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## Strategies for Analyzing Complex Organization in the Nervous System. II. A Case Study: Directed Movement and Spatial Representation in the Frog

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In chapter 3 in this volume, I provided a series of reasons for believing that an intermediate level experimental strategy, as distinct from strategies in which one begins with the neuron and works up or begins with computational problems and works down, provides a viable and productive way to explore the complex information-processing characteristics of the nervous system (see also Grobstein 1987, 1988a, 1989). That general discussion reflected a series of experiences in trying to make sense of the neuronal organization that intervenes between the retinotectal projection and directed movement in the case of orienting behavior in the frog. In this chapter, I want to provide somewhat more detail about these experiences. My hope is that this chapter will serve not only as a concrete illustration of the strengths of an intermediate level approach to complex information-processing systems but also as a contribution to the development of specific intermediate information-processing concepts valuable in discussing brain organization. Of concern in this regard is the nature of the relation between neuronal networks and input-output relations in brain function, and the problem of how spatial information is represented in the nervous system.

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### Beginning in the Middle

It has long been known that in the frog, as in other vertebrates, the retina projects to the opposite tectal lobe in a topographic fashion, that stimuli activating particular retinal and tectal loci trigger ballistic movements directed toward the stimulus, and that local lesions of the tectum result in a failure to turn toward prey stimuli at locations in the visual field predictable from the organization of the retinotectal projection (for reviews see Ewert et al. 1983; Ewert 1987; Grobstein et al. 1983; Grobstein 1988a, 1989; Ingle 1983). Our own interests in the posttectal circuitry involved in orienting in the frog began with the discovery that orienting movements apparently identical to

those elicited by visual stimuli could also be triggered by appropriate tactile stimulation (Comer and Grobstein 1978, 1981a). This led to lesion experiments designed to test, in the sense defined in chapter 3, a then (and still) prevalent, intermediate-level, general hypothesis: that tectum is an essential final common path for the triggering of orienting movements by all relevant sensory modalities. Our finding that tactile orienting survives tectal lesions (Comer and Grobstein 1978, 1981b) clearly established that tectum in the frog is not an essential component of the circuitry underlying tactually elicited orienting: tactile information need not pass through tectum to cause directed movements. The experiments showed not only that there exist adequate nontectal paths by which tactile information can reach premotor circuitry underlying directed movements but, more importantly in the present context, that directed movements themselves survive tectal lesions and, hence, that premotor circuitry adequate to generate such movements also exists outside the tectum. This seemed to us to provide an approach to a behavioral phenomenon in terms of intermediate level neuronal concepts: the problem of accounting for orienting behavior could be tentatively regarded as the problem of characterizing the nature of the coupling between locations in a sensory map and elements of a repertoire of directed movements created by premotor circuitry at some nontectal location.

Given this phrasing of the problem, prior work by others in both anuran orienting and primate saccade control (see Grobstein 1988a for references), and our own work on tactile orienting, a reasonable intermediate level model of the circuitry underlying orienting emerged, as illustrated in figure 1A. Two two-dimensional sensory maps, a visual map in the tectum and a tactile map in the underlying torus semicircularis (Comer and Grobstein 1981c), were each presumed to project in a map-like fashion and to converge onto common premotor circuitry, circuitry responsible for generating the various motoneuron discharge patterns that constitute the frog's repertoire of directed movements. The maps were known to exist. Distinct pattern-generating circuitry, convergence, and map-like projections were all inferences, reasonable from existing information but unproven. In this regard, what is of particular relevance in the present context is that the model was made up entirely of intermediate level elements; the reality of these elements can, at least in principle, be evaluated without concern for cellular details

(chapter 3). Additionally significant is that relatively few such elements seemed to be necessary to account for orienting behavior.

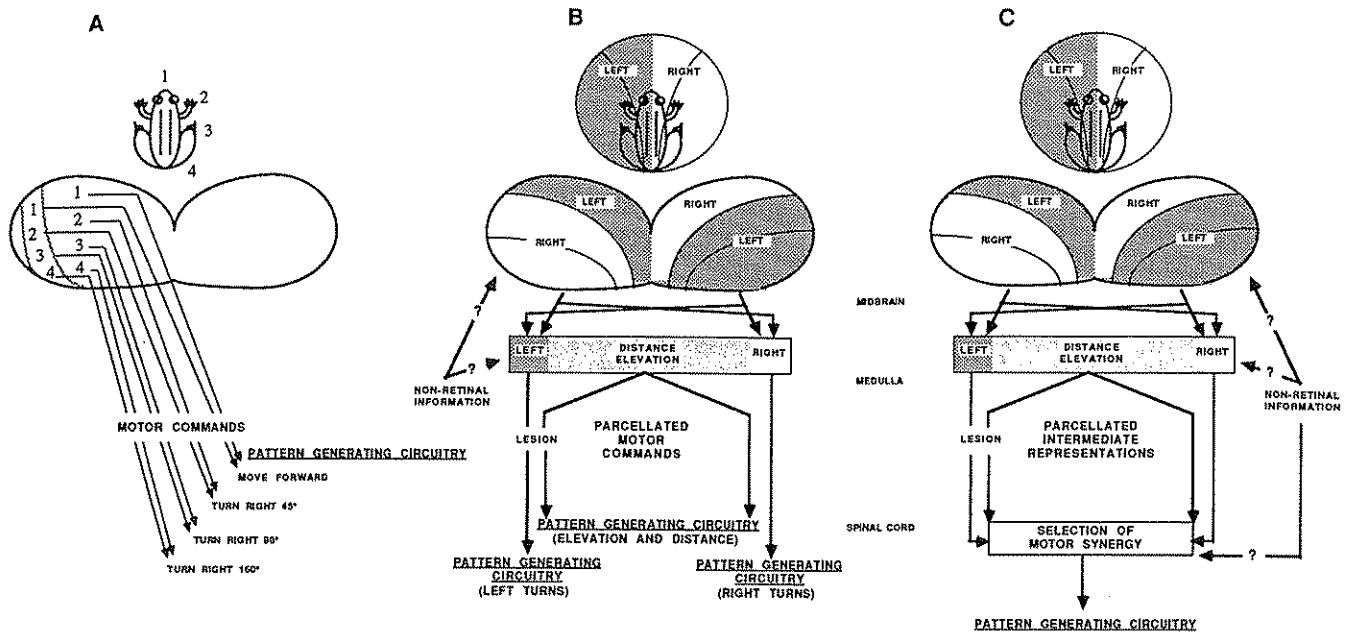
In the following, I want to consider the validity of two particular aspects of this model: the notion that the linkage between sensory maps and pattern-generating circuitry is "map-like," and the issue of whether the number of intermediate level processing elements in the model is in fact adequate to account for directed movement in the frog. The observations to be discussed also bear on the existence and character of pattern-generating circuitry, and on the hypothesis that visual and tactile signals converge at or prior to such circuitry.

