Directed movement in the frog: motor choice, spatial representation, free will?

The sooner we recognize the fact that the complex higher functional Gestalts which leave the reflex physiologist dumbfounded in fact send roots down to the simplest basal functions of the CNS, the sooner we shall see that the previously terminologically insurmountable barrier between the lower levels of neurophysiology and higher behavioral theory simply dissolves away.

von Holst and Mittelstaedt (1950)

13.1. Introduction

There might, on the face of it, seem to be nothing in the way of 'complex higher functional Gestalts' in the directed movements made by frogs in response to prey items. Indeed, until quite recently, a large part of the appeal of anuran orienting responses for experimental neuroscientists was the apparent simplicity of the behaviour, and a belief that the underlying neuronal organisation was clearly understandable in reflex terms with only the anatomical and physiological details remaining to be filled in. However, as has happened with notable frequency in a variety of other contexts over the past ten years or so (Grobstein, 1990a), efforts to fill in the details of frog orienting behaviour have revealed an unexpected complexity in neuronal organisation, and forced a recognition that the behaviour itself is far more sophisticated than one might have thought. Frogs respond rapidly and accurately to prey items, but the processes involved in doing so have proven to have so little in common with stereotyped stimulus/response relations that explorations of alternative ways of thinking about how the nervous system works are necessary (Grobstein, 1988a,b, 1989). Frogs get where they need to go, but how they get there, I will suggest in this chapter, is a matter not of reflexes but instead of choices, of gestalts, and perhaps of a rudimentary form of free will.

The appropriateness of using, in a discussion of nervous system organisation, terms whose origins reflect observations of a quite different sort may not be obvious, particularly when the meaning and even the putative significance of the terms being used is a matter of no little disagreement. What I hope to show is that if terms such as 'choice', 'gestalt', and 'free will' did not exist, something very like them would have had to be

invented to make sense of observations on nervous system organisation, and, further, that by at least temporarily borrowing the existing terms for this purpose one can contribute to a clearer understanding of what they actually mean in the context from which they arose. The existence of varying degrees of unpredictability of output in response to external perturbation, and that of distinctive overall forms which persist despite variations in the elements making them up, are characteristics of most biological systems at all levels of organisation (Grobstein, 1988c). While both the material substrates giving rise to these characteristics and the roles they play in biological function almost certainly differ at different levels of organisation (Grobstein, 1988c, 1990a), the admonition of von Holst and Mittelstaedt suggests that a recognition of similar and related phenomena at different levels of organisation should not only enrich studies of 'the lower levels of neurophysiology' but also contribute to those of 'higher behavioral theory' as well. One may ultimately want to acknowledge differences between phenomena at different levels of organisation with appropriate terminological distinctions, but this is best done with full awareness of how they relate to one another rather than across an 'insurmountable barrier'.

13.2. From the reflex frog to activity-gated divergence: of choices and choice

Classical work on anuran orienting behaviour led to working models which were clearly reflex in character (cf. Ewert *et al.*, 1983; Grobstein *et al.*, 1983; Ingle, 1983; see Fig. 13.1). A prey item at a given location in space is imaged by the optics of the eye at a given location on the retina. This in turn, by way of the topographic retinotectal projection, causes activity at a given location in superficial layers of the optic tectum. Different locations in the latter, it was supposed, are individually and distinctively linked to motor pattern generating circuitry in such a way as to cause the particular directed movement appropriate for the corresponding target location. The essence of such models was the presumption that what one was dealing with was an ensemble of parallel reflex pathways, each associating in a one-to-one fashion a given retinal and superficial tectal locus with a given movement.

Models of this sort were appealing to experimental neurobiologists because they seemed to provide a full explanation of behaviour in terms requiring no more than two already well understood neurobiological entities: sensory maps and motor pattern generating circuitry (Grobstein, 1988b). Such models were additionally appealing in that they reduced the seemingly vague and operationally undefined problem of accounting for directed movement to the more obvious and technically feasible problem of characterising the presumably different patterns of projection of differ-

