC ablation appears to remove the visual receptive-fields of units in the deep layers of the SC (Schiller et al.). It is difficult to accept, however, that the cortical projections to the superficial layers of the rat and monkey SC have no influence at all on units in the superficial layers of the SC. It is even more difficult to accept that the cortico-tectal projection in the rat has no influence at all on any layer of the rat SC.

Several electrophysiological unit recording studies have produced results which suggest that cortico-tectal projections may play an important role in modulating SC excitability (Berman and Sterling, 1976; McIlwain and Fields, 1970; Ogasawara, McHaffie, and Stein, 1984; Stein and Arigbede, 1972; Wickelgren and Sterling, 1969b). The possibility of such a role was first suggested by the results of a study by Wickelgren and Sterling (1969b).

In yet another attempt to understand how visual cortex influences the receptive-field properties of SC cells, Wickelgren and Sterling (1969b) examined the effect of cortical removal in visually deprived cats. They found that after monocular deprivation, cells in the SC responded primarily to the experienced eye. However, after VC was ablated (including areas 17, 18, and 19 and the lateral bank

of the suprasylvian gyrus), the deprived eye regained its capacity to drive cells in the contralateral colliculus. Wickelgren and Sterling permitted their cats to recover for periods of two to four weeks following the cortical ablations, leaving open the question of whether the "recovery" of the deprived eye following the VC ablation was immediate or gradual. A gradual recovery would suggest a recovery mechanism like sprouting or an increase in synaptic effectiveness due to a long-term metabolic alteration. Alternatively, a rapid or immediate recovery of the retino-tectal input from the deprived eye would suggest that VC suppressed this input by an inhibitory synaptic mechanism and that recovery was due to removal of this inhibitory mechanism.

Berman and Sterling (1976) obtained results favoring the latter interpretation, reporting that units in the contralateral SC regained responsiveness to visual stimulation of the deprived eye 15-60 minutes following cortical ablation. Berman and Sterling also observed that a few units were responsive to both the deprived and experienced eyes, and that two of these demonstrated directional selectivity when driven by the experienced eye and no directional selectivity when driven by the deprived eye, suggesting that the retinal (non-directional) and cortical (directional) inputs involve independent pathways. Finally, Berman and Sterling suggested that the cortical suppression of retinal input may be present in normal animals, stating that directionally selective units in the SC virtually require suppression of non-directionally selective input.

McIlwain and Fields (1970) investigated the influence of visual cortex on the response properties of units in the SC of the cat by electrically stimulating VC and simultaneously recording from units in the SC. They reported that in all colliculus units investigated, electrical stimulation of VC

resulted in discharge of SC neurons. In addition, it was noted that following the excitation of the SC neuron, the SC unit entered a phase of depressed responsiveness lasting from 50-100 msec. It was also noted that the cortical stimulation need not initially excite the SC neuron in order to produce the inhibition. This inhibitory phenomenon was present for the majority of the tectal units driven by cortex. Furthermore, the effects of stimulation of VC were similar for directionally selective and non-directionally selective units in the cat SC.

Stein and Arigbede (1972) examined the response properties of unimodal and multimodal units in the cat SC. They reported that the receptive-fields of the units that responded only to visual stimuli gradually increased in size with increased depth in the SC. Most units responded only to moving edges, and many of these exhibited directional selectivity. Some units responded to pulsed stationary stimuli. In the SGM layer and below, Stein and Arigbede located units that could be activated by either somatic or acoustic stimuli and some that were multimodal. These multimodal units, in contrast to the superficial unimodal units, did not respond well to each stimulus presentation. In units which responded to more than one modality, one was often dominant. Cooling of VC rendered 74% of the visual unimodal units completely unresponsive, reduced the responsiveness of another 15%, and 11% were left unaffected by the manipulation. Although the response to visual stimulation was reduced in bimodal and trimodal units, the response to somatic and acoustic stimuli remained unaltered. Stein and Arigbede postulated that the cooling elicited seizure discharge from visual cortex, rather than deactivating it, and that this seizure discharge actively inhibited the response of deep layer SC units to the visual stimuli, and as a result Stein and Arigbede suggested that the primary influence of visual cortex upon the SC is an

inhibitory one. However, it seems equally likely that cooling of VC simply depressed a facilitatory visual input to the SC, thereby depressing the response of deep layer SC units to visual stimuli.

Ogasawara, McHaffie, and Stein (1984) noted that whereas cat areas 17 and 18 project mainly to the superficial layers of the SC and only sparsely to the deeper layers, the posterior regions of suprasylvian cortex (PSSC) project quite densely to the deep layers of the SC. Ogasawara et al. recorded from units in both the superficial and deep layers of the SC before, during, and after the cooling of either of these two regions of cortex and reported that cortical cooling had a profound depressive effect on units in the SC. Cooling cortex resulted in a decrement in the number of spikes evoked or a complete absence of response to previously optimal stimuli regardless of the area being cooled. Cooling areas 17 and 18 of visual cortex resulted in depressed activity of binocular and directionally selective units in the superficial layers of the SC. Units in the deep layers of the SC were unaffected by cooling of the primary VC but were affected by cooling of the PSSC in the same way that units in the superficial layers of the SC were affected by cooling areas 17 and 18. Cooling of the PSSC had a slight effect on the excitability of some superficial lamina units. Ogasawara et al. concluded that there are two functionally independent cortico-tectal systems that serve to maintain the excitability and complex receptive-fields of target cells in the SC. Based upon their findings that some units demonstrated increased excitability and receptive-field complexity after cortical cooling, Ogasawara et al. inferred the existence of a minor tonic inhibitory cortico-tectal influence in the intact cat, and based upon findings of depression in most units in the superficial layers of the cat SC following cooling of VC, Ogasawara et al. inferred that VC exerts a tonic

facilitatory influence on the SC.

In summary, the nature of cortical-tectal interaction is not at all clear. Several studies indicate that the primary function of cortical-tectal interaction is to confer certain receptive-field properties on SC units. Other studies have failed to note any influence at all of the VC over the SC. Still others have suggested that the cortico-tectal projections may play a modulatory role over the operations of the SC. It seems that there is a need for further research on the nature of cortical-tectal interaction.

Section 3: The 2-DG Technique

The assumption that 2-DG uptake reflects glucose uptake which in turn reflects the metabolic demand and functional activity of the cell is a basic tenet of research using the 2-DG technique. The 2-DG molecule is a radioactive glucose analogue that competes with plasma glucose for transport across the blood-brain barrier. Once the 2-DG has been transported into a cell, it is phosphorylated by the enzyme hexokinase to form the molecule deoxyglucose-6-phosphate. Normally, the next step in glycolysis involves the restructuring of glucose-6-phosphate from a six-sided ring to a five-sided form called fructose-6-phosphate. In this case, however, because of a structural difference between 2-DG and glucose (namely the replacement of a hydroxyl group on the second carbon atom by a hydrogen atom), deoxyglucose-6-phosphate is not able to form the 5-sided fructose-6-phosphate structure. Deoxyglucose-6-phosphate is not able to pass through the cell membrane and, as a result, the radioactive carbon is trapped within the brain tissue. The tissue containing the radioactive isotope can then be exposed to x-ray sensitive film to produce autoradiographs, and then densitometric readings taken from the autoradiographs can be used to estimate the activity of the tissue.

Sokoloff et al. (1977) developed the 2-DG technique to

provide an absolute measure of the rate of local cerebral glucose utilization. Sokoloff et al.'s 2-DG technique involves the measurement of the time course of the relative concentrations of glucose and [^{14}C]deoxyglucose in the plasma, the rate constants for the turnover of free glucose and [^{14}C]deoxyglucose pools in the tissue, and of the ratios of the kinetic constants for the transport and phosphorylation of glucose and [^{14}C]deoxyglucose. Sokoloff et al. recommend 30 to 45 minutes be allowed for the clearance of 2-DG from the plasma. With this information, one can use the formula developed by Sokoloff et al. to compute the rate of glucose utilization from the [^{14}C]deoxyglucose-6-phosphate concentration in the tissue.

Presently, there is some question over whether 2-DG uptake occurs primarily at the cell soma or in the neuropil. Sharp (1976) suggested that 2-DG labels primarily the neuropil. Mata et al. (1980) demonstrated that 2-DG uptake was closely associated with the increased activity of the sodium pump which is activated by the influx of sodium ions and efflux of potassium ions that occur during an action potential. Furthermore, Mata et al. hypothesized that the increment in energy utilization which accompanies membrane depolarization is a function of the surface-to-volume ratio of the tissue, and because the highest surface-to-volume ratio is found in the nerve endings and dendrites (i.e. neuropil), it is likely that the greatest uptake of 2-DG would be in the neuropil. However, several researchers have used the [^3H]2-deoxyglucose technique, which permits analysis of the individual labeled units, and have reported heavy labeling of the perikarya and proximal dendritic processes (Durham and Woolsey, 1985; Durham, Woolsey, and Kruger, 1981), although using this technique Ryan and Sharp (1982) reported that uptake in individual nerve fibers can reach the highest levels observed in the cell soma. Peschanski et al. (1986) found a high correlation between

the electrophysiological activity of units and the 2-DG labeling of neurons, suggesting that 2-DG uptake is related to the activity level of the neuron.

Kadekaro, Crane, and Sokoloff (1985) reported no change in the uptake of 2-DG by the cell bodies of the dorsal root ganglion in response to electrical stimulation, but reported an increase in 2-DG uptake in the dorsal horn, the site of the nerve terminals in this pathway. Kadekaro et al. suggest that this pattern of uptake may be peculiar to these units in the central nervous system, which do not generate action potentials in the soma or dendrites. In their experiment, Kadekaro et al. orthodromically stimulated the superior cervical ganglion, which excited both the pre- and post-synaptic elements, making it impossible to determine whether the uptake of 2-DG was limited to the terminal processes or extended into the postsynaptic elements. Yarowsky, Crane, and Sokoloff (1985) demonstrated that antidromic stimulation produced 2-DG uptake in the postsynaptic elements, although Yarowsky et al. were unable to determine whether it was the perikaryonal soma, initial segment, dendritic processes or the glia that were responsible for the uptake of 2-DG.

Nudo and Masterton (1986) made use of the afferent and efferent connections of two auditory nuclei to try and determine whether the 2-DG technique reflects primarily activity of the cells within the CNS nuclei or the afferent activity arriving at the nuclei. Nudo and Masterton (1986) concluded that 2-DG autoradiographs provide a snapshot of the afferent activity arriving at a nucleus and that the activity of the neuropil dominates the autoradiographs.

Auker, Meszler, and Carpenter (1983) reported that although visual and infrared stimuli produced similar spiking activity in tectal units of the rattlesnake, the optic tectum was heavily labeled by visual stimulation but not by infrared stimulation. Based on the results of

evoked potential studies and the fact that field potentials reflect synaptic activity rather than spike activity when recorded at a distance from the site of generation, Auker et al. concluded that visual stimulation produced greater excitatory synaptic activity in the rattlesnake's optic tectum than infrared stimulation, but that the number of spikes produced by both sources of stimulation is equivalent. Therefore, Auker et al. reasoned that 2-DG labeling may be a function of synaptic activity generated by afferent input, not spike production of tectal units.

A modification of the 2-DG technique employed by Sokoloff et al. has been employed to examine the metabolic activity of rat SC under several conditions. Kennedy et al. (1975) demonstrated interhemispheric differences between the two colliculi in rat when one eye was enucleated and the other was left open to ambient light. The SC contralateral to the enucleated eye showed a reduced metabolic rate relative to the SC contralateral to the remaining eye. Toga and Collins (1981), in a similar experiment, made the same observation in rats which had their remaining eye exposed to a reversing checkerboard pattern. Cooper and Thurlow (1985), however, demonstrated that even if the remaining eye was lid-sutured shut, thereby simply eliminating visual stimulation, the SC contralateral to the enucleated eye would show a metabolic rate lower than the SC contralateral to the lid-sutured eye. This suggested that the differences observed by Kennedy et al. and Toga and Collins may have reflected denervation effects primarily, and introduced the question of whether or not visual stimulation actually had an effect on 2-DG uptake in the SC. Rooney and Cooper's (1988) results demonstrated that visual stimulation does have an effect on the uptake of 2-DG in rat SC. They observed in rat that if one eye was simply lid-sutured shut and the other eye exposed to a stationary pattern of square-wave gratings, the SC contralateral to the eye

exposed to the pattern stimuli would take up more 2-DG than the SC contralateral to the lid-sutured eye. On the other hand, they also observed that the SC contralateral to an eye exposed to a diffuse light stimulus would take up less 2-DG than the SC contralateral to a lid-sutured eye. Further investigation demonstrated that even subtle differences in visual stimulation could elicit different levels of 2-DG uptake. McIntosh and Cooper (1988) observed that SC uptake was greater when the stripes display moved slowly and intermittently than when it remained stationary. Therefore, there appear to be a number of studies which suggest that the 2-DG technique can be used to evaluate activity in the SC under different visual conditions.

Preliminary work (Thurlow and Cooper, 1985) has also revealed that 24 h after a unilateral visual cortex ablation, glucose metabolism in the ipsilateral SC is reduced below that of the contralateral SC when both eyes are lid-sutured. This finding, as well as the work on 2-DG uptake in rat SC under different visual conditions, prompted the present investigation, the major objective of which was to determine whether cortical ablation alters the tectal response to moving gratings and to diffuse light. If, as some studies suggest, VC governs the overall excitability of the SC, then VC ablation might have some effect on 2-DG uptake under the moving gratings and diffuse light visual stimulation conditions, which normally increase and decrease, respectively, 2-DG uptake in rat SC.

Chapter 2. Experiment I: The Effect of Unilateral Visual Cortex Ablation on [^{14}C]-2-deoxyglucose Uptake in Superior Colliculus of Rat

Experiment I examined the effects of unilateral VC ablation at various post-operative time intervals on SC 2-DG uptake in binocularly lid-sutured rats tested in a dark box. The purpose of the experiment was threefold: (1) Previous work (Thurlow and Cooper, 1985) indicates that there is a reduction in ipsilateral SC metabolic activity 24 h after a unilateral VC ablation. It was not established, however, whether this effect was temporary or enduring, and this suggested that a time-course study be carried out, if only to determine whether the diffuse and moving gratings experiment (Experiment II) should involve animals tested at different post-operative intervals. (2) Knowing the effects of a cortical ablation on the "resting" unstimulated SC is also important for interpreting the significance of any alterations in metabolic activity occurring under diffuse and moving gratings stimulation conditions. (3) Finally, Experiment I provided an opportunity to test Thurlow and Cooper's (1985) speculation that "generalized cortical depression" may contribute to tectal depression.