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### Activity-Gated Divergence

I have treated this topic at some length elsewhere (Grobstein, 1988a, 1989), from a somewhat more theoretical point of view, and will briefly summarize that argument here, before considering the matter from a different perspective, one more germane to this chapter. The basic point is that the hypothesis of a map-like linkage between a sensory map and a repertoire of directed movements is tenable only in a restricted set of circumstances: those in which not only activity in the sensory map but also the repertoire of directed movements can both be described in terms of coordinate frames that have the same dimensionality and that are, in addition, stable with respect to one another. If this is not true, and it turns out to be not true in some perhaps surprisingly simple situations (Fukson et al. 1980), the hypothesis of a map-like sensorimotor interface can be eliminated on theoretical grounds.

The situation of prey orienting in the frog turns out to satisfy neither of the two requirements. The retinotectal projection, at least to a first approximation for present purposes, is a two-dimensional structure: the locus of activity within it can be adequately described in terms of two independent variables. The orienting movements of frogs, in contrast, vary with stimulus location in all three dimensions of Euclidean space: there is no way to describe the repertoire of orienting movements using fewer than three independent variables (Ingle 1970, 1972; Comer and Grobstein 1981a; Reyes and Grobstein 1984; Grobstein et al. 1985; Grobstein 1988a). Less abstractly put, the input-output relations of frog orienting are more complex than would exist if there was a one-to-one correspondence between retinotectal locus and element of a



**Figure 1.**

Evolution of intermediate level models to account for prey-orienting behavior in the frog. (A) An early model involving sensory maps, and map-like motor command projections to pattern-generating circuitry. Numbered stimulus positions indicate locations of prey items around a diagrammatic frog. These locations are mapped by the retinotectal projection to the contralateral lobe of the optic tectum, as shown by the right set of numbers on a drawing of the tectum as seen from a dorsal view. The locations are also mapped by an unknown somatosensory projection to the underlying torus semicircularis (the left set of numbers within curved, lighter lines). Each local tectal and toral region is presumed to give rise to a distinctive pattern of projections that converges on pattern-generating circuitry at some unknown brain location. As shown by the arrows, the projections are presumed to engage pattern-generating circuitry in a map-like fashion, i.e., such that activity at any given tectal or toral location causes a particular and distinctive movement. The projections thus constitute a spatially organized motor command system. Adapted from Grobstein et al. 1983.

(B) A later model involving a sensory map, and an intermediate-processing stage creating a lateralized and parcellated motor command signal. The upper part of the figure schematizes the visual world of a frog as represented on a hemispherical dome centered on the frog. Curved lines show the edges of the visual fields of the right and left eyes. Space between these lines is seen by both eyes and represented on both tectal lobes as schematized in the middle part of the figure. Each hemifield is represented in both tectal lobes, as indicated by labels and by shading corresponding to the left hemifield. Subsequent to the midbrain but prior to the medulla, information leaving the tectum (arrows) is presumed to be reorganized (rectangle). The effect of this reorganization is to produce a lateralized and parcellated motor command (arrows going

to pattern-generating circuitry). Signals from either tectal lobe that trigger left turns descend on the left side of the brain and those that trigger right turns on the right. A separate, bilateral projection system carries signals related to stimulus elevation and distance. The model presumes that normal three-dimensional movements result from parallel and independent activation of pattern-generating circuitry for turns and for components of movement related to stimulus elevation and distance. A left-sided lesion, as illustrated, spares rightward turning because of the lateralization of the turning components of motor commands. It also spares movements related to stimulus elevation and distance, because of the bilateral projection of the component of the parcellated motor command related to these variables. Nonretinal information involved in determining the particular movement associated with activation of a given tectal locus may enter the system at either of two levels, as indicated. Adapted from Grobstein 1988a.