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4

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4

MOTOR COMMANDS

PATTERN GENERATING
CIRCUITRY

MOVE FORWARD

TURN RIGHT 45°

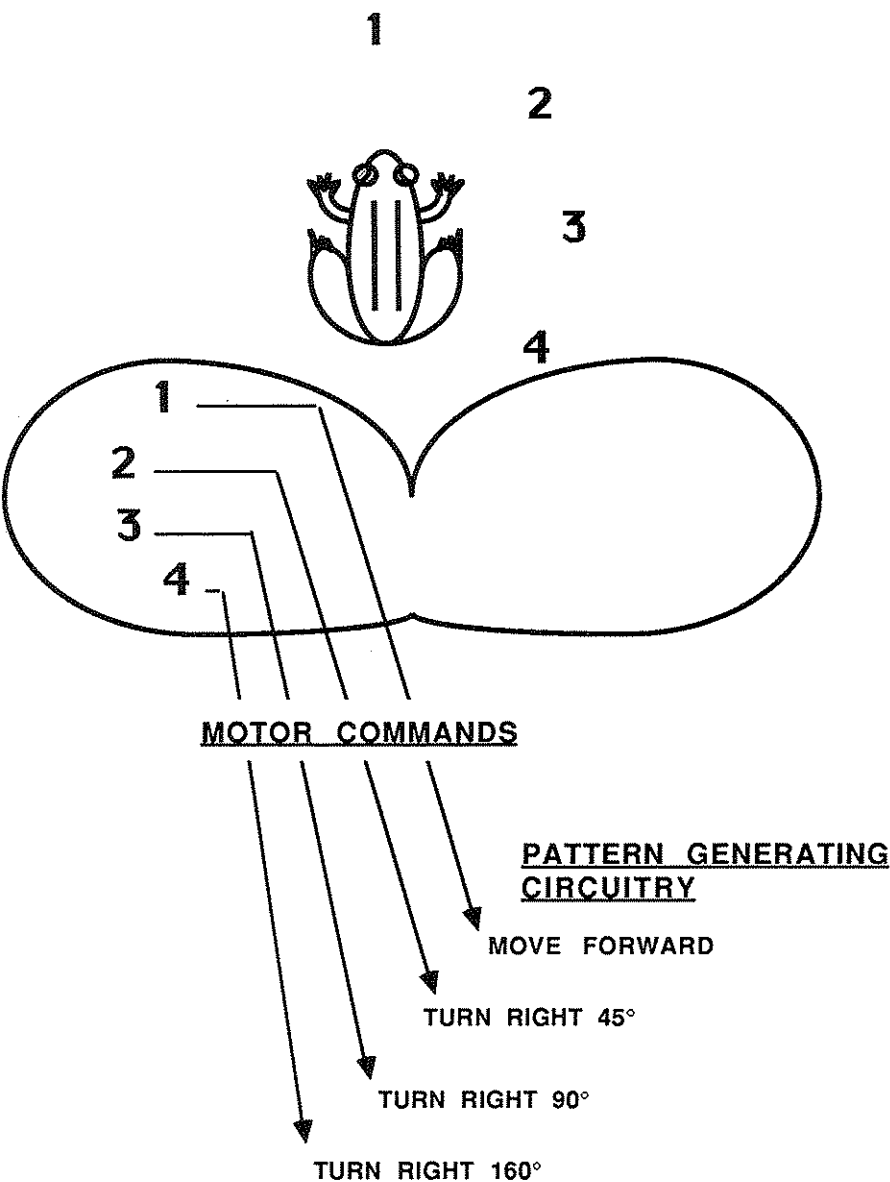**TURN RIGHT 90°**

TURN RIGHT 160°

Fig. 13.1. Schematic illustration of early models of the neuronal organisation underlying frog prey orienting behaviour. Locations in visual space are represented by numbers around the frog. Below is shown the representation of these locations in the left lobe of the optic tectum. The descending parallel paths ('motor commands') link each of these tectal locations with 'pattern-generating circuitry' in such a way that activity at each causes a distinct and appropriate motor pattern, as diagrammed.

ent tectal locations. There was thus a certain amount of both scepticism and frustration when it began to be reported that neither lesion analyses (Grobstein *et al.*, 1983) nor anatomical studies (Masino and Grobstein, 1990, and references therein) were consistent with a simple parallel coupling between the optic tectum and directed movements. I have reviewed elsewhere the kinds of evidence that encouraged a re-evaluation of the information processing requirements involved in anuran orienting (Grobstein, 1988b, 1989, 1990b), and discussed some of the methodological implications of this and similar stories for strategy and tactics in integrative neurobiology generally (Grobstein, 1988a, 1989, 1990a). Here I want to focus on the new theoretical perspective, and on the significance of finding that the neuronal circuitry involved in orienting proved to be more complicated than it was expected to be.