As well as finding that a unilateral VC ablation in the rat produced, 24 h later, a depression in 2-DG uptake in the SC ipsilateral to the VC ablation, Thurlow and Cooper (1985) noted that the greatest depression relative to the contralateral colliculus occurred in stratum griseum intermediale (SGM) of the SC. Thurlow and Cooper had expected that the greatest depression would occur in the superficial layers of the SC (stratum griseum superficiale (SGS) and stratum opticum (SO)), because these layers receive the greatest number of the projections from VC (Cadusseau and Roger, 1985; Goodman and Horel, 1966; Lund, 1966; Nauta and Bucher, 1954; Olavarria and Van Sluyters, 1982; Takahashi, 1985); and because the depression observed

in the rat SC layers contralateral to an enucleated eye corresponds to the number of projections they receive from the retina (Cooper and Thurlow, 1985). The nature of the depression of 2-DG uptake observed 24 h following VC ablation was brought into question as a result of this unexpected finding in SGM.

Thurlow and Cooper (1985) hypothesized that the depression in 2-DG uptake in SGM of the rat SC following unilateral VC ablation might be due to a reduction in the activity of descending extravisual cortical inputs to SGM as a result of the VC ablation. There is evidence for the existence of projections to the deeper layers of the SC from motor cortex, somatosensory cortex, and auditory cortex (Cadusseau and Roger, 1985; Takahashi, 1985) as well as for the existence of polymodal units in SGM (Chalupa and Rhoades, 1977; Drager and Hubel, 1975; Merideth and Stein, 1983; Stein and Arigbede, 1972).

Thurlow and Cooper (1985) suggested that a possible mechanism for the depression of the extravisual projections to SGM might be "generalized cortical depression" induced by the VC ablation. Pappius (1981) and Cooper and Thurlow (1984) noted that cortical damage resulted in a temporary generalized cortical depression of 2-DG uptake. Pappius, using Sokoloff et al.'s (1977) 2-DG technique, demonstrated that following unilateral freezing lesions to parietal cortex, a significant decrement in 2-DG uptake occurred throughout the ipsilateral cortex for up to three days following the ablation. The decrement was significant in the undamaged hemisphere only in the parietal and olfactory areas. In addition, by five days following the freezing lesion, 2-DG uptake had returned towards normal in all cortical areas; however, it remained slightly lower than normal ipsilateral to the lesion. In 1984, Cooper and Thurlow noted that even four days following a neocortical ablation, 2-DG uptake in the ipsilateral frontal cortex and

striatum was greatly depressed relative to the contralateral hemisphere. Therefore, generalized cortical depression of 2-DG uptake following cortical damage is well documented, and could be responsible for some or all of the depression observed in SGM following VC ablation.

However, generalized cortical depression appears to be a temporary phenomenon. If generalized cortical depression is responsible for a portion of the depression observed in SGM 24 h following VC ablation, then it follows that recovery from depression in SGM should occur simultaneously with recovery from generalized cortical depression. Therefore, in Experiment I, uptake of 2-DG by cortex and the SC following unilateral VC ablation was examined at several post-operative intervals to determine whether a recovery occurs in SGM and whether or not this recovery coincides with recovery from generalized cortical depression.

In addition, if the hypothesis that generalized cortical depression is responsible for depression in SGM is correct, then a generalized cortical depression induced by a short-term unilateral parietal cortex ablation should also produce a depression in ipsilateral SGM. Therefore, as an additional test of this hypothesis, the uptake of 2-DG by cortex and the SC was examined in a group of rats that had undergone unilateral parietal cortex ablations 48 h prior to 2-DG administration.

Method

Procedure

Subjects. Twenty male, Long-Evans black-hooded rats, bred from parent stock obtained from Canadian Breeding Farms and Laboratories, served as subjects. The rats weighed 170 to 320 g. They were kept on a 12 h-on 12 h-off light-dark cycle.

Three rats underwent unilateral parietal cortex ablations, 17 rats underwent unilateral VC ablations. The post-operative survival interval for the rats with parietal

cortex ablations was 2 days. The post-operative survival intervals of the rats with unilateral VC ablations followed in parentheses by the number of rats examined at each interval were: 1 day (3), 2 days (3), 4 days (2), 7 days (2), 14 days (2), 30 days (2), 60 days (2), and 90 days (1).

Surgery. Cortical ablations were produced by gently removing the pia mater which eliminated the arterial supply to the tissue. The unilateral parietal cortex ablations, located in either the left or right hemisphere, included Kreig's cortical areas 1, 3, 4 and 7 (Kreig, 1946) and may have infringed upon the most anterior portions of Kreig's areas 17 and 18. The unilateral VC ablations, also located in either the left or right hemisphere, were similar to those described by Thurlow and Cooper (1985). These ablations included most or all of Kreig's areas 17, 18, and 18a, and extended anteriorly into Kreig's area 7. The posterior occipital pole under the transverse sinus remained intact (see Figure 1 for examples of ablations).

The final surgery was carried out 24 h prior to the administration of the 2-DG. For the 17 rats with unilateral VC ablations, the final surgery involved a binocular lid suture and the implantation of a chronic external jugular catheter. The eyelids of the rat were sutured shut using five to eight interrupted sutures. The chronic external jugular catheter was filled with heparin and inserted in the right jugular vein. The tubing was then brought under the skin to the back, where approximately 10 cm. of tubing was coiled under the skin. The end of the tubing was plugged and extended through a slit in the skin between the shoulders where it was anchored with sutures. For the three rats with parietal cortex ablations, the jugular catheter was implanted at the time of the cortical ablation (2 days prior to 2-DG administration) and the eyelids were sutured 24 h prior to the 2-DG administration. All operations were carried out under deep sodium pentobarbital

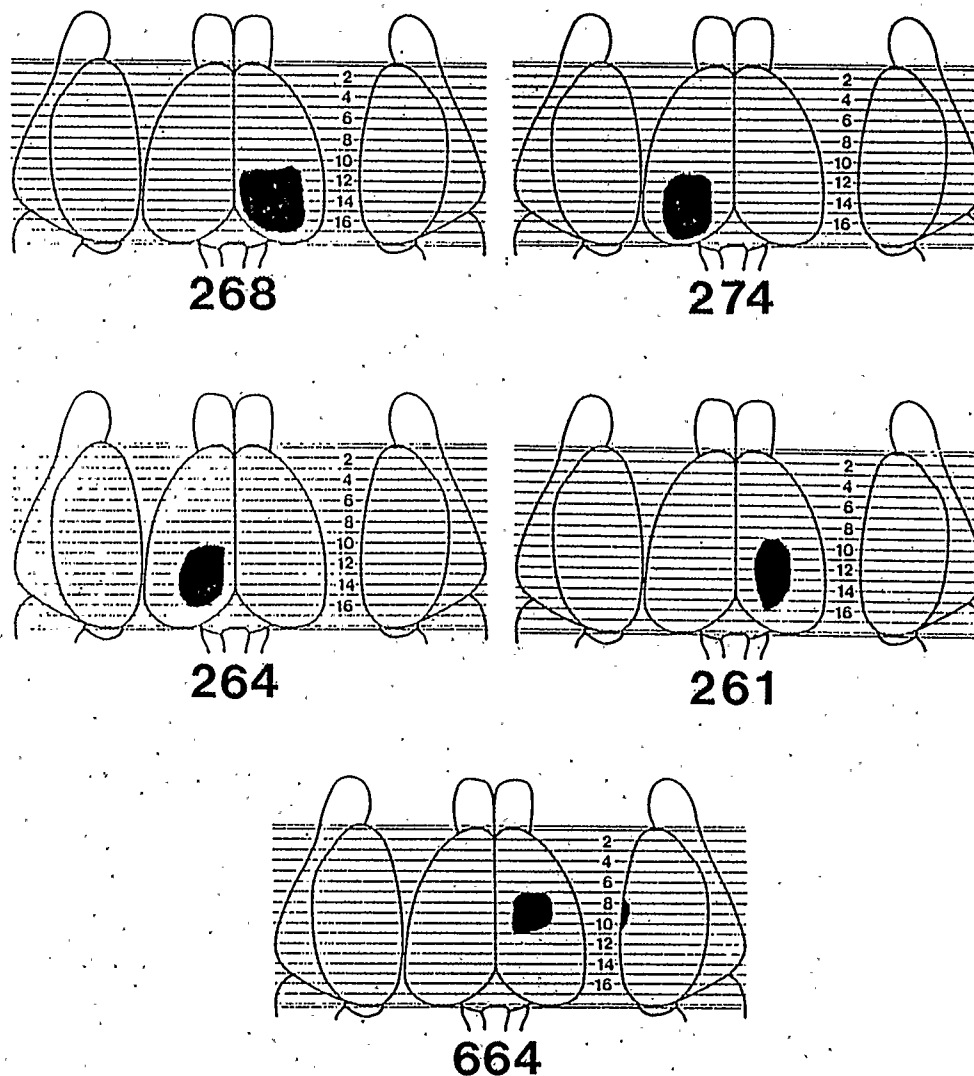


Figure 1. Examples of cortical ablations. Rats 268 and 274 underwent VC ablations 48 h prior to 2-DG administration, rats 261 and 264 underwent a VC ablation 30 d prior to 2-DG administration. Rat 664 underwent a 48 h parietal cortex ablation.

anesthesia (65 mg/kg i.p.).

2-DG Injections and Autoradiographs. Twenty-four hours after the final surgery the rats were injected via the jugular catheter with 100-110 $\mu\text{Ci/kg}$ of 2-deoxy-D-[U- ^{14}C]glucose of high specific activity (303 mCi/mmol). The rats were then placed in a dark box, to ensure that there was no response to light by the retina, for a 45 minute incubation period as recommended by Sokoloff et al. (1977). This procedure was similar to that carried out by Cooper and Thurlow (1985) and Thurlow and Cooper (1985).

After 45 minutes, the rats were removed from the dark box, sacrificed with an injection of sodium pentobarbital via the jugular catheter, and perfused with 40 ml of saline solution and 80 ml of Hand's solution (Hand, 1981). The brain was then covered in Lipshaw embedding matrix and frozen in 2-methyl butane at approximately -20°C and mounted on a pedestal with O.C.T. embedding compound (Fisher). The brains were then cryostat-cut at 30 μm at approximately -16°C and relevant sections were mounted on warm slides and immediately dried on a hot plate. The dried sections were apposed to Dupont Lo-Dose X-ray film together with sets of Amersham [^{14}C]methacrylate standards for approximately three weeks, after which the film was developed.

Autoradiographic Analysis. The analysis was similar to that of Thurlow and Cooper (1985), where measures were taken of relative tissue radioactivity rather than tissue metabolic rate.

The generalized cortical depression was estimated in rats with unilateral VC ablations by examining entorhinal cortex and sensorimotor cortex (area 4) for hemispheric asymmetry in 2-DG uptake. The choice of entorhinal cortex and sensorimotor cortex was based on anatomic considerations. Entorhinal cortex is not believed to receive a significant

projection from visual cortex, therefore it reflects generalized depression with a minimal emphasis on denervation effects. Area 4 lies just anterior to the lesion site and sends projections to SGM (Cadusseau and Roger, 1985; Takahashi, 1985), and therefore is representative of an area of cortex that may be affected by generalized cortical depression and that also projects to the deeper layers of the SC. In rats with parietal cortex ablations, entorhinal cortex was examined for asymmetry of 2-DG uptake, and VC was examined for asymmetry in place of sensorimotor cortex, because sensorimotor cortex was at least partially ablated by the parietal cortex ablation.

Film densities were determined using Spectra brightness spot meter (UB1/4) readings digitized by a Cromemco microprocessor. A circular reticule 260 μ m in diameter, centered within a 2.75 mm viewing field, delineated the six sample loci in SGS, SO, and SGM (See Figure 2 for sampling loci), the ten sample loci through anterior entorhinal cortex and dorsomedial area 4 of sensorimotor cortex, and the 13 sample loci through VC (layer 4). The sampling procedure was repeated for at least five sections from different rostro-caudal coronal planes of the SC and from three sections through each cortical area (See Figure 3 for sampling loci of cortical areas). Means of densitometric readings were calculated for each SC layer, for sensorimotor, entorhinal, and visual cortex, and for additional readings taken through "light" (corpus callosum) and "dark" (posterior mamillary nucleus) areas of the autoradiographs. These densitometric means were converted to measures of tissue ^{14}C as determined by densitometric readings through the standards of known radioactivity. To improve intersubject comparability, ^{14}C measures were transformed using the formula $(L - X)/(L - D) \times 100$, where L = the mean of the "light" readings, D = the mean of the "dark" readings, and X = the mean of the area under study.

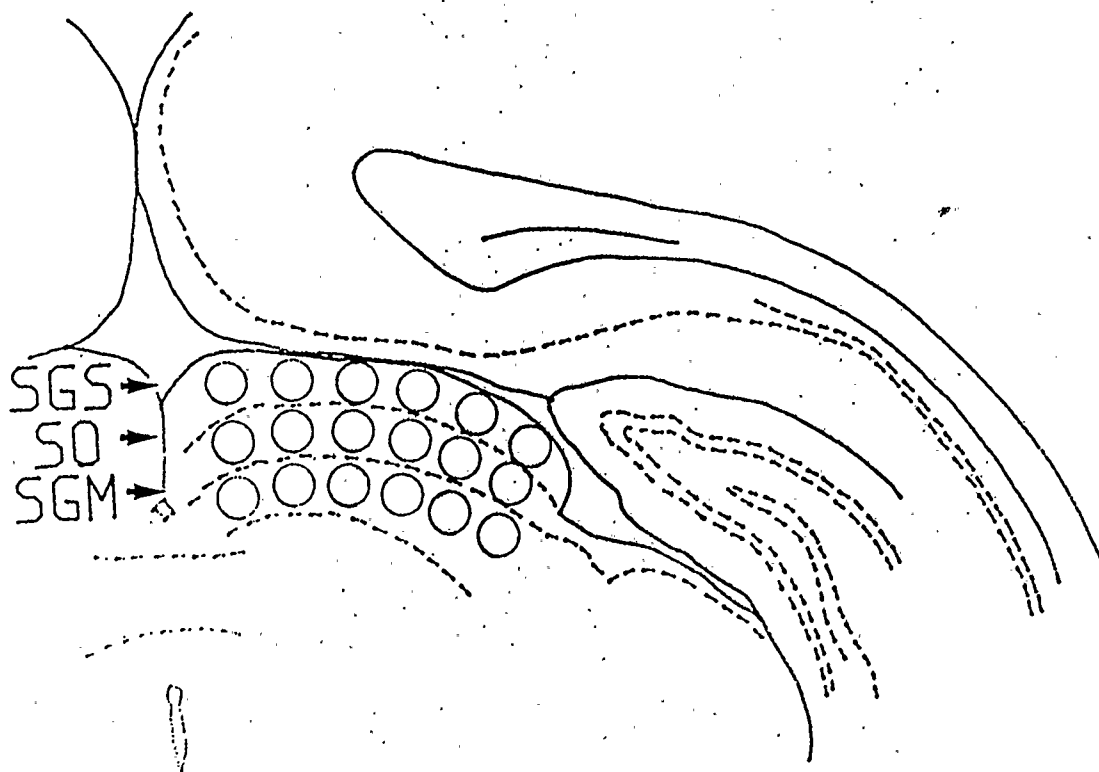
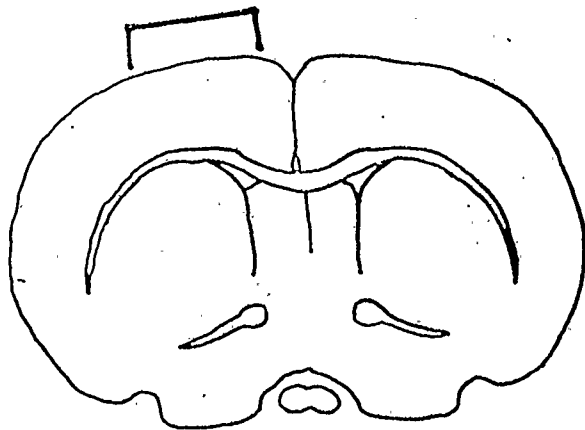
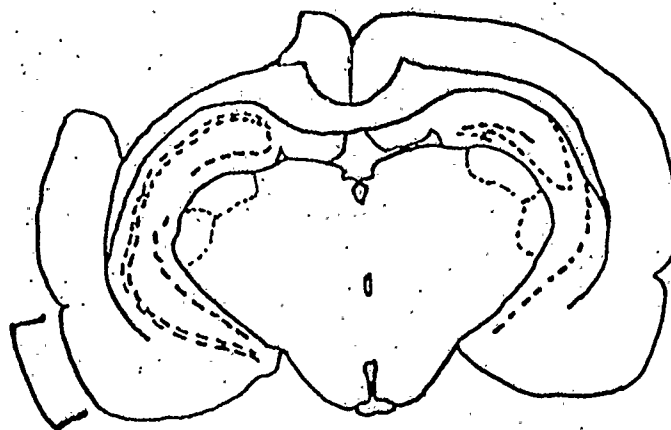


Figure 2. The six sample loci through the SGS, SO, and SGM of the SC. Readings were taken through the SC in both hemispheres.