(C) Our current model, involving an intermediate spatial representation and an additional processing step that, like pattern-generating circuitry, is located in the spinal cord. The model is identical to that in B through the caudal midbrain and the production of lateralized and parcellated descending signals. These signals, however, rather than being components of a motor command in the sense of directly addressing pattern-generating circuitry, are components of a spatial representation signal that must be combined prior to the selection of particular response motor synergy and subsequent activation of pattern generators. A left-sided lesion, in this case, selectively eliminates leftward turning by eliminating the leftward horizontal eccentricity component of the parcellated spatial representation signal. Since the lesion is prior to circuitry involved in motor synergy selection, the model accounts for the parallel alterations in turning and motor synergy observed in lesioned animals. Adapted from Grobstein 1988a.

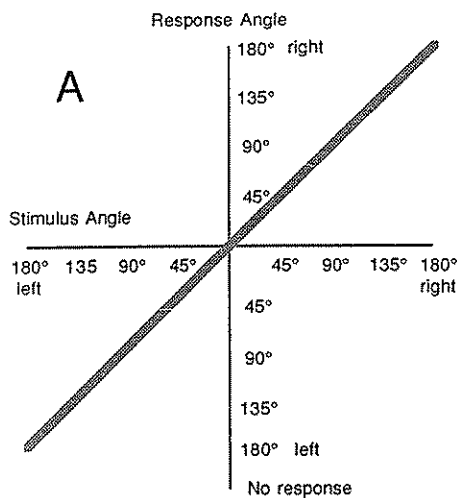
movement repertoire. Activation of a given locus in the retinotectal map is not associated with a single invariant movement. Instead activation of a given locus must be associated with an array of possible movements, with the actual movement triggered being determined by some other signal (probably not retinal) related to stimulus distance (Ingle 1972; Collet and Harkness 1982; Grobstein et al. 1985). This provides a specific example of what I have called an "activity-gated divergent network" (Grobstein 1988a,b, 1989), an organization in which activity at a given location in the nervous system may have any of a variety of outcomes, depending on the pattern of some other contemporaneous activity. A similar requirement for an activity-gated divergent network, rather than for a map-like relation between the retinotectal projection and movement, follows from the instability of the retinal relative to the movement coordinate frame. Frogs accurately direct movements from a variety of different postures, indicating that the movement triggered by activation of a given retinotectal locus must vary with signals related to postural control (Ingle 1970; Reyes and Grobstein 1984). Other signals too are probably involved (Grobstein et al. 1985).

In the present context, two points are worth making in connection with these conclusions. The first is that they call attention to an aspect of neuronal information processing that seems to me to have been somewhat neglected in recent years, as argued in Chapter 3 of this volume. Network structure is unquestionably an important determinant of the information-processing characteristics of the brain, but it is by no means the only such determinant. To predict the output associated with a given input, one needs to know not only the network structure but the pattern of activity in the network at the time the input occurs. Lashley was, to my knowledge, the last person to call general attention to this important reality (Lashley 1951), but it is by no means an idiosyncrasy of frog orienting (Forssberg et al. 1975; Fukson et al. 1980; Mays and Sparks 1980; Croll et al. 1985). The background activity pattern is an important store of information relevant to the processing of any given input signal, in some ways comparable to the software contribution to information processing in a computer, although in general probably less temporally stable. It stems in part from other current and recent inputs (many of which may be reafferent rather than genuinely exteroceptive signals) but also from endogenous activity. My suspicion

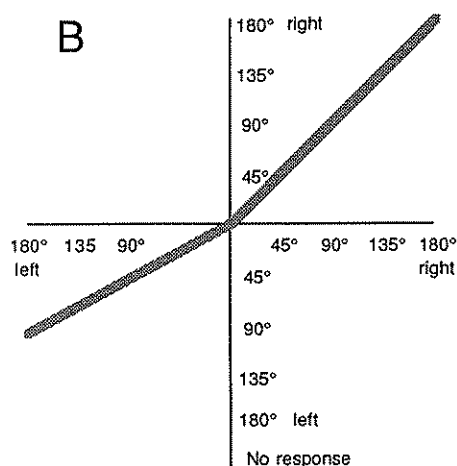
is that neuronal computation (and probably computation in general) will not be fully understood until, as Lashley urged, more explicit attention is given to the forms of representation of information in background activity patterns and to how these interact with information arriving along input pathways (see chapter 3 for more general discussion).

The other aspect of the theoretical arguments for the existence of an activity-gated divergence network underlying orienting in the frog that is significant in the present context is that the theoretical issues were recognized post hoc. What actually followed from our original studies on tactile orienting behavior was a second set of lesion studies (Kostyk and Grobstein 1982, 1987a,b,c) aimed, as discussed below, at an entirely different intermediate level question. It was oddities in the behavior of the animals in these studies, similar to some we had seen in our tactile studies (Comer and Grobstein 1981b), that first suggested to us the existence of an activity-gated divergent network. Theoretical considerations of why such a network might be present (Grobstein et al. 1983), and efforts to determine whether these applied to the frog (Reyes and Grobstein 1984; Grobstein et al. 1985), actually followed from the experimental observations, rather than preceding them. The point is worth making not only as an example of the usefulness of lesion experiments and of the style of an intermediate-level analysis (chapter 3) but also because the original observations are significant in their own right, and have proven useful in a subsequent context, as I will describe further below.