In essence, what was recognised was a fundamental inconsistency between neural model and behavioural reality: the latter requires that each retinal and superficial tectal locus must be related to elements of the movement repertoire, not in an obligatory one-to-one fashion, but rather in a way which makes possible the association of a given input with any of an array of outputs. The most straightforward evidence for this divergent organisation comes from the observation that the prey-orienting movements of a frog vary with stimulus location in all three dimensions of space (Grobstein *et al.*, 1985; Grobstein, 1988b). While not in itself particularly surprising, and indeed earlier documented (Ingle, 1970, 1972; Comer and Grobstein, 1981), the implications of this variation are profound but were largely unrecognised until recently. The retina, and the superficial retinotectal projection, are both two-dimensional surfaces, and there is simply no way to associate, in a one-to-one fashion, locations in a two-dimensional surface with elements of a motor repertoire which itself varies continuously in three dimensions. Instead what one should be looking for is another kind of neuronal organisation which I have termed 'activity-gated divergent' (Grobstein, 1988b; see Fig. 13.2). Each point in the superficial tectum must be linked by intervening circuitry not in an invariant fashion with a particular movement but rather in a labile fashion with an array of possible movements, including at a minimum all of those appropriate for all of the stimulus locations which are imaged at the same point on the retina but differ in distance. The particular movement which occurs at any given time must reflect not only the pattern of connections from a particular superficial tectal locus but also other activity in the nervous system at that time, relaying information related to stimulus distance. Other important parameters not represented in the location of superficial tectal activity must also be involved (Grobstein, 1988b, 1989).

That an activity-gated divergent network, rather than parallel paths, intervenes between superficial tectum and anuran orienting movements very much changes one's expectations of the efferent anatomical organ-
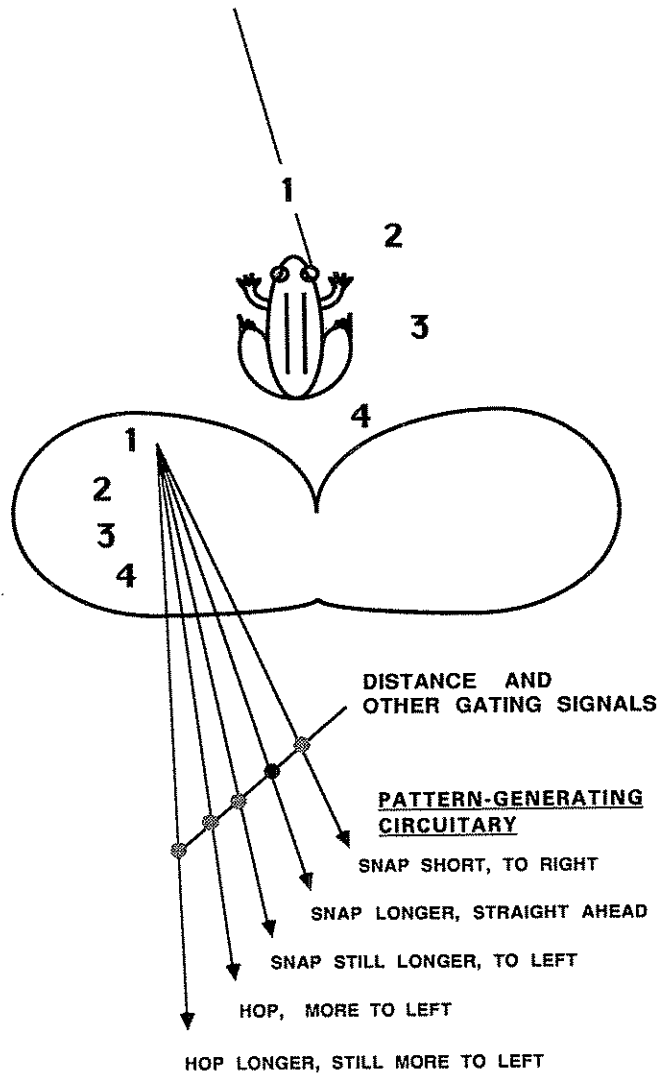
Fig. 13.2. Schematic illustration to show the more realistic, activity-gated divergent character of the linkage between tectum and motor output in the case of frog orienting behaviour. A given retinal and tectal locus receives input not from a particular point in three-dimensional space but rather from all points along a given line of sight from the eye. One such line of sight, passing through location '1' in space, is diagrammed. Stimuli at different points along this line of sight must trigger different movements. Hence, the pathways linking each tectal locus with movement pattern must be divergent, as diagrammed, rather than parallel, with the particular pathway effective at a particular time (black dot in contrast to shaded dots, presuming a stimulus at the distance of '1') reflecting other signals, including those related to stimulus distance ('distance and other gating signals').

isation of superficial tectum in anurans, and has in the present context a quite specific additional significance as well. Inherent in the concept of an activity-gated divergent network is the notion that a fundamental design requirement of many neural networks is not that of associating a given input with a particular output, but rather that of supporting 'choice', in the sense of making possible the association of a given input with any of several outputs. I do not expect all readers to instantly accept that my use of the term 'choice' is appropriate