Area 4 of Sensorimotor Cortex



Entorhinal Cortex



Visual Cortex

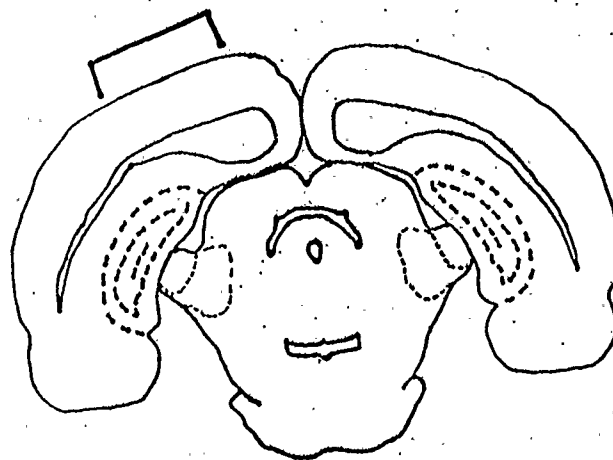


Figure 3. Top left: Area of the ten sample loci through dorsomedial area 4 of sensorimotor cortex. Top right: Area of the ten sample loci through anterior entorhinal cortex. Bottom: Area of the thirteen sample loci through layer 4 of VC.

This procedure arithmetically equated the light-dark range of each autoradiograph to 100, and positioned each area of interest within that range. The transformed value for the area of interest in the ablated hemisphere was subtracted from the transformed value of the area in the intact hemisphere and the resulting difference score for each animal in each area was graphed in Figure 4 for the animals with VC ablations, and Figure 5 for the animals with parietal cortex ablations.

Results

Figure 4B reveals that up to 7 days after unilateral VC ablation, the depression in metabolic activity in the ipsilateral SC was least in SGS, greater in SO, and greatest in SGM. By about 14 days these profiles changed so that the order of the difference scores across the layers was reversed (Figure 4B). The reversal coincided with the obvious reduction in generalized cortical depression which occurred in both area 4 and entorhinal cortex at about 14 days post-operative (Figure 4A).

Figure 4B also shows an absolute decline in the overall amount of tectal depression as a function of post-operative interval. The recovery was most evident and consistent in SGM. Recovery also appeared to occur in SO and SGS, although it was not always evident in all long-term recovery animals (for example see second 60 day recovery animal in Figure 4B).

Figure 5A indicates that 48 h following unilateral parietal cortex ablation, generalized cortical depression was present in both entorhinal and visual cortex in all three animals, but that in two of these animals it was very slight. Rat number 677, in which the generalized cortical depression was greater than in the other two rats of this group, demonstrated asymmetry between the three layers of the SC resembling the asymmetry produced by a short-term VC ablation (Figure 5B). However, rats 664 and 675, although

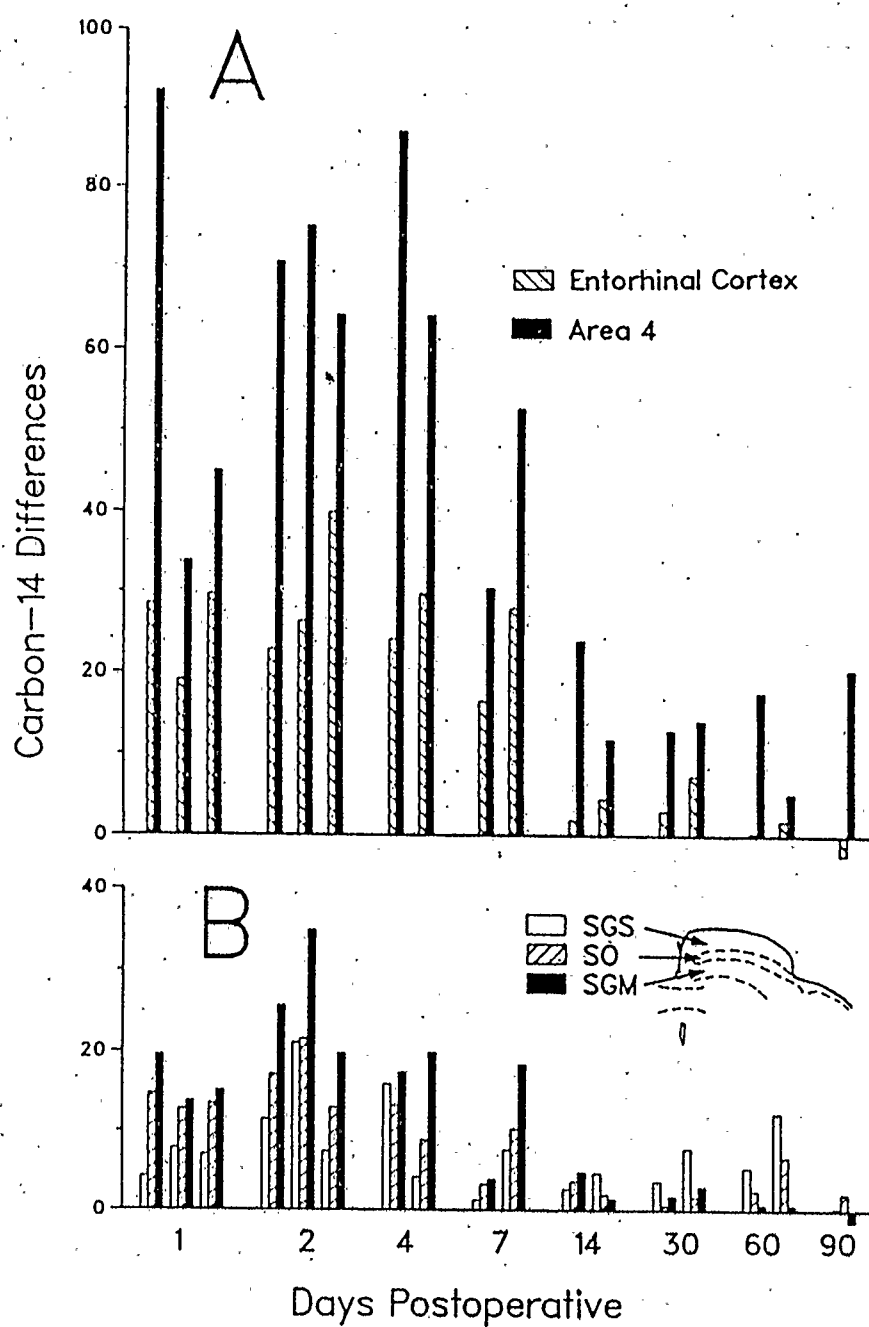


Figure 4. Carbon-14 differences between the two hemispheres for entorhinal and area 4 cortex (A) and upper colliculus layers (B) from 1 to 90 days after a unilateral VC ablation. Positive values indicate that the hemisphere contralateral to the VC ablation is more active than the ipsilateral hemisphere.

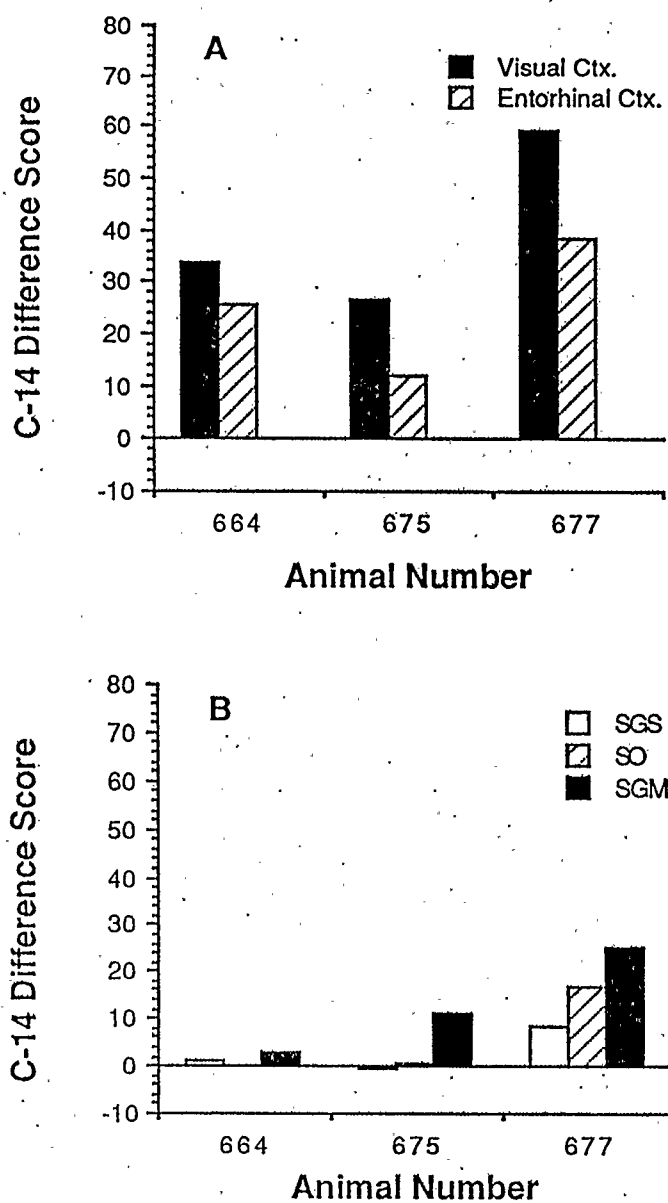


Figure 5. Carbon-14 differences between the two hemispheres for VC and entorhinal cortex (A) and upper colliculus layers (B) at 48 h after a unilateral parietal cortex ablation. Positive values indicate that the hemisphere contralateral to the cortical ablation is more active than the ipsilateral hemisphere.

demonstrating generalized cortical depression in both VC and entorhinal cortex, did not demonstrate SC asymmetry typical of rats with short-term VC ablations. Rat 664 shows very little asymmetry in any of the SC layers, and rat 675 shows very little asymmetry in SGS or SO, and only a small asymmetry in the SGM layer of the SC.

Discussion

The results support Pappius's (1981) and Cooper and Thurlow's (1984) claims of generalized cortical depression following unilateral VC ablations and the time course of recovery from this depression proposed by Pappius. Depression in both ipsilateral cortex and the SC appeared to peak 48 h following the ablation. By 30 days following the VC ablation, there was a noticeable reduction in the depression of 2-DG uptake in both the ipsilateral SC and cortex.

In both the VC ablation and parietal cortex ablation groups, the depression in 2-DG uptake observed in the ipsilateral SGM corresponded with the presence of a rather large degree of generalized cortical depression of 2-DG uptake. In animals in which only relatively slight amounts of generalized cortical depression were observed, very little depression was observed in ipsilateral SGM, suggesting that for cortical depression to have a noticeable effect on subcortical 2-DG uptake, cortical depression must reach a certain magnitude. It is not clear from Experiment I what factors are involved in determining the magnitude of the cortical depression. However, the results of this experiment support the hypothesis that generalized cortical depression may account for a large portion of the depression observed in ipsilateral SGM shortly after a unilateral VC ablation.

In the VC ablation groups, recovery also appeared to occur in SGS and SO, and because these layers receive cortical projections primarily from area 17, this could

indicate that denervation-produced depression also abates with time. However, because area 17 removal may have been incomplete, the lifting of a generalized depression in remaining posterior portions of area 17 may also have contributed to recovery in SGS and SO.

In the parietal cortex ablation group, rat number 677 showed depression in the SGS and SO layers of the SC. This is likely attributable to the depression of VC via generalized cortical depression induced by parietal cortex ablation, creating a depression in the superficial layers of the SC that resembles that produced by VC ablation.

Finally, it is possible that the depression in 2-DG uptake in the SC as a result of VC ablation is specific to nonstimulating visual conditions (i.e. binocular lid-suture). It would therefore be useful to examine the effects of VC ablation on 2-DG uptake in the SC under stimulating visual conditions. Such an examination may provide a better understanding of the effects of visual decortication on the SC.

Chapter 3. Experiment II: Effects of Moving Gratings and Diffuse Light on 2-Deoxyglucose Uptake in Rat Superior Colliculus following Visual Cortex Ablation

Several reports on the cat, ground squirrel, hamster, and rabbit have emphasized the effect decortication has on directional selectivity and ocular dominance (Berman and Cynader, 1975; Chalupa and Rhoades, 1977; Cynader and Berman, 1972; Graham, Berman, and Murphy, 1982; Ogasawara, McHaffie, and Stein, 1984; Palmer and Rosenquist, 1974; Rosenquist and Palmer, 1971; Schiller, Stryker, Cynader, and Berman, 1974; Sterling and Wickelgren, 1969; Wickelgren and Sterling, 1967) as well as on hypercomplex (Michael, 1972b) and bimodal or trimodal units (Stein and Arigbede, 1972) in the SC. Other reports have stated that ablation of VC has little or no effect on the response properties of units in the SC (Hoffmann and Straschill, 1971; Horn and Hill, 1966b; Humphrey, 1967; 1968; Marchiafava and Pepeu, 1966; Maslund, Chow, and Stewart, 1971; Rizzolatti, Tradardi, and Camarda, 1970). It is clear that the nature of cortical-tectal interaction warrants further investigation.