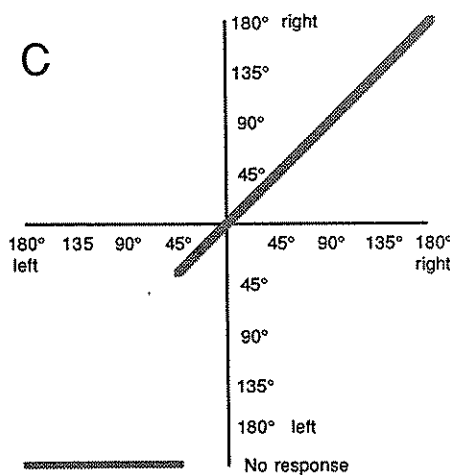
What we observed is that subtotal lesions of what we believed to be the descending tectofugal pathways did not either disconnect any given region of tectum from pattern-generating circuitry or result in movements whose internal organization was itself recognizably abnormal. Instead, they caused a systematic alteration in the particular motor patterns (apparently themselves normal) triggered from all of one or both tectal lobes; this consisted typically of a reduction in horizontal turn amplitude for stimuli at locations throughout one or both visual hemifields (Kostyk and Grobstein 1982, 1987a,b,c; compare figure 2A and B). The lesion observations sufficed to establish that the organization of descending pathways is such as to allow the triggering of not one but a number of different normal movements from a given tectal locus, but not, given the logic of interpretation of lesion experiments (Grobstein, this volume), to show that this kind



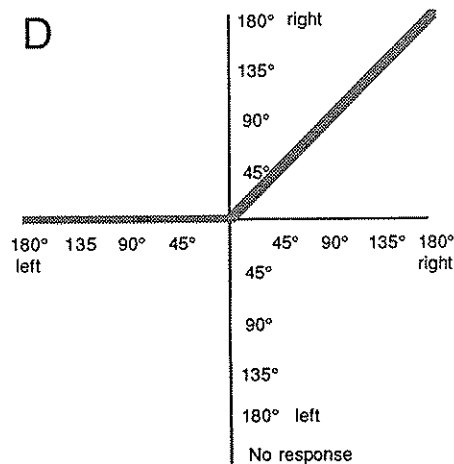
NORMAL ANIMALS



PARTIAL UNILATERAL MEDULLARY LESION



UNILATERAL TECTAL LESIONS



COMPLETE UNILATERAL MEDULLARY LESIONS

Figure 2.

Schematized representations of behavior observed in normal and lesioned frogs. (A) Normal animals. Stimulus angle, in terms of degrees around the frog to the right and left of the mid-sagittal plane, is shown on the abscissa. Response angle, similarly measured, is on the ordinate. Any stimulus locations at which animals fail to respond are noted in this and the following at the bottom of the display (No response). Normal frogs typically respond for all stimulus positions with a rapid movement directed toward the stimulus, as indicated by the angled line. Actual data for individual animals are given in Kostyk and Grobstein 1982, 1987a. (B) Animals with partial unilateral lesions of an identified white tract in the caudal midbrain or at the junction between the medulla and the spinal cord. Typical behavior is shown as for normal animals; a left-sided illustration is presumed. Note that the slope of the angled line is less than normal, indicating that movements undershoot the stimulus locations. The slope varies substantially from case to case in a population of lesioned animals. In a small number of cases, the slope in one region of the hemifield differs somewhat from that in another region. Actual data for individual animals are given in Kostyk and Grobstein 1987b and Masino and Grobstein 1989a. (C) Animals with unilateral tectal ablation. Typical behavior is shown as for normal animals; a right-sided lesion is presumed. Note that animals fail to respond to stimuli in the monocular visual field (peripheral to about 45°) contralateral to the lesion. Normally directed movements occur for remaining stimulus positions that comprise the entire visual field of one eye. Response frequency for binocular field positions in a population of lesioned animals varies somewhat from case to case. Actual data for individual animals are given in Kostyk and Grobstein 1982, 1987a. (D) Animals with complete unilateral interruption of an identified white tract in the caudal midbrain or at the junction between the medulla and the spinal cord. Typical behavior is shown as for normal animals; a left-sided lesion is presumed. Note that animals respond normally only within one visual hemifield, an area smaller than the visual field of one eye. For all stimulus locations in the ipsilateral hemifield, animals respond with forwardly directed movements, as discussed in the text. Actual data for individual animals are given in Kostyk and Grobstein 1982, 1987a,b and Masino and Grobstein 1989a.

of potential variability is significant in normal behavior. There exist a number of alternate interpretations of the finding that damage alters the movement triggered by activity at a given tectal locus (Kostyk and Grobstein 1987b); hence our concern for establishing whether different movements actually ought to result from, and in fact result from, such activity in normal animals.

The lesion findings alone, however, did allow us to eliminate from further consideration some otherwise likely forms of organization of the descending pathways, including the one with which we started. Perhaps the simplest neural realization of the hypothesis of a map-like coupling between tectum and pattern-generating circuitry would consist of a topographically organized motor command system [a "motor map," see Grobstein (1988a) for discussion in this and other systems] involving distinctive projections from each tectal region which when active cause particular movements (as shown in figure 1A). Partial damage to the projections of such a topographically organized command system should disconnect some local tectal regions from pattern-generating circuitry, and leave others normally connected. There is no reason why they should produce systematically altered movements across the entirety of one or both tectal lobes.

The one reservation that had to be dealt with before concluding from our lesion observations that a simple motor map organization does not exist related to the possibility that our lesions actually produced their effects by damaging an unknown ascending projection rather than the descending tectofugal projections. Our initial studies involved white matter lesions in the caudal mesencephalon (Kostyk and Grobstein 1982, 1987a). Retrograde labeling studies showed that tectofugal information passes through the critical lesion sites but that so too did ascending projections from structures in the medulla (Kostyk and Grobstein 1987b). More recently, we have found that identical deficits result from restricted white matter lesions at the junction of medulla and spinal cord, a location caudal to the origin of the previously identified ascending projections (Grobstein and Masino 1986; Masino and Grobstein 1986, 1989a,b). The recent findings provide strong support for our presumption that the behavioral deficits observed reflect the consequences of damage to the descending tectofugal system, and hence that this system is not organized so as to associate a particular and different movement with activity at each distinct tectal locus.