In Experiment I it was found that a unilateral VC ablation resulted in a temporary ipsilateral reduction in SC uptake of 2-DG in binocularly lid-sutured awake rats. In Experiment II, the effects of unilateral visual decortication were examined in two other visual conditions that are known to have certain effects on the uptake of 2-DG in the rat SC. McIntosh and Cooper (1988) reported that moving gratings produced an intertectal asymmetry in monocularly lid-sutured rats, with the SC contralateral to the open eye taking up more 2-DG in the SGS, SO, and SGM than the SC contralateral to the lid-sutured eye. Rooney and Cooper (1987) reported that diffuse light produced an asymmetry between the superior colliculi of monocularly lid-sutured rats, with the SC contralateral to the open eye taking up less 2-DG in the SGS and SO than the SC

contralateral to the lid-sutured eye. Therefore, slowly moving gratings is an excitatory stimulus relative to lid-suture for the uptake of 2-DG in the SC, and diffuse light is a depressive stimulus relative to lid-suture. These two visual conditions were used to compare the degree of asymmetry produced by unilateral VC ablation in binocularly lid-sutured rats to the degree of asymmetry produced by unilateral VC ablation in rats binocularly exposed to these two visual conditions. They were also used to determine whether the normal intertectal asymmetry observed in animals monocularly exposed to these two conditions is affected by bilateral VC ablation.

Method

Procedure

Subjects. Thirty male, Long-Evans black-hooded rats, bred from parent stock obtained from Canadian Breeding Farms and Laboratories, served as subjects. The rats weighed 170 to 320 g. They were kept on a 12 h-on 12 h-off light-dark cycle.

Apparatus. The stimulus chamber consisted of a plastic box 29 x 29 x 38 cm in size. For the moving square-wave gratings condition, the walls, ceiling and floor were covered with black and white, horizontal and vertical intersecting stripes of various widths ranging from .02 cm to 2.0 cm. For the diffuse light condition the surfaces were covered with plain white paper. In both conditions, the ceiling and walls were back-lit with five 60 watt incandescent bulbs. During stimulus exposure the rats were housed in a clear plastic cylinder with a radius of 10.5 cm. The cylinder was located inside the stimulus chamber. The rats wore diffusing goggles over both eyes in the diffuse light condition. A fan supplied ventilation and background noise.

Surgical Procedure. The rats were anaesthetized with sodium pentobarbital and then they underwent either

unilateral or bilateral visual cortex ablations similar to those described in Experiment I. The skull, dura mater, and pia mater overlying VC areas 17, 18, and 18a were removed, thus eliminating the blood supply and therefore creating a lesion. A jugular catheter was inserted 48 h prior to the 2-DG administration. Rats with bilateral ablations and rats with intact cortex underwent a monocular lid-suture 24 h prior to administration of 2-DG. Rats in the diffuse light groups also had a post cemented to the top of the skull 48 h prior to 2-DG administration that anchored the light diffusing goggles worn by the rats in the diffuse light condition at the time of 2-DG administration.

Experimental Procedure. At the time of 2-DG administration, the rats received 100-110 $\mu\text{Ci/kg}$ injections of 2-DG via the jugular catheter. They were then placed in either the moving square wave gratings or diffuse light stimulus conditions. Forty-five minutes after 2-DG injection, the rats were overdosed with sodium pentobarbital, and the brain was removed and processed for autoradiography as described in Experiment I. Densitometer readings were taken from coronal autoradiographs through the SGS, SO, and SGM layers of the SC in the same locations as in Experiment I. Finally, the densitometer values were converted to carbon-14 transformed values and the differences between the carbon-14 transformed values in SGS, SO, and SGM in one hemisphere and the carbon-14 values in SGS, SO, and SGM in the contralateral hemisphere were determined, again as in Experiment I.

Table 1 summarizes the different treatments for the animals of Experiment II.

Results

Nothing emerged from the results to suggest that the intertectal asymmetry produced by unilateral VC ablation in binocularly lid-sutured rats differs from the intertectal asymmetry produced by unilateral VC ablation in rats

Treatment of Groups Used in Experiment II

Unilateral Visual Cortex Ablations

Darkness	Moving Gratings	Diffuse
48h-UVC-LS	48h-UVC-MG	48h-UVC-DF
30d-UVC-LS	30d-UVC-MG	30d-UVC-DF

Bilateral Visual Cortex Ablations

Moving Gratings	Diffuse
48h-BVC-MG	48h-BVC-DF
30d-BVC-MG	30d-BVC-DF

Normals (No Visual Cortex Ablations)

Moving Gratings	Diffuse
N-ULS-MG	N-ULS-DF

48h = 48 h recovery from VC ablation
 30d = 30 day recovery from VC ablation
 BVC = bilateral VC ablation
 DF = diffuse visual condition
 LS = lid-suture
 MG = moving gratings visual condition
 N = normals (no VC ablation)
 ULS = unilateral lid-suture
 UVC = unilateral VC ablation

binocularly exposed to either moving gratings or diffuse light. In addition, the results indicated that bilateral VC ablation does not affect the intertectal asymmetry typically observed in rats monocularly exposed to either moving gratings or diffuse light. The only significant finding, already observed in Experiment I, was that following unilateral VC ablation, interhemispheric difference scores were larger in the rats tested at 48 h than in rats tested at 30 days. This finding provides additional evidence for recovery of 2-DG uptake in the SC after unilateral VC ablation. The following paragraphs describe the results in detail along with the appropriate statistical tests.

Figure 6 shows the intertectal differences obtained in SGS, SO, and SGM in each of the rats that underwent a unilateral VC ablation. Observe that in each visual condition the 48 h unilateral ablation groups (48h-UVC-LS, 48h-UVC-MG, and 48h-UVC-DF) show a large degree of depression in the SC ipsilateral to the VC ablation, which contrasts with the smaller degree of depression in the 30 day groups (30d-UVC-LS, 30d-UVC-MG, and 30d-UVC-DF). Note that the differences between the 48 h and 30 day groups are consistent in all three layers but are most striking in SGM and SO. Of further interest is the finding that at each recovery interval the degree of depression in each layer of the SC does not differ across the various stimulation conditions. For example, the interhemispheric differences observed in SGM in the 48h-UVC-LS group do not appear to differ from the interhemispheric differences in SGM in the 48h-UVC-MG and 48h-UVC-DF groups. Nor do the interhemispheric differences in SGM in the 30d-UVC-LS group appear to differ from the interhemispheric differences in SGM in the 30d-UVC-MG and 30d-UVC-DF groups.

For each layer of the SC, a statistical analysis was carried out using multiple regression, with survival time and stimulus condition as the two independent variables, and

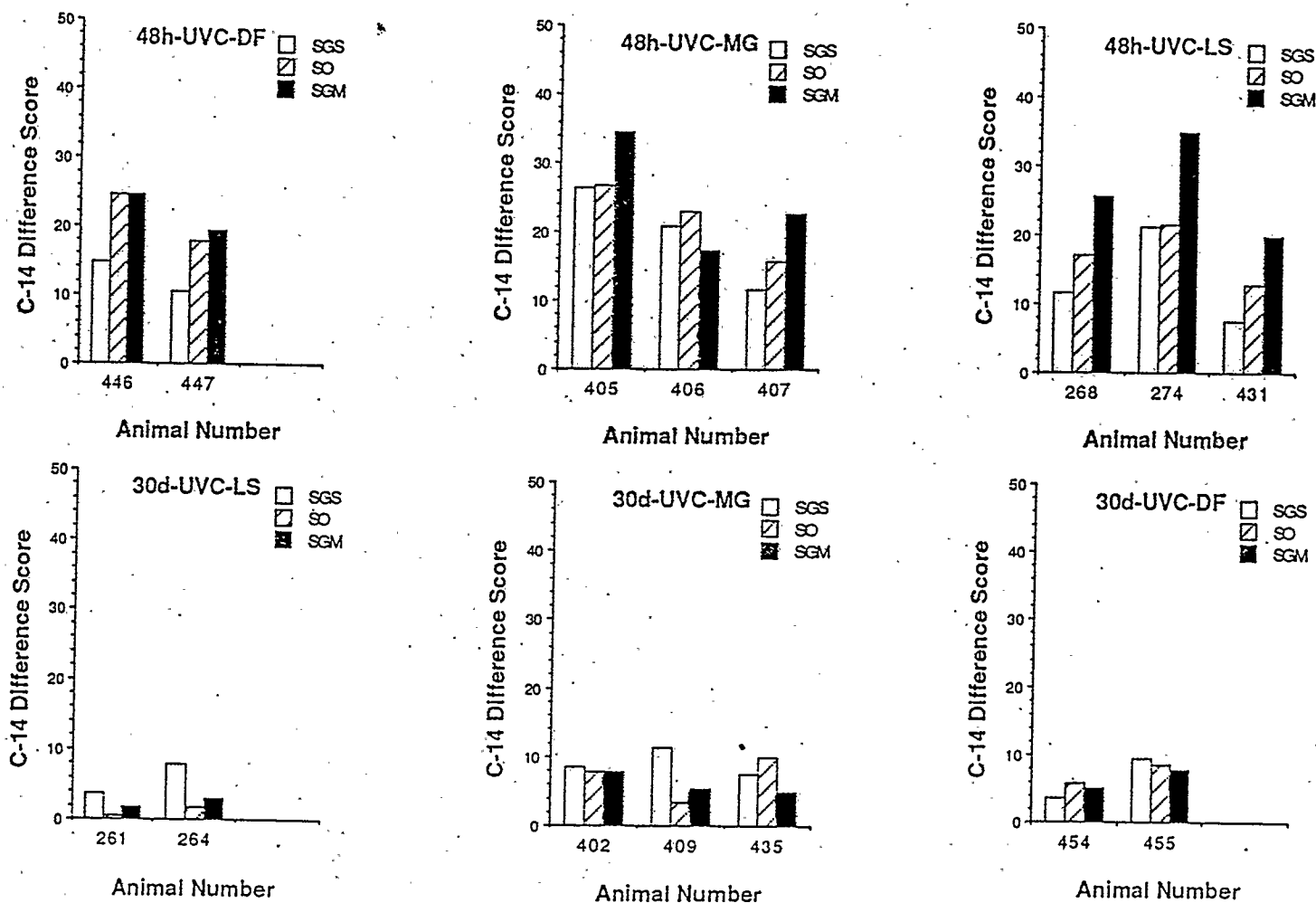


Figure 6. Intertectal C-14 differences in SGS, SO, and SGM for each rat with a unilateral VC ablation. Positive values indicate that the contralateral SC is more active than the ipsilateral SC.

the difference between the contralateral and ipsilateral SC as the dependent variable.

In the SGS, the test of the interaction between survival time and stimulus condition was not significant ($F(2,9) = 0.23$, $p > .05$). This was also the case for SO ($F(2,9) = 0.075$, $p > .05$) and SGM ($F(2,9) = 1.76$, $p > .05$).

Figure 7 shows the mean intertectal differences in SGS, SO, and SGM across the three stimulus conditions at survival times of 48 h and 30 days. The mean difference between the contralateral and ipsilateral SGS for the 48 h recovery interval across the three stimulus conditions was 15.21, and the mean difference between the contralateral and ipsilateral SGS for the 30 day recovery interval across the three stimulus conditions was 7.14. The test of the main effect of survival time in the SGS proved to be significant ($F(1,9) = 8.38$, $p < .05$). The mean difference between the contralateral and ipsilateral SO for the 48 h recovery interval across the three stimulus conditions was 20.06, and for the 30 day recovery interval was 5.12. The test of the main effect of survival time in the SO also proved to be significant ($F(1,9) = 48.28$, $p < .01$). The mean difference in SGM for the 48 h recovery interval across the three stimulus conditions was 24.52, and the mean difference for the 30 day recovery interval was 4.96. The test of the main effect of survival time in the SGM also proved to be significant ($F(1,9) = 107.86$, $p < .01$).

The group means of the difference scores between the contralateral and ipsilateral SGS in the 48 h recovery groups in the binocular lid-suture, moving gratings, and diffuse light groups were 13.4, 19.59, and 12.52, respectively. The group means of the difference scores in the 30 day recovery groups in the binocular lid-suture, moving gratings, and diffuse light groups were 5.77, 9.09, and 6.57, respectively. The test of the main effect of stimulus condition proved not to be significant in SGS

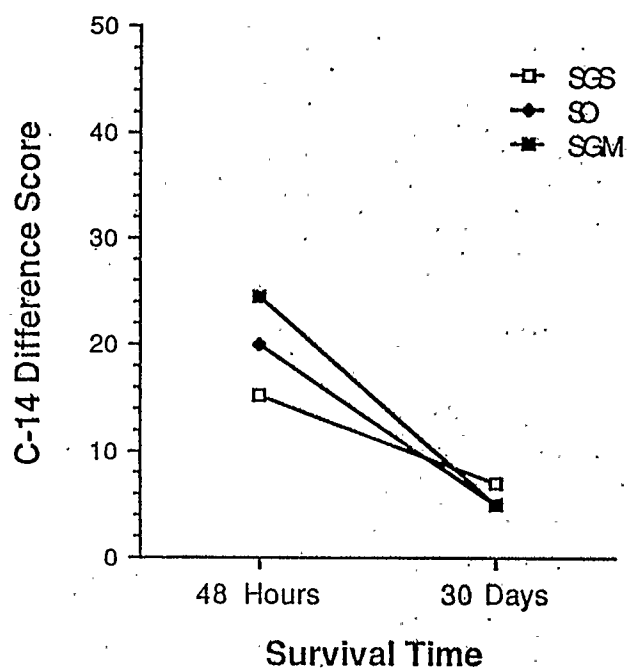


Figure 7. Intertectal C-14 differences in SGS, SO, and SGM, averaged across all three stimulus conditions at survival times of 48 h and 30 days.

($F(2,9) = 1.44$, $p > .05$). The group means of the difference scores in SO in the 48 h recovery groups in the binocular lid-suture, moving gratings, and diffuse light groups were 17.26, 21.73, and 21.17, respectively, and in the 30 day recovery groups were 1.18, 7.04, and 7.13, respectively. Once again, in SO, the test of the main effect of stimulus condition proved not to be significant ($F(2,9) = 2.51$, $p > .05$). The group means of the difference scores in SGM in the 48 h recovery group in the binocular lid-suture, moving gratings, and diffuse light groups were 26.8, 24.7, and 21.98, respectively, and in the 30 day recovery groups were 2.4, 6.05, and 6.41, respectively. In this layer as well, the test of the main effect of stimulus condition proved not to be significant ($F(2,9) = 0.15$, $p > .05$).

Figure 8 shows the difference scores in all three SC layers for the rats with bilateral VC ablations monocularly exposed to moving gratings after 48 h and 30 day recovery intervals and the difference scores for the rats with intact visual cortex that were also exposed to the moving gratings. From Figure 8 it appears that the differences in each layer of the SC are similar in the 48h-BVC-MG, 30d-BVC-MG, and N-ULS-MG groups. For each of the three layers of the SC, an analysis of variance was carried out to determine whether the difference scores in either the 48h-BVC-MG or 30d-BVC-MG group differed significantly from the difference scores in the N-ULS-MG group.