This conclusion is, of course, consistent with our theoretical conclusions, as well as, interestingly, with a number of different anatomical findings on tectofugal projections in an array of organisms (Grantyn and Grantyn 1982; Masino et al. 1984; Sereno 1985; Sereno and Ulinski 1985, Sharma et al. 1985, Masino and Grobstein 1985; Dacey and Ulinski 1986; Masino and Grobstein 1990). Noteworthy, however, is that the lesion findings described eliminated one form, but by no means all forms, of a motor map organization. MacIwain (1976, 1982) has called attention to the fact that, in mammals, a local signal in superficial tectum rapidly diverges to activate a wide array of deep tectal neurons, implying that the descending signal is coded as activity across a population of neurons coming from a fairly large tectal region; the same is true of toads (Ewert 1987). If this divergence incorporated additional signals, of the kind discussed earlier, the tectal outflow might still be regarded as a topographically organized motor command signal, one in which movement direction is coded as the activity pattern across a population of neurons rather than as activity in a small number. MacIwain suggested that partial damage to such a population coded signal might, as we observed, systematically alter the movements associated with a wide array of superficial tectal loci.

What is at issue is not whether activity-gated divergence characterizes the link between the retinotectal projection and directed movement, but where the divergence occurs. Does the tectal outflow signal code for a particular movement or is there a subsequent processing step that must occur before the movement to be made has been determined? Here, too, our lesion findings in the case of partial damage in the descending paths turned out, in hindsight, to provide an important hint. For more frontal stimuli, normal frogs characteristically respond with a directed head movement, without moving their limbs. For increasingly eccentric stimuli, the movement patterns change to involve first more forelimb movement, and then stepping components using all four limbs. What is noteworthy about the behavior of animals with partial lesions is that the deficits seemed to involve not only alterations in the amplitude of turn associated with activation of particular superficial tectal loci, but also alteration of the general character of the movements: the motor synergies (head movement, forelimb movement, stepping movements) involved in reduced amplitude turns were those appropriate for the turn amplitude seen, rather than

those that would normally be triggered by stimuli activating particular tectal regions (Kostyk and Grobstein 1987b). There is no obvious explanation for such a correlated disturbance in movement amplitude and pattern in the topographically organized command system model, even assuming some kind of distributed coding. There is, however, an explanation in terms of an unexpected intermediate processing level, as discussed in the following sections.

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### An Intermediate Spatial Representation

The partial-lesion effects that motivated our interest in activity-gated divergence, and an additional set of findings implying the existence of an unexpected form of spatial representation, both emerged from studies having a much more straightforward motivation. The organization of the retinotectal projections in the frog is such as to produce a double representation of binocular visual field, one representation in each tectal lobe (figure 1B and 1C). Correspondingly, unilateral tectal lobe lesions produce a scotoma restricted to the contralateral monocular visual field (figure 2B). Lesioned frogs fail to respond to prey items in this area, while continuing to turn accurately toward stimuli both in the ipsilateral monocular visual field and at locations to both sides of the mid-sagittal plane throughout binocular visual field. Sperry (1948) had reported that, in the newt, unilateral lesions caudal of the tectum affect orienting toward contralateral rather than toward ipsilateral stimuli, suggesting that tectal outflow, like retinal input, follows a crossed path. Sperry's observations caused us to wonder whether such a lesion in the frog would result in a monocular field deficit, like that from unilateral tectal lesions, or a hemifield deficit, implying convergence on one side of the brain of information from both tectal lobes that relates to one side of visual space. The latter proved to be the case (Kostyk and Grobstein 1982, 1987a). Following either complete unilateral hemisection or smaller unilateral lesions of a ventral white tract in the caudal midbrain, frogs fail to turn toward stimuli at any location throughout the entire ipsilateral visual hemifield, including both monocular visual field and the adjacent half of the binocular visual field, to one side of the mid-sagittal plane (figure 2D). More recently, we have found that the same deficit can be produced by similar lesions as far caudal as the junction

between the medulla and the spinal cord (Grobstein and Masino 1986; Masino and Grobstein 1986, 1989a,b).

The finding of a hemifield deficit is consistent with a convergence in the visual pathways, and has additional important implications for analysis of the anatomical structures linking tectum with spinal cord; both matters are considered at greater length elsewhere (Kostyk and Grobstein 1987b,c; Grobstein and Masino 1986; Masino and Grobstein 1989a,b 1990). What is important here is that the lesion findings established that there exists in the medulla a form of representation of spatial information that is quite different from that in the tectum. For one thing, it is oppositely and more strictly lateralized. Unilateral tectal lesions produce deficits restricted to the monocular field contralaterally; more caudal lesions affect the entire hemifield ipsilaterally. It turned out that there is an additional striking difference between the behaviors resulting from unilateral lesions in the tectum and those placed more caudally. The deficit with more caudal lesions does not involve a scotoma. Lesioned animals respond quite readily to stimuli in the ipsilateral visual hemifield. What they fail to do is to turn toward such stimuli (see Ingle 1983, for related observations). Regardless of stimulus eccentricity on the horizontal, lesioned frogs respond with an otherwise normal looking, forwardly directed movement. While not varying with the horizontal eccentricity of the stimulus, these movements, as well as those in the unaffected hemifield, do vary with stimulus elevation and distance. What this implies is that the representation of spatial information in the medulla differs from that in the tectum not only in being oppositely and more completely lateralized but also in being "parcellated," organized so that damage can selectively affect one component of a multidimensional signal, that related to turning. What it also implies is that forwardly directed movements can be triggered by descending pathways on either side of the brain and, further, that they do not require simultaneous activation of both.

What is particularly noteworthy about the form of spatial representation evident in what we presume to be the descending tectofugal pathways is not only that it is different from that in the tectum but that it has turned out to be different from that of premotor circuitry as well. Our original, straightforward interpretation of the hemifield deficit was that it reflected lateralization and parcellation of the pattern-generating circuitry for orienting, and of the descending projections linking tectal loci with such

circuitry (see figure 1B). The hypothesis, in essence, was that the forwardly directed responses of lesioned animals to stimuli in the ipsilateral hemifield reflected selective interruption of one component, that addressing pattern-generating circuitry for lateralized movement, of a multi-component descending signal, the surviving components of which addressed pattern-generating circuitry for more symmetric movements (those relating to stimulus elevation and distance). A prediction of such an hypothesis is that the movements made by lesioned animals for stimuli in the affected hemifield should be precisely those made for such stimuli by normal animals, except for the missing turn component. This turns out not to be the case.

The orienting movements of frogs vary with stimulus distance, as they do with eccentricity, not only quantitatively but also qualitatively (Ingle 1970; Grobstein et al. 1985). For nearer stimuli, the movement is a directed snap. A hop, a different motor pattern lacking a downward lunge and a tongue projection, is used for more distant stimuli. In normal frogs, the shift from one motor pattern to the other occurs at a distance of about two body lengths for frontal stimuli and at a distance of about one body length for lateral stimuli (Ingle 1970; Grobstein et al. 1985; Kostyk and Grobstein 1987a; Masino and Grobstein 1989a). If the abnormal movements associated with the hemifield deficit reflected the specific elimination of a turning component from an otherwise normal movement, the lesioned animals would be expected to snap forward for stimuli out to a distance of one body length for lateral stimuli in the affected hemifield and to hop forward for stimuli at greater distances. What they in fact do is to switch from snapping to hopping not at a distance of one body length but rather at a distance of two body lengths, the same distance at which they and normal frogs switch between motor patterns for frontal stimuli (Kostyk and Grobstein 1987a; Grobstein and Masino 1986; Masino and Grobstein 1989a).

That the qualitative character of the movement triggered by stimuli at particular distance (between one and two body lengths) is different in normal and lesioned animals clearly indicates that the deficit cannot be attributed simply to selective elimination of a signal specific to turn-generating circuitry; the deficit involves not only an absence of turning but a correlated change in motor synergy as well. More generally, the latter implies that what has been directly disturbed by the lesion is not the actual production of a motor pattern itself, regardless

of how one hypothesizes this to be accomplished. What has instead been disturbed is the outcome of a logically prior computational step, one involved in determining the selection of a particular motor pattern to be generated (figure 1C). Nor does it appear to be the computational process per se that has been disturbed. Lesioned frogs continue to exhibit orderly changes in motor pattern usage with stimulus distance. The abnormality is that these changes are those appropriate for frontal rather than for lateral stimuli. What this suggests is that the lesion, rather than disturbing a signal related specifically to horizontal movement, has disturbed one that is related more generally to horizontal stimulus eccentricity. Both the alteration from snapping to hopping in frogs that fail to turn, and the alternations in motor synergy accompanying under-shooting in animals with partial lesions as described earlier, make sense in these terms. In normal animals, the motor synergies used for stimuli at given locations vary with both horizontal eccentricity and distance. Alteration in a horizontal eccentricity signal should thus produce correlated variations in turn amplitude and motor synergy, precisely as seen in our lesioned animals.

What our lesion observations establish is the existence in the frog nervous system of a form of representation of spatial information that is experimentally distinguishable from that observed in the retinotectal projection, as well as from that inherent in any form of immediately premotor organization. It differs from the former in its lateralization, as well as its coding of horizontal eccentricity separately from other parameters of stimulus location. It differs from the latter in that, when disturbed, what results for a stimulus at a given location is not an abnormal movement pattern but rather a normal movement pattern appropriate for some other stimulus location. In this sense, what our lesion findings unexpectedly revealed to be involved in anuran orienting is an intermediate form of spatial representation, one not clearly associated with either the sensory or motor sides of the nervous system, and one of some general interest, for reasons discussed in the next section.

The simplest interpretation of our findings is that the lateralized and parcellated spatial representation is intermediate in an anatomical sense as well: that it is a characteristic of the tectofugal pathways, established somewhat between the retinotectal projection and the ventral mid-brain, and remaining stable until at least the rostral spinal cord. Assuming this to be true, our findings imply that



what leaves tectum probably ought not to be thought of as a motor command, even one of the population coded sort. The horizontal eccentricity signal presumably comes from the tectum, but a given signal horizontal eccentricity is compatible with any one of a number of movements, depending on a distance signal that can be nonretinal (see earlier references), and hence may well not come from the tectum at all. In any case, it is not until the two signals have combined, apparently in the spinal cord, that a single signal related to a particular movement could be said to exist.