The mean difference score between the ipsilateral and contralateral SGS in the 48h-BVC-MG group was 27.37, in the 30d-BVC-MG group was 31.51, and in the N-ULS-MG group was 34.35. The differences between these means proved not to be significant ($F(2,5) = 0.64$, $p > .05$).

The mean difference score between the ipsilateral and contralateral SO in the 48h-BVC-MG group was 11.68, in the 30d-BVC-MG group was 11.29, and in the N-ULS-MG group was 17.31. The differences between these means proved not to be

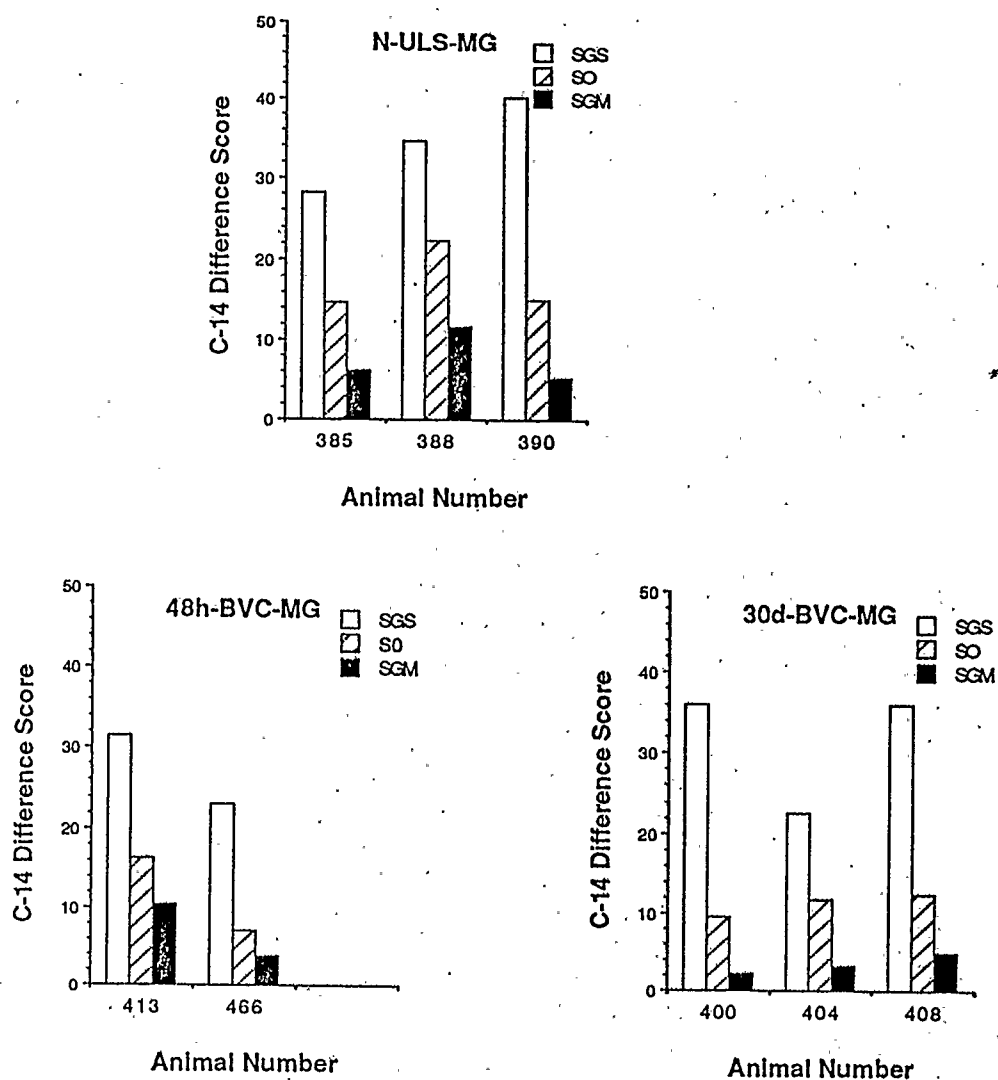


Figure 8. Carbon-14 differences between the colliculi in SGS, SO, and SGM in each rat monocularly exposed to moving gratings. Positive values indicate that the SC fed by the eye exposed to the moving gratings stimuli is more active than the SC fed by the lid-sutured eye.

significant ($F(2,5) = 1.94, p > .05$).

The mean difference score between the ipsilateral and contralateral SGM in the 48h-BVC-MG group was 7.10, in the 30d-BVC-MG group was 3.59, and in the N-ULS-MG group was 7.63. The differences between these means also proved not to be significant ($F(2,5) = 1.4, p > .05$).

Figure 9 shows the difference scores in all three SC layers for the rats with bilateral VC ablations monocularly exposed to the diffuse light condition after 48 h and 30 day recovery intervals and the difference scores for the rats with intact VC also monocularly exposed to the diffuse light condition. From Figure 9, it appears that the differences are similar within each layer of the SC in the 48h-BVC-DF, 30d-BVC-DF, and N-ULS-DF. For each of the three layers of the SC, an analysis of variance was carried out in an attempt to determine whether the difference scores in either the 48h-BVC-DF or 30d-BVC-DF groups differed significantly from the difference scores in the N-ULS-DF group.

The mean difference score for the SGS in the 48h-BVC-DF group was -10.31, in the 30d-BVC-DF group was -3.64, and in the N-ULS-DF group was -9.47. The overall F proved to be significant ($F(2,4) = 7.55, p < .05$), however, the post hoc analysis using a Scheffe test indicated that the difference between the 30d-BVC-DF group and the N-ULS-DF groups was not statistically significant ($F(2,4) = 9.13, p > .05$) and that the difference between the 48h-BVC-DF group and the N-ULS-DF group was not significant either ($F(2,4) = 11.96, p > .05$).

The mean difference score for the SO in the 48h-BVC-DF group was -4.13, in the 30d-BVC-DF group was -2.74, and in the N-ULS-DF group was -5.52. The overall F proved not to be significant ($F(2,4) = 1.86, p > .05$).

The mean difference score for the SGM in the 48h-BVC-DF group was -0.92, in the 30d-BVC-DF group was -0.34, and in the N-ULS-DF group was 0.14. The overall F proved not to be significant ($F(2,4) = 0.1, p > .05$).

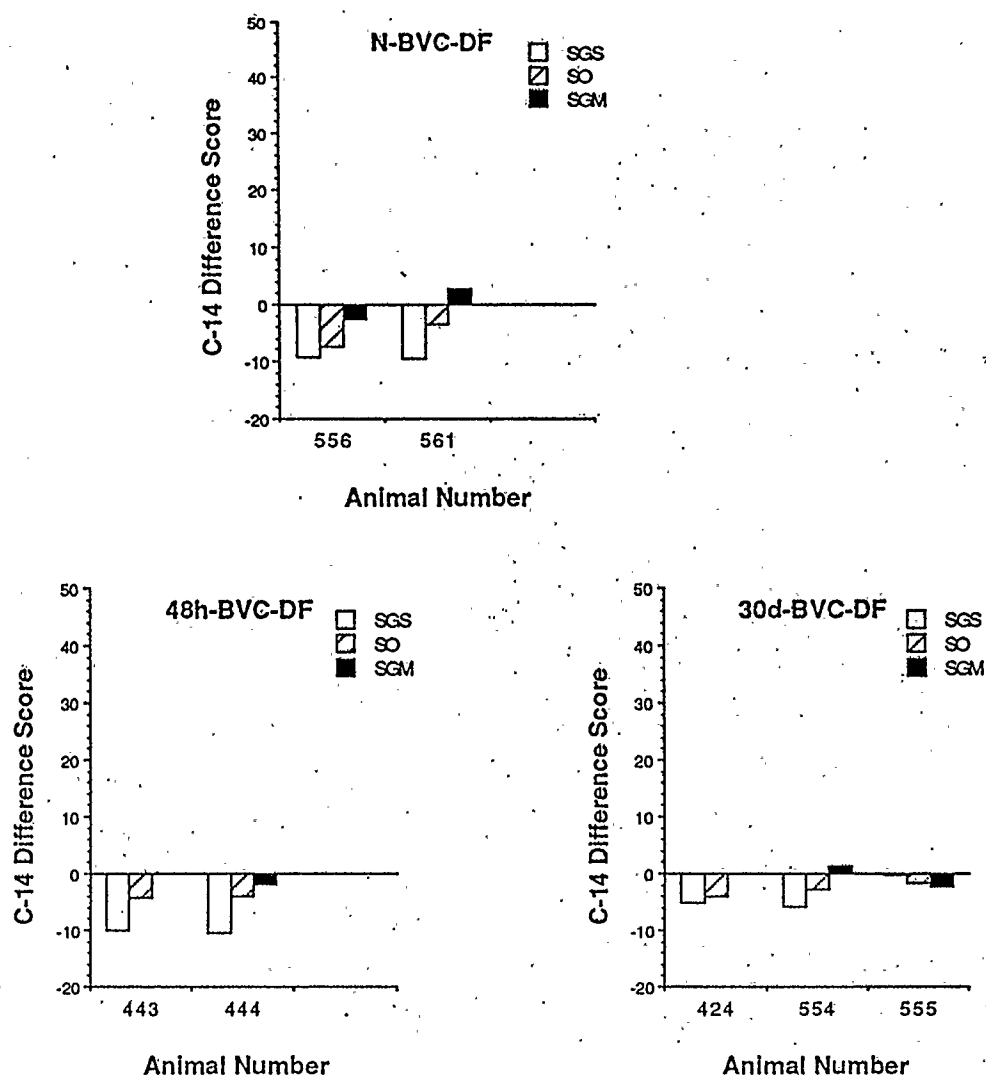


Figure 9. Carbon-14 differences between the colliculi in SGS, SO, and SGM in each rat monocularly exposed to diffuse light. Negative values indicate that the SC fed by the lid-sutured eye is more active than the SC fed by the eye exposed to the diffuse light.

Therefore, the results demonstrate that the asymmetry between the superior colliculi for rats with unilateral VC ablations is of the same amount regardless of the visual condition, provided that the comparisons are made between rats that have been allowed similar recovery intervals. Furthermore, within each visual condition, the bilateral VC ablation monocularly exposed groups and intact monocularly exposed control groups do not differ significantly from one another in terms of collicular asymmetry regardless of the recovery interval of the bilaterally ablated animals.

Discussion

The asymmetry observed between the contralateral and ipsilateral SC of the unilateral VC ablation animals in the moving gratings condition and diffuse light condition did not differ significantly from the asymmetry observed in unilateral VC ablation animals of equivalent recovery times in the binocular lid-suture condition. Both the contralateral and ipsilateral SC of animals with unilateral VC ablations respond to the moving gratings and diffuse light conditions with equivalent increases or decreases in 2-DG uptake. In addition, the moving gratings and diffuse light displays had their normal effects on tectal 2-DG uptake in rats with bilateral VC ablations. Therefore, the results of Experiment II suggest that under the three visual stimulation conditions used, cortico-tectal and retino-tectal projections act independently in governing uptake of 2-DG in the rat SC. Cortico-tectal and retino-tectal afferents appear to combine in an additive manner to affect 2-DG uptake in the SC under these three visual conditions.

Currently, it is not clear whether the 2-DG technique reflects primarily afferent activity or activity of the cell soma. It has been suggested by several researchers that the 2-DG technique reflects primarily afferent activity (Auker, Meszler, and Carpenter, 1983; Kadekaro, Crane, and Sokoloff,

1985; Nudo and Masterton, 1986; Ryan and Sharp, 1982; Sharp, 1976), whereas others have suggested that 2-DG uptake occurs primarily in the cell soma and proximal dendritic processes (Durham and Woolsey, 1985; Durham, Woolsey, and Kruger, 1981) and that there is a high correlation between the electrophysiological activity and 2-DG labeling of neurons (Peschanski et al., 1986). The results of this experiment may be interpreted in two very different ways depending upon whether 2-DG uptake reflects primarily afferent activity or the activity of the cell soma.

If it is true that 2-DG uptake reflects primarily afferent activity, then the intertectal asymmetry observed in Experiments I and II following unilateral VC ablation suggests the removal and/or depression of cortical-tectal afferent activity. The results would also carry with them the implication that under these three visual conditions, retinal and cortical afferents to the SC do not interact prior to synapsing on units in the SC. The studies of Wickelgren and Sterling (1969b) and Berman and Sterling (1976) suggest that cortical suppression of retinal input may be present in visually deprived and normal cats. The results of Experiment II suggest that if this phenomenon occurs in the rat, it is not the result of presynaptic control of ganglion activity by cortical neurons. For example, if cortico-tectal projections had been responsible for inhibiting ganglion cell afferent activity in the SC via presynaptic inhibition, a unilateral VC ablation should have produced disinhibition, and this should have resulted in an increase in 2-DG uptake in the ipsilateral SC. This in turn would have produced an intertectal asymmetry less than that observed following unilateral VC ablation under binocular lid-suture conditions. However, the intertectal asymmetry observed in the unilateral VC ablation animals was similar under all visual conditions when the survival times were also equivalent. Therefore, if 2-DG uptake reflects

primarily afferent activity, then this experiment suggests that cortical and retinal afferents do not interact prior to synapsing upon units in the SC under the three visual conditions presented.

If the 2-DG technique reflects primarily the activity of the cell soma, then the intertectal asymmetry observed in Experiments I and II reflects a SC that has not changed its relationship with the retina, but that is metabolically depressed as the result of the removal of a facilitatory cortical afferent activity. It is possible that such a SC could be functionally depressed due to a reduction in the output of units in the SC.

Sprague (1966) used perimetric testing to determine the functional visual fields of unilateral visually decorticate cats and demonstrated a total contralateral hemianopia similar to that found in cats with unilateral SC ablations (Dreher, Marchiafava, and Zernicki, 1965; Myers, 1964; Sprague and Meikle, 1965), a finding which provides some support for the suggestion that the intertectal asymmetry observed in Experiments I and II represents a functionally depressed SC and not just the removal of afferent activity from the neuropil. Sprague hypothesized that following unilateral VC ablation, the SC no longer carried out its normal role of mediating visually guided behavior because it was functionally depressed, partially as a result of the removal of a facilitatory cortical input. Furthermore, Goodale (1973) examined the visually evoked potentials in the SC of rats before and after destruction of ipsilateral VC, and reported that following ipsilateral ablation of the VC, there was a depression of the light-evoked response in the ipsilateral SC. Goodale suggested, in agreement with Sprague's position, that normally the intact SC is under the influence of an ipsilateral cortical-tectal facilitation. Moreover, Schneider (1975) reported that after near-total unilateral removal of neocortex, adult hamsters demonstrate

a complete contralateral hemianopia on tests of visually elicited turning. This deficit is followed by very slow recovery, with some responsiveness beginning to return at about six weeks following the ablation. However, normal pursuit movements appear to never return. Schneider concluded that unilateral VC ablation resulted in a functionally depressed ipsilateral SC, and described this phenomenon as a cortico-tectal diaschisis effect. Finally, Ogasawara et al. (1984), using the electrophysiological unit recording technique, reported that VC inactivation depresses units in the cat SC, and concluded that cortico-tectal projections were primarily of a tonic facilitatory nature. Therefore, there is evidence in the literature that unilateral VC ablation results in a functionally depressed ipsilateral SC.