This last set of inferences depends on one reasonable but not absolutely certain presumption. It remains at least logically possible that what has been disturbed by our lesions is not the tectofugal pathways themselves, but some other unknown ascending or descending system that alters the expression of information in the tectofugal pathway. This seems improbable for a variety of reasons (Masino and Grobstein 1989b, 1990), but means the issue of whether the tectal outflow is actually a motor command cannot be regarded as conclusively settled. On the other hand, the existence of an intermediate spatial representation that is somehow involved in orienting in the frog is certain, and the tentative identification of the intermediate representation with the tectofugal pathways, like any good bootstrapping hypothesis (chapter 3), defines a number of new areas of exploration. It is the outcome of these that will undoubtedly serve as the best test of not only the validity but the usefulness of the identification, and ultimately of the motor command issue as well. One would like to know, for example, whether there is any sign in tectal efferent anatomy of an organization that would extract from signals in a two-dimensional map a signal related to horizontal eccentricity. At the other end of the system, one would like to know whether there is some aspect of spinal cord organization that could account for the computational step of motor synergy selection.

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### From the Middle Outward

Our findings raise, as noted, new questions for exploration at more cellular levels, using neuroanatomical and neurophysiological techniques. At the same time, they relate to some intriguing higher order and computational problems as well, having to do with the nature of spatial representation in general. A lateralized and parcellated

organization of the kind revealed by our studies of the frog is by no means unique to this situation or organism. An organization that establishes a relation between one side of the brain and one side of behavioral space, irrespective of the laterality of the sensory surfaces generating relevant input signals, is quite common. Parietal cortex lesions in humans, for example, frequently result in neglect of visual stimuli to one side of the body midline, regardless of eye position at the time the stimulus occurs (Critchley 1953; Hyvärinen 1982). For many nonvisual modalities, it has long been known that receptors on both sides of the body are activated by stimuli to either side of the body midline. Unilateral lesions of the central nervous system, nonetheless, produce hemifield deficits in situations as diverse as mammalian sound localization (Masterton and Imig 1984), water wave localization in aquatic frogs (Elepfandt 1988a,b), and cockroach escape behavior in response to wind puffs (Comer and Dowd 1987).

The latter two cases are particularly intriguing in that, as in frogs, unilateral deficits may relate to the ipsilateral rather than to the contralateral hemifield, and be relatively specific to one component of stimulus direction. Unilateral transection of the abdominal nerve cord in cockroaches does not abolish responses to wind puffs; it disturbs the turn angle of responses to stimuli from particular directions. Certain unilateral midbrain lesions in aquatic frogs field a deficit in response to water wave stimulation very similar to what we see for grassfrogs in response to visual stimulation: absence of turns with persistence of forwardly directed movements. A similar lateralization and parcellation has been described in connection with head movement in humans (Beever 1909; Ianonne and Gerber 1982): lesions can produce a loss of ipsiversive head turns while contralateral and vertical movements are spared. The same is true of saccade control in monkeys: unilateral lesions in the pontine reticular formation abolish ipsilateral saccadic eye movements while sparing contralateral as well as vertical saccades (Raphan and Cohen 1978).

It is hard to avoid the inference that there is some rather general significance to representation of spatial information in a lateralized and parcellated form of the sort we have seen in the frog. Location in space, for most people, is probably most comfortably described in terms of three independent variables. The segregation of information related to turning from that related to

stimulus elevation and distance in the frog appears to make sense in these terms, and leads one to expect that two additional pathways, related respectively to the two additional variables of spatial location, will ultimately be identified in the frog and other organisms. Whether this proves true or not, it should be made explicit that neither lateralization nor parcellation, intuitively appealing as they may be, is an obvious consequence of the early stages of spatial processing. Initial stages typically involve map-like representations of largely contralateral sensory space, representations in which two variables are coded simultaneously in terms of representation within one structure. The need to extract one of these two variables (horizontal position) for representation separately and frequently, perhaps at some stage always, on the opposite side of the brain, is not obvious. It does, however, appear to be general, in that it occurs not only for a variety of organisms, but for a variety of stimulus modalities.

An alternate possibility to be considered is that the lateralized and parcellated spatial representation reflects characteristics of the motor side of the nervous system. Indeed, in the case of primate saccade control, it has been presumed that this is the case, that there are independent pattern-generating circuits for vertical and horizontal eye movements, with the latter subdivided into leftward- and rightward-generating circuits on the left and right sides of the brain, respectively. While this may be true for saccade control, it clearly does not hold in the frog, for reasons discussed previously, or provide a good basis for explaining the generality of a parcellated and lateralized organization. While an abstract description of spatial location can be given in terms of three independent variables, and at least three are necessary to describe a repertoire of directed movements, it is not at all clear that the motor side of the nervous system actually works in terms of the theoretical minimum of three independent variables. If the organization of the neural circuitry underlying orienting in the frog is such as to allow independent control of all involved muscles, then the number of independent motor control variables would be equal to the number of involved muscles, a number much greater than three. Given the existence of pattern-generating circuitry, which determines the activities of sets of muscles in relation to one another, a more appropriate and smaller estimate would be the number of independently controllable pattern-generating circuits. This number is unknown, but might be approximated by further lesion studies, aimed

at characterizing motor deficits following spinal cord lesions. In any case, it is almost certainly at least six (movements can vary independently not only with regard to endpoint in the three dimensions discussed here, but also with regard to endpoint pitch, roll, and yaw), and may well be higher. Regardless of the exact number, there is no obvious explanation on the motor control side of the frog nervous system for the independent representation of precisely three variables, and particularly of those three variables that one would use to characterize stimulus location in space. Nor is there any reason to see the same variables in an array of situations in which the kinds of movement involved (eye, head, body) are quite different from one another. Whatever the appropriate representation of spatial location is for motor control purposes, it is likely to vary from organism to organism, to involve more than three independent variables, and to have these relate to muscle synergies rather than to Euclidean axes.