In summary, from Experiment II, it can be concluded that cortical and retinal projections affect 2-DG uptake in the SC independently and additively under binocular lid-suture, moving gratings, and diffuse light stimulation. However, what this experiment reveals about cortico-tectal interactions is dependent upon whether 2-DG uptake reflects primarily afferent activity or the activity of the cell soma. If 2-DG uptake reflects primarily afferent activity, then Experiment II reveals nothing about the nature of cortico-tectal interactions. It does suggest, however, that under the three visual conditions presented in Experiment II, cortico-tectal and retino-tectal projections do not interact prior to synapsing on tectal units. If the 2-DG technique reflects primarily the activity of the cell soma, then it can be concluded that cortico-tectal projections are primarily facilitatory, and that a VC ablation does not alter the relationship between the SC and the retina.

Chapter 4. Experiment III: Role of Retino-Tectal Projections in Recovery from Depressed 2-Deoxyglucose Uptake in Rat Tectum following Visual Cortex Ablation

Experiment III was an additional test of whether the relationship between the eye and the tectum is altered by VC ablation. If the 2-DG technique reflects primarily afferent activity, then the recovery observed in Experiments I and II over the 30 day interval may represent the gradual replacement of the vacated synapses by collaterals from other inputs to the SC. Thurlow and Cooper (1985) found that following optic nerve section, there is an initial reduction in 2-DG uptake in the denervated SC, that this is followed by recovery towards normal 2-DG uptake, and that a subsequent cortical ablation results in a greater than normal decline in 2-DG uptake in the SC. Thurlow and Cooper hypothesized that the recovery towards normal 2-DG uptake following optic nerve section was possibly due to a proliferation of cortico-tectal nerve endings. Several studies (Cotman and Nieto-Sampedro, 1984; Liu and Chambers, 1958; Raisman, 1969) have demonstrated that when the afferents from one source are removed via denervation, remaining afferents take over the vacated synapses.

The purpose of this experiment was to determine if the recovery in 2-DG uptake by the SC in the days and weeks following a unilateral VC ablation is due to an increase in the dependence of the SC's 2-DG uptake on the activity of the retino-tectal projection. Experiment III reversed the procedure used by Thurlow and Cooper (1985). If retino-tectal neurons increase their influence on 2-DG uptake in the SC after visual decortication then their destruction should have a greater effect on 2-DG uptake in the recovered decorticate animal than the same surgery would in the intact animal. This was not found to be the case.

Method

Procedure

Subjects. Six male, Long-Evans black-hooded rats, bred from parent stock obtained from Canadian Breeding Farms and Laboratories, served as subjects. The rats weighed 170 to 320 g. They were kept on a 12 h-on 12 h-off light-dark cycle. The rats were divided into one control group and one experimental group of three subjects each.

Surgical Procedure. The rats in the experimental group were anaesthetized with sodium pentobarbital and then underwent unilateral VC ablations similar to those described in Experiment I. The rats were allowed to recover from the VC ablation for 30 days before being administered 2-DG. The rats in the control group did not receive VC ablations. For both groups, a jugular catheter was inserted 24 h prior to 2-DG administration. Also during this surgery, the rats in both groups underwent a contralateral eye enucleation followed by a binocular lid-suture.

Experimental Procedure. At the time of 2-DG administration, the rats received 100-110 μ Ci/kg injections of 2-DG via the jugular catheter. They were then placed in a dark box during the 45 minute incubation period. Forty-five minutes after 2-DG injection, the rats were overdosed with sodium pentobarbital via the jugular catheter, and the brain was removed and processed for autoradiography as described in Experiment I. Briefly, densitometer readings were taken from coronal autoradiographs through the SGS, SO, and SGM layers of the SC, converted to carbon-14 transformed values, and the differences between the carbon-14 transformed values in SGS, SO, and SGM in the contralateral and ipsilateral hemispheres obtained, as in Experiment I.

Results

The results showed that the control and experimental groups did not differ significantly from one another either in the degree or direction of asymmetry observed between the ipsilateral and contralateral SC in the SGS and SO, but that

they did differ significantly from one another in the degree of asymmetry observed between the ipsilateral and contralateral SGM.

Figure 10 shows the difference score for each rat in the control and experimental groups in SGS, SO, and SGM. Observe that the control and experimental groups do not appear to differ in the degree of depression observed in the ipsilateral SGS and SO, but that the depression in the ipsilateral SGM appears to be greater in the experimental group. The mean difference score in the SGS for the control group was 24.9. The mean difference score in the SGS for the experimental group was 23.2. The difference between the two groups was not significant in SGS ($t(4) = 0.58$, $p > .05$).

The mean difference score in the SO for the control group was 19.2, and for the experimental group was 19.5. In the SO, the two groups were not found to differ significantly in the degree of asymmetry observed ($t(4) = 0.11$, $p > .05$).

The mean difference score in the SGM for the control group was 3.6, and for the experimental group was 9.8. The control and experimental groups were found to differ significantly in the degree of asymmetry observed in the SGM ($t(4) = 4.87$, $p < .05$).

Discussion

There was no evidence to suggest that the relationship between the retina and the SC changes following VC ablation in the rat. Although the asymmetry observed in SGM following a monocular enucleation in recovered decorticate animals was significantly greater than the asymmetry observed in otherwise intact animals following a monocular eye enucleation, the difference is not of a magnitude that would suggest an increased dependence of the ipsilateral SC on retino-tectal projections following a unilateral VC ablation. If the ipsilateral SC did increase its dependence on retino-tectal projections in the SGM following unilateral

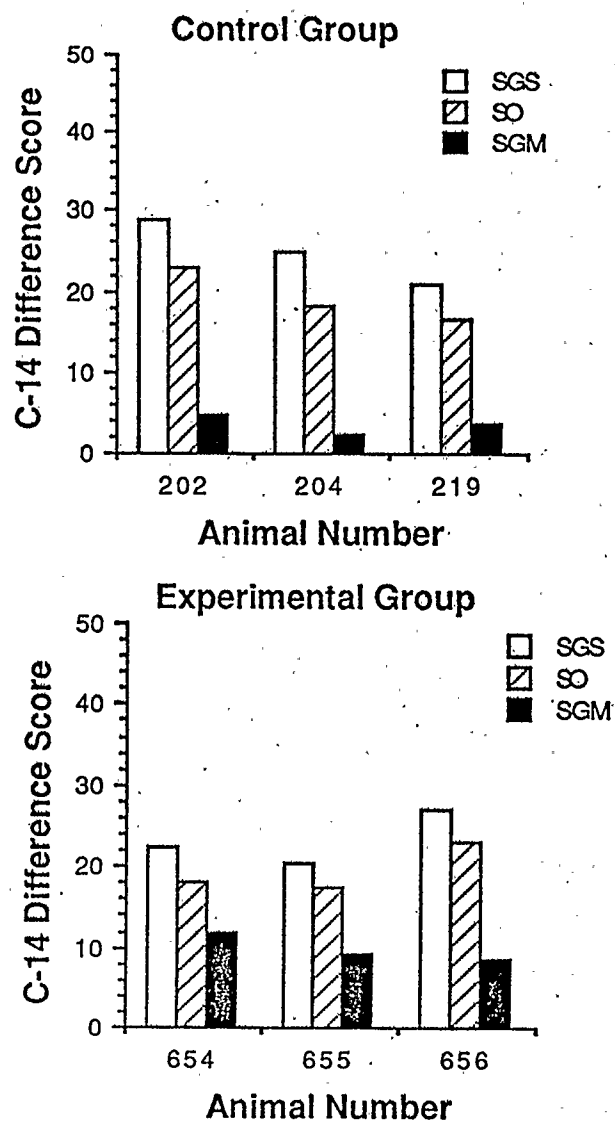


Figure 10. The C-14 difference score in SGS, SO, and SGM for each rat in the control (enucleation only) and experimental (enucleation plus 30 day unilateral VC ablation) groups.

VC ablation, then a contralateral monocular enucleation should result in an asymmetry between the colliculi in the SGM, the magnitude of which should reflect the sum of the effects of short-term VC ablation and short-term eye enucleation. From the mean transformed difference score in SGM of the control group in this experiment, one can see that the magnitude of the asymmetry usually observed in SGM following short-term monocular enucleation is approximately 3.6. In experiment I it was demonstrated that a short-term (48 h) unilateral VC ablation, in rats that had undergone binocular lid-suture 24 h prior to 2-DG administration, creates an asymmetry between the SC in SGM with a magnitude of approximately 26.8. Therefore, one would predict that if the reduction in asymmetry observed over the 30 day interval following a unilateral VC ablation were due entirely to an increased dependence of SC 2-DG uptake on the retino-tectal projection, the experimental group in this experiment would have shown an asymmetry in the SGM of approximately 30.4. The actual intertectal asymmetry observed in the SGM in the experimental group (9.8) does not begin to approach this magnitude.

The significant difference between the control and experimental groups in SGM asymmetry can be explained when one considers the asymmetry that normally exists between the SC in SGM 30 days following a unilateral VC ablation. The magnitude of this asymmetry is approximately 4.96, which is the mean depression exhibited by the three 30 day recovery groups in Experiment II. The addition of the asymmetry remaining from the VC ablation after 30 days recovery to the asymmetry that arises in SGM 24 h following a monocular enucleation (3.6) creates an expected magnitude of 8.56, which is very close to the asymmetry observed in SGM in the experimental group (9.8).

Therefore, it appears that in SGS, SO, and SGM, the decline in asymmetry of 2-DG uptake observed over a 30 day

interval following unilateral VC ablation in the rat is not due to the development of an increased dependence on retino-tectal projections by the SC. This conclusion is in agreement with the conclusion reached by Goodman and Horel (1966), who examined axonal sprouting of optic tract projections as a result of occipital cortex removal using the Nauta-Gygax method for degenerating axons, and reported that sprouting of the optic tract did not appear to occur in any layer of the SC. It is possible that some source of afferents to the SC other than the optic tract may replace the synapses vacated by the cortico-tectal afferents. However, the results of Experiment III suggest that VC ablation does not appear to change the relationship between the retina and the SC.

Chapter 5. Experiment IV: Effect of Tectal Commissure

Section on Depressed 2-Deoxyglucose Uptake in Rat

Superior Colliculus following Visual Cortex Ablation

Shortly following unilateral VC ablation in the rat, the ipsilateral SC shows a reduction in the uptake of 2-DG relative to the contralateral SC (Thurlow and Cooper, 1985) that is followed in the subsequent days and weeks by a gradual recovery towards symmetrical 2-DG uptake by the two colliculi (Experiments I and II of this study). It is not clear whether the initial reduction in 2-DG uptake by the ipsilateral SC reflects only the removal of cortical afferent activity, or whether it also reflects functionally depressed units within the ipsilateral SC.

Sprague (1966) found that cats with unilateral occipito-temporal cortex ablations exhibit visual deficits in the contralateral visual field in perimetric tests that resemble the deficits exhibited by cats following tectal ablations (Dreher, Marchiafava, and Zernicki, 1965; Myers, 1964; Sprague and Meikle, 1965). Unilateral occipito-temporal ablations produce an almost complete hemianopia in the contralateral visual field. Sprague hypothesized that this contralateral hemianopia results from the removal of an ipsilateral facilitatory cortico-tectal influence. In addition, Sprague demonstrated that ablation of the contralateral SC following a unilateral cortical ablation results in the return of visual responses to the previously hemianopic visual field. Sprague concluded that removal of the ipsilateral facilitatory cortico-tectal influence created an imbalance in an inhibitory tecto-tectal interaction, and that the combined effect of these two factors resulted in a functionally depressed ipsilateral SC. A tectal commissure section produces effects similar to ablation of the contralateral SC in cats with unilateral occipito-temporal cortex ablations, suggesting that the intertectal interaction occurs via the tectal commissure.

Several other studies also indicate that tecto-tectal interactions play a role in functional depression of the SC following VC ablation. Goodale (1973) observed an increase in the size of the visually evoked potential in the rat SC following ablation of the contralateral SC and a reduction in the size of the visually evoked potential after ablation of the ipsilateral VC. Goodale also observed that if a unilateral VC ablation is followed by ablation of the contralateral SC, the light-evoked response in the remaining SC will return to near normal levels. In agreement with Sprague's speculations, Goodale concluded that the SC is under the influence of two opposing and tonic inputs - an ipsilateral cortico-tectal facilitation and a contralateral tecto-tectal inhibition. Sherman (1974) confirmed that occipito-temporal decorticate cats are capable of visually guided behavior when intercollicular influences are removed via tectal commissure section, and Schneider (1975) demonstrated that recovery from near total contralateral hemianopia in hamsters with unilateral ablations of neocortex occurred more rapidly if the contralateral SC was undercut at the time of the neodecortication. Schneider concluded that a unilateral neocortex ablation resulted in a functionally depressed ipsilateral SC, which Schneider described as a cortico-tectal diaschisis effect. Moreover, Robert and Cuenod (1969a; 1969b) reported results consistent with the existence of an inhibitory intertectal pathway in the pigeon via the posterior and/or tectal commissures that distributed itself throughout all the layers of the optic tectum except the most superficial layers. The results of the studies cited above suggest that it is possible that the reduction in 2-DG uptake by the ipsilateral SC following unilateral VC ablation may in part be attributable to a resulting imbalance between the denervated and normal superior colliculi.

The purpose of this experiment was to examine the effects

of unilateral VC ablation on SC 2-DG uptake in rats that have undergone a tectal commissure section prior to VC ablation. If the depression in 2-DG uptake by the ipsilateral SC is reduced by tectal commissure section, then it may be concluded that intertectal interactions are partially responsible for the depression in 2-DG uptake typically observed 48 h following unilateral VC ablation. Any depression that might be observed in the ipsilateral SC following both tectal commissure section and unilateral VC ablation may be attributed to factors other than tecto-tectal interactions, such as reduction in the activity of the units within the SC as the result of the removal of a facilitatory cortico-tectal influence, and/or a reduction of activity in the neuropil as a result of the removal of afferent activity originating from VC.

Method

Procedure

Subjects. Five male, Long-Evans black-hooded rats, bred from parent stock obtained from Canadian Breeding Farms and Laboratories, served as subjects. The rats weighed 170 - 320 g. They were kept on a 12 h-on 12 h-off light-dark cycle. The data from rats with 48 h and 30 day unilateral VC ablations from Experiment II of this study were used for comparison purposes.

Surgical Procedure. The initial surgery was carried out under sodium pentobarbital anaesthesia. A small hole was drilled medially in the skull above the anterior SC through which a Scouten knife was lowered to a depth that permitted sectioning of the tectal commissure. One and a half months following this surgery, and 48 h prior to 2-DG administration, a unilateral VC ablation was carried out and a jugular catheter was implanted under sodium pentobarbital anaesthesia using a procedure identical to that described in Experiment I.

Experimental Procedure. At the time of 2-DG

administration, the rats received 100-110 $\mu\text{Ci/kg}$ injections of 2-DG via the jugular catheter. They were then placed immediately in the moving gratings condition. Forty-five minutes after 2-DG injection, each rat was overdosed with sodium pentobarbital, and the brain was removed and processed for autoradiography as described in Experiment I. During cryostat sectioning, the location of the tectal commissure section was identified (see Figure 11 for location of section in each animal). Densitometer readings were taken from coronal autoradiographs through the SGS, SO, and SGM layers of the SC in the same locations as in Experiment I. Finally, the densitometer values were converted to carbon-14 transformed values and the differences between the carbon-14 transformed values in SGS, SO, and SGM in one hemisphere and the carbon-14 values in SGS, SO, and SGM in the contralateral hemisphere were examined. The difference scores in each layer of the SC were then compared to those obtained from the rats with 48 h and 30 day unilateral VC ablations in Experiment II.

Results

The analysis was carried out separately for each layer of the SC. When 48 h unilateral VC ablations were preceded by tectal commissure sections, the asymmetry observed in SO and SGM differed significantly in magnitude but not direction from animals in which 48 h and 30 day unilateral VC ablations had not been preceded by tectal commissure section. In the SGS, the 48 h unilateral VC ablation-tectal commissure animals did not differ significantly in either size or direction of asymmetry from 48 h and 30 day unilateral VC ablation animals that had not undergone a tectal commissure section previous to the VC ablation.

Figure 12 shows the differences obtained between the superior colliculi in the SGS, SO, and SGM of the rats that underwent tectal commissure section 1.5 mo. prior to unilateral VC ablation.

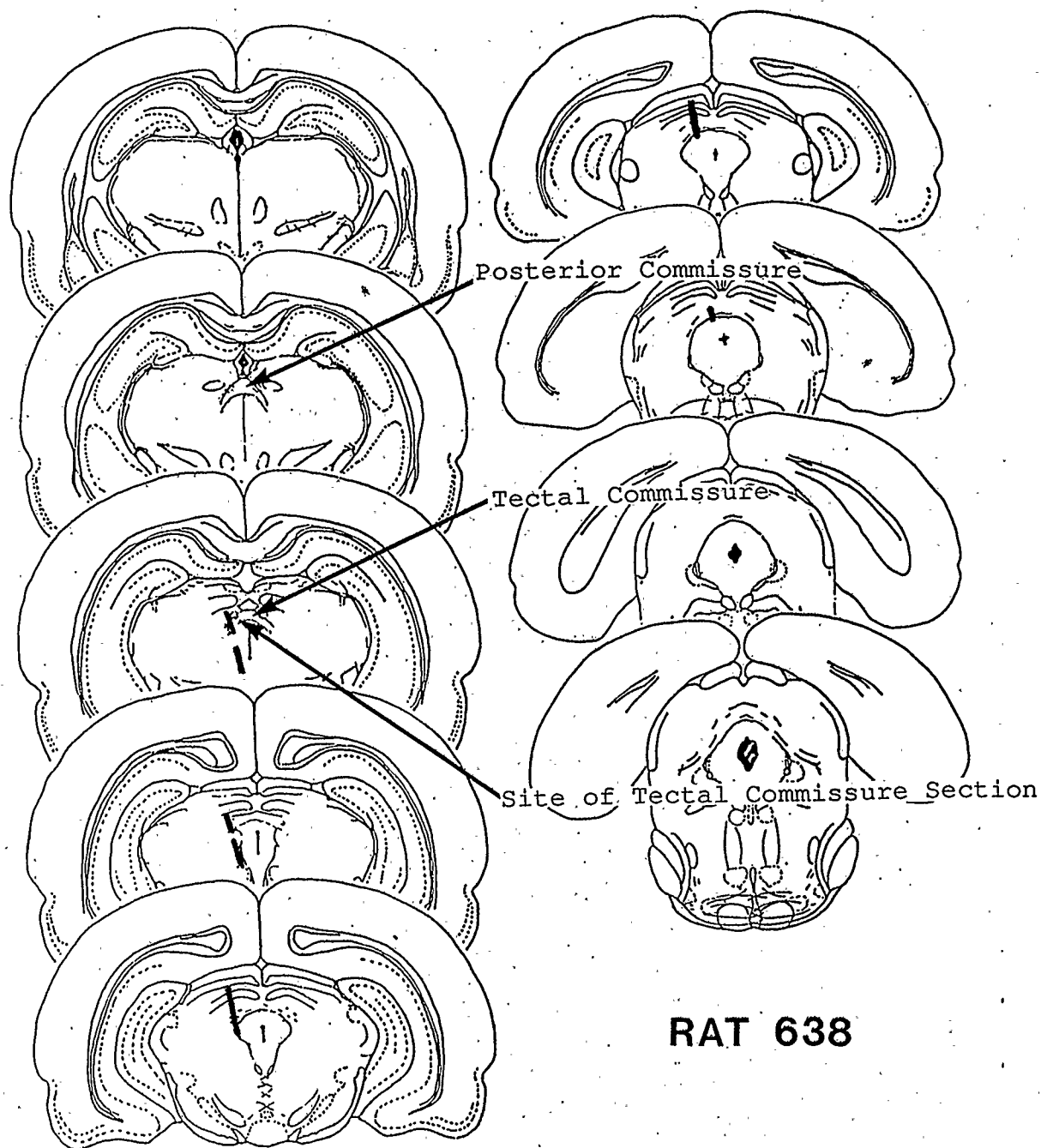
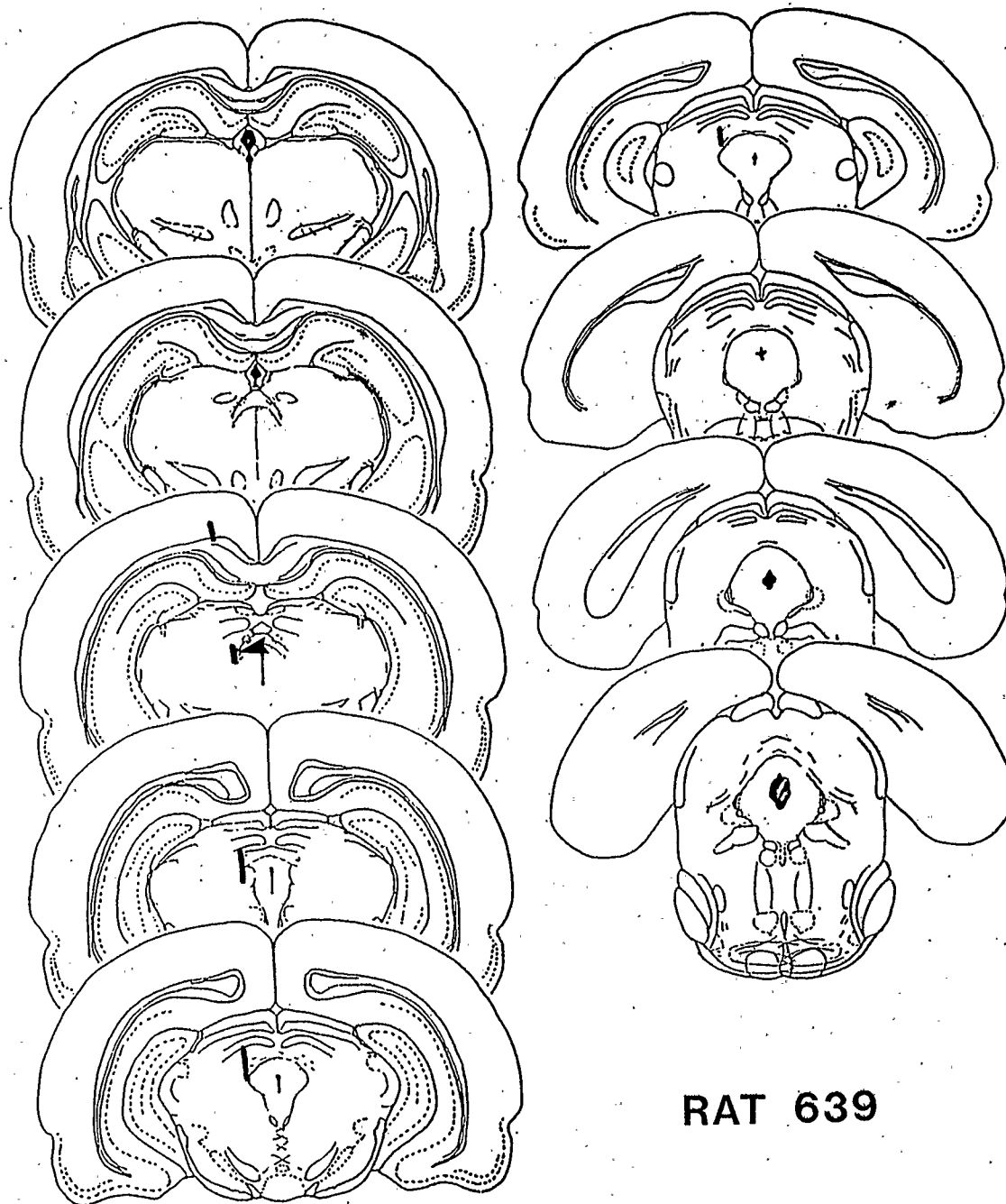


Figure 11. The location of the tectal commissure sections in rats 638, 639, 651, and 652. The location of the tectal commissure section for rat 653 could not be identified.

**RAT 639**

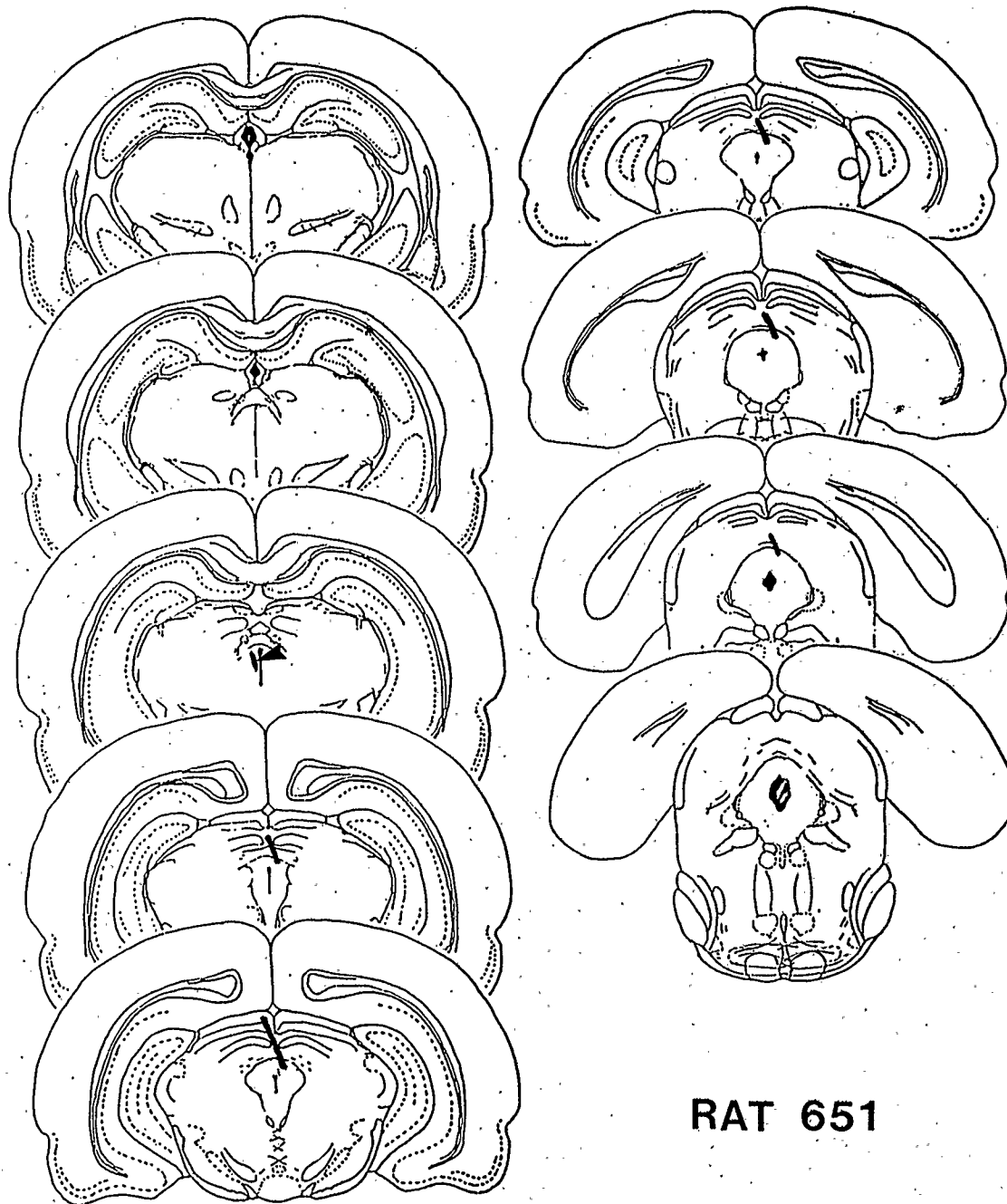
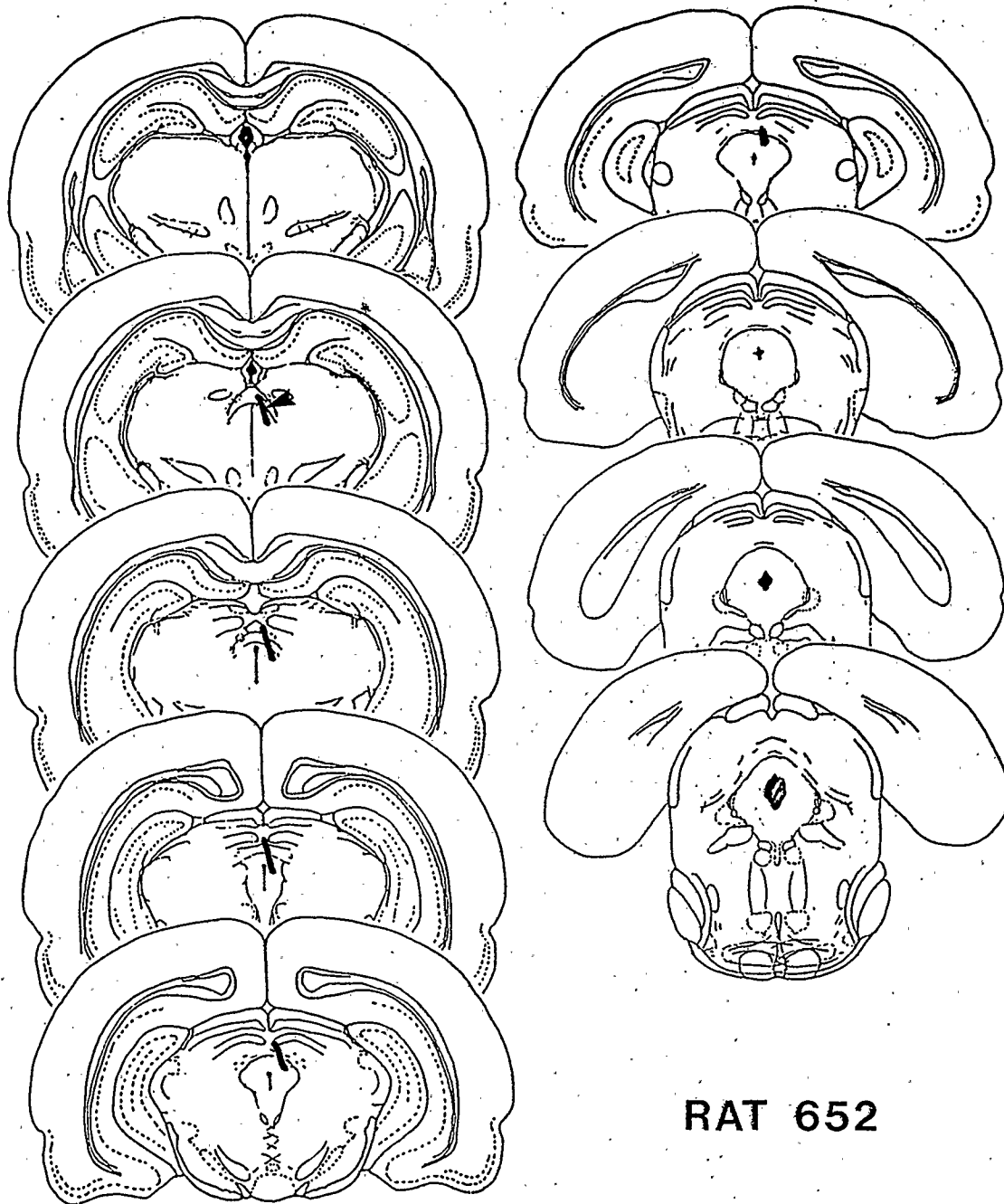


Figure 11. continued. . . .