In short, a parcellated and lateralized form of representation of spatial information follows logically from known properties of neither the sensory nor the motor sides of the nervous system, yet appears general in that it occurs in relation to a number of different sensory and motor systems. What this suggests is that such a form of representation may reflect a computational solution to a general problem, rather than a hardware idiosyncrasy of particular nervous systems. The problem of linking diverse sensory and motor representations comes up not only in thinking about a variety of animals and behaviors, but within individual animals as well. Orienting behaviors, as in the frog, can in general be triggered by inputs of a number of different modalities, and can involve a variety of different sorts of movement. Given that sense has to be made of input from a variety of different sensory systems, each with its own coordinate representation, and signals appropriately conveyed to influence circuitry responsible for a number of different motor synergies, some form of intermediate, generalized representation of spatial location may be necessary. Such a generalized form of spatial representation must of course have three independent variables but need not have any more than that. Representing the three variables in separate locations might be important to facilitate the independent variation of the variables. Other considerations, as yet to be understood, may account for the lateralization of components of a generalized spatial representation signal as well as the fact that either side of the brain alone suffices to carry signals

related to stimulus elevation and distance. Consistent with the notion that the intermediate form of spatial representation observed in the frog is a generalized one are preliminary findings indicating that parallel visual and tactile deficits result in the case of several of the lesions used to characterize visual orienting circuitry (Kostyk and Grobstein 1987a,b,c; Grobstein et al. 1988; Grobstein 1989). It may well be then that our findings on the frog can be valuable not only for issues of brain organization but for matters of abstract computation as well, complementing more formal analyses of similar problems (cf. Pellionisz 1983; Grossberg and Kuperstein 1986; Bullock and Grossberg 1988).

In this regard, there is an additional characteristic of the parcellated and lateralized form of spatial representation that should be remarked on in the present context. The representation has a distributed rather than a map-like character, certainly in one sense and probably in two. It is clearly a distributed representation in that location in space is represented by activity occurring in at least two separate structures, rather than by the location of activity in one. Given the prevalence of map-like structures in the nervous system, one has a tendency to presume that the processing of spatial information should have a map-like character. The situation in the frog should serve as a caution against the general validity of such presumptions. The representation may well also be distributed rather than map-like in the sense that even within each of the involved structures information is probably coded in ways other than the locus of activity. The partial lesion effects, discussed earlier, suggest at a minimum that a given horizontal eccentricity signal corresponds to a pattern of activity across a number of fibers rather than to activity in any particular fiber or well-defined subset of fibers. We have not systematically studied a large variety of different partial lesions, but our findings suggest that removal of any subset of fibers similarly reduces the amplitude of the horizontal eccentricity signal. If this is so, one needs to begin entertaining the notion of information representation in some form other than place-coding, such as in total activity across a fiber population. Also relevant in this regard is that what we presume to be complete removal of a population of fibers does not disrupt subsequent processing steps. It is apparently interpreted as a normal absence of activity, itself corresponding to a stimulus on the mid-sagittal plane. Taken collectively, these characteristics, together with the described lateral-

ization and parcellation, point to a form of sensory representation quite different from what one might imagine based on studies on individual neurons, and one the future analysis of which should be quite instructive.

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## Conclusions

In the past 20 years there has been an explosion of information about the properties of the cellular and subcellular constituents of the nervous system. This wealth of observation has substantially enriched the repertoire of processes that can be invoked in efforts to account for the more complex information-processing characteristics of the brain, without, however, greatly increasing understanding of the actual information processing underlying any but the simplest behavioral acts. More recently, increasing attention has been paid to the problem of characterizing at an abstract level the information-processing demands placed on the nervous system by particular behavioral acts. These efforts have contributed significantly to the creation of new contexts within which cellular observations can be considered and, more generally, have provided some explanation for the complexity of the nervous system when viewed from the cellular level. At the same time, as I argued in chapter 3, the abstract approach too can be misleading with regard to neuronal information processing, and fails to exploit the insights into computation in general that are intrinsic in the unknown computational characteristics of the brain. What is needed is an intermediate approach, at a level somewhere between the neuron and a consideration of information-processing strategies and methods in the abstract.

My hope is that this chapter will have served to supplement the general arguments for an intermediate level approach by providing an explicit example of their use in a particular case, the characterization of the organization of neuronal circuitry intervening between the retinotectal projection and directed movement in the frog. Our studies proceeded neither from an assumption that one must work up from basic elements nor an assumption that one must work down from a global analysis, but rather in both directions from the phenomenology at a level where disturbing the computational process reveals both meaningful subdivisions and the characteristics of interactions among such subdivisions. Quite rigorous and significant conclusions can be reached with this style of

analysis: that the linkage between a sensory map and the circuitry responsible for the elaboration of ballistic movement is not itself map-like but instead involves an activity-gated divergence, and that an apparently general, non-map-like form of spatial representation is involved in the linking circuitry provide two examples. These sorts of conclusions provide new questions for an approach at more cellular levels. More importantly, perhaps, the intermediate level analyses reveal the existence of computational processes from which new understandings of the computational strategies and tasks that the nervous system is designed to accomplish are provided.

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