**RAT 652**

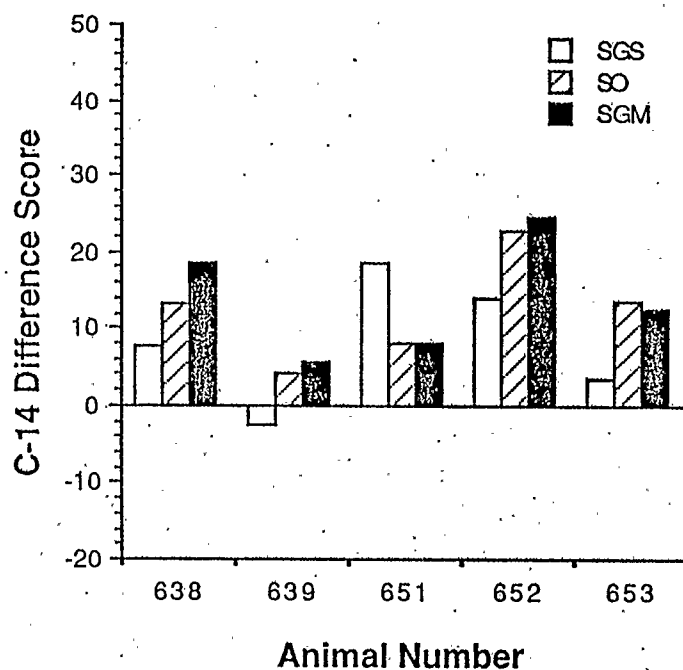


Figure 12. The C-14 differences in SGS, SO, and SGM for each of the rats with tectal commissure sections 1.5 months prior to unilateral VC ablation. Positive values indicate that the SC contralateral to the VC ablation is more active than the ipsilateral SC.

In the SGS, the mean difference between the contralateral and ipsilateral SC (positive difference scores indicate that the ipsilateral SC is depressed relative to the contralateral SC) for the unilateral VC ablation-tectal commissure sectioned animals was 9.1. Recall from Experiment II of this study that the mean difference in SGS for the 48 h recovery, unilateral ablation animals across all three stimulus conditions was 15.5, and for the 30 day recovery animals was 7.0. The difference scores in the SGS for the tectal commissure section group did not differ significantly from either the 48 h recovery animals ($t(11) = 1.5$, $p > .05$) or the 30 day recovery animals ($t(10) = 0.588$, $p > .05$), suggesting that there was a great deal of variability in the difference scores in this layer.

In the S0, the mean difference between the contralateral and ipsilateral SC for the tectal commissure sectioned animals was 12.7. Recall from Experiment II that the mean difference in S0 for the 48 h recovery, unilateral VC ablation animals across the three stimulus conditions was 19.9, and for the 30 day recovery animals was 5.4. The difference scores in the S0 for the tectal commissure ablation animals differed significantly from both the 48 h ($t(11) = 2.34$, $p < .05$) and 30 day ($t(10) = 2.53$, $p < .05$) recovery animals.

In the SGM, the mean difference between the contralateral and ipsilateral SC for the tectal commissure sectioned animals was 14.3. Recall from Experiment II that the mean difference in SGM for the 48 h recovery, unilateral VC ablation animals across the three stimulus conditions was 24.8, and for the 30 day recovery animals was 5.1. The difference scores in the SGM for the tectal commissure ablation animals differed significantly from both the 48 h ($t(11) = 6.33$, $p < .01$) and 30 day ($t(10) = 3.15$, $p < .05$) recovery animals.

Discussion

The results suggest that in the SO and SGM, tecto-tectal interactions are at least partially responsible for the depression in 2-DG uptake observed 48 h following a unilateral VC ablation. The depression in 2-DG uptake that remains after tectal commissure section and VC ablation may reflect the effects of factors other than tecto-tectal interaction, such as a reduction in the activity of units within the SC resulting from the removal of a facilitatory cortical-tectal influence, or a reduction of activity in the neuropil as a result of removal of afferent activity originating in the VC.

In the SGS, the effect of tectal commissure section is less clear. The extreme variability of the results in this layer of the SC makes it difficult to draw any conclusions regarding the influence of intertectal interactions in SGS on the uptake of 2-DG following VC ablation. The reason for the great deal of variability in this layer of the SC is unclear.

Whereas the tectal commissure section group shows significantly less depression of 2-DG uptake in the SO and SGM than the 48 h ablation groups from Experiment II, the tectal commissure sectioned group shows a significantly greater degree of depression in the ipsilateral SO and SGM than the 30 day ablation groups from Experiment II. This suggests that recovery towards more normal 2-DG uptake following unilateral VC ablation involves factors other than a reduction of the contralateral SC's inhibitory control over the ipsilateral SC during the 30 day recovery interval. For example, one factor that has already been implicated in the recovery in SGM towards more normal 2-DG uptake is recovery from the effects of generalized cortical depression (Experiment I). This experiment suggests, however, that the initial effects of generalized cortical depression may explain only a portion of the depression observed in the ipsilateral SO and SGM following unilateral VC ablation, and

that tecto-tectal interactions may account for an additional portion of the depression observed in the ipsilateral SC.

The effect of the tectal commissure section on the uptake of 2-DG in the SO and SGM is important because it demonstrates that a manipulation that affects behavior, as demonstrated by Schneider (1975), Sherman (1974), and Sprague (1966), also affects uptake of 2-DG. This supports the idea that regional cerebral utilization of glucose reflects the functional activity of this region in addition to the activity of the afferent inputs to this region. If the 2-DG technique only reflects afferent activity, then a tectal commissure section, which removes the same number of afferent inputs to each colliculus, should not affect the intertectal asymmetry observed 48 h following unilateral VC ablation. This experiment shows that tectal commissure section reduces the intertectal asymmetry in SO and SGM. Therefore, one can conclude that the 2-DG technique reflects the activity of units within the SC, although it is likely that the 2-DG technique also reflects afferent activity.

The observation that the 2-DG technique reflects the metabolic activity of units within the SC provides a basis for further interpretation of the results of Experiment II. Because it appears that units in the ipsilateral SC are depressed following unilateral VC ablation, it can be concluded that the cortico-tectal projections are primarily facilitatory for 2-DG uptake in the SC. However, it is not clear whether the cortico-tectal projections bring about this facilitation by exciting units in the SC directly or by producing disinhibition of inhibitory tecto-tectal projections. Moreover, since the intertectal asymmetry that results from 48 h unilateral VC ablation can be partially alleviated by section of the tectal commissure, there must be an inhibitory intertectal pathway in the rat.

Chapter 6. Summary and Conclusions

The effects of unilateral VC ablation on 2-DG uptake in the rat SC under conditions of binocular lid-suture were examined in Experiment I. This experiment revealed that the depressive effects of unilateral VC ablation on 2-DG uptake change with time, suggesting that in the future, studies examining changes in tectal function after a VC ablation should do so at more than one recovery interval. Additionally, the finding that the recovery from generalized cortical depression and the recovery from depressed 2-DG uptake in SGM follow similar time-courses is consistent with the notion that generalized cortical depression may be responsible for the reduction in 2-DG uptake which occurs in the deep layers of the ipsilateral SC. It also appears that the generalized cortical depression must reach a certain magnitude before this effect in the deep layers of the SC becomes obvious. However, the factors that induce generalized cortical depression and that determine its magnitude are not well understood, and should be investigated further (see Pappius and Wolfe, 1984).

In Experiment II, the effects of VC ablation on 2-DG uptake by the SC under two visual stimulation conditions, moving gratings and diffuse light, were compared to the effect of VC ablation on 2-DG uptake under lid-suture conditions. It was concluded that the ipsilateral SC reduces its baseline of 2-DG uptake as a result of a VC ablation, but that it still responds with increases in 2-DG uptake to moving gratings stimulation and decreases in 2-DG uptake to diffuse light stimulation that are of the same magnitudes as the increases and decreases demonstrated by the SC of intact animals.

Several researchers have adopted the position that 2-DG uptake largely reflects afferent activity (Auker et al., 1983; Kadekaro et al., 1985; Mata et al., 1980; Nudo and Masterton, 1986; Sharp, 1976) whereas others claim that 2-DG

uptake also reflects the metabolic activity of the cell soma (Durham and Woolsey, 1985; Durham, Woolsey, and Kruger, 1981; Peschanski et al., 1986; Yarowsky et al., 1985). The results of Experiment II left open the possibility that the 2-DG effect in the rat SC observed in Experiments I and II may have been the result of the removal and/or depression of cortical afferents to the SC. However, it was also possible that the 2-DG effect may have been caused by a depression in the activity of units intrinsic to the SC as the result of the removal of tonic facilitatory inputs from VC.

Experiment III was a further attempt to detect a change in SC operation after a VC ablation. In this case, however, the focus was on possible changes in presynaptic activity. Previous 2-DG work (Thurlow and Cooper, 1985) demonstrated that after the initial reduction and recovery in SC 2-DG uptake which occurs following optic nerve section, a subsequent cortical ablation produces a greater than normal decline in 2-DG uptake. Thurlow and Cooper's finding suggested that following optic nerve section, cortico-tectal control over SC metabolic activity is increased, perhaps by proliferation of the axonal endings of the cortico-tectal projections. This particular interpretation fits well with the position that the 2-DG technique primarily measures afferent activity. Moreover, the proliferation of remaining inputs to cells after their partial denervation is a well-established phenomenon (Cotman and Nieto-Sampedro, 1984; Liu and Chambers, 1958; Raisman, 1969). In experiment III, the procedure used by Thurlow and Cooper was reversed. First VC ablations were performed, then the animals were allowed to "recover" for 30 d and then optic nerve section was performed in order to determine whether the resulting depression was greater than normal. There was no evidence to indicate that the optic nerve had gained a greater control over tectal metabolic activity. Therefore, it was concluded that if axonal proliferation is responsible for

recovery after a VC lesion then it must come from some source other than retinal ganglion cells.

Experiment IV was designed to determine whether the depression in 2-DG uptake by the ipsilateral SC following VC ablation is primarily a reflection of the removal of afferent activity, or whether it is at least in part a reflection of a depression in the metabolic activity of units within the SC. A brief description of the rationale follows. If the 2-DG technique reflects only afferent activity, then a tectal commissure section, which removes an equivalent number of afferent inputs to each SC, should have no effect on the degree of asymmetry normally observed following VC ablation. Conversely, if the asymmetry reflects changes in metabolic activity of units within the SC, then inactivation of the intertectal pathway, a procedure that produces functional recovery in visually decorticate cats (Sherman, 1974; Sprague, 1966) and hamsters (Schneider, 1975), should reduce the asymmetry typically observed shortly following unilateral VC ablation. The results of Experiment IV suggested that the depression in 2-DG uptake in the ipsilateral SC typically observed shortly following unilateral VC ablation reflects the metabolic activity of units within the SC. However, it is still likely that 2-DG uptake reflects afferent activity in addition to the activity of units within the SC. In addition, because it appears that units in the ipsilateral SC are depressed following unilateral VC ablation, it is possible to conclude that cortico-tectal projections are primarily of a facilitatory nature to SC activity, although it is not clear whether this is brought about by direct excitation of SC units or by disinhibition of inhibitory intertectal influences. Furthermore, since this depression is partially alleviated by section of the tectal commissure, it is possible to conclude that intertectal interactions are primarily inhibitory in nature following unilateral VC

ablation.

Furthermore, based on the findings of Experiment IV, it is possible to further interpret the results of Experiment II. The results of Experiment II indicate that the retinal and cortical pathways act independently of one another in governing uptake of 2-DG in the SC, at least under lid-suture, moving gratings, and diffuse light visual stimulation conditions. If these two pathways did not act independently, then one would expect that the tectal asymmetry in the unilateral VC ablation groups in Experiment II would have varied with stimulus condition. For example, if VC were responsible for inhibiting ganglion afferent activity to the SC during diffuse light stimulation, then a 48 h unilateral VC ablation should result in disinhibition and produce an increase in 2-DG uptake in the ipsilateral SC, and therefore produce an intertectal asymmetry less than that observed 48 h following unilateral VC ablation in the binocular lid-suture condition. In fact, the observed effect was an inter-tectal difference no different from that typically observed in 48 h unilateral VC ablation animals under moving gratings and binocular lid-suture stimulation.

In summary, as a result of this research, it is possible to conclude that under the three visual conditions examined (darkness, diffuse light, and moving gratings), the projections from VC to the SC primarily facilitate uptake of 2-DG in the SC. Some of the findings of this investigation suggested that 2-DG activity in the SC might primarily reflect the afferent activity reaching the SC. However, it was concluded that 2-DG uptake in the SC must reflect, at least partially, the activity of units intrinsic to the SC. Following this, it was concluded that the retinal and cortical afferent pathways act on the SC independently of one another. Finally, it appears that tecto-tectal pathways are primarily of a tonic inhibitory nature.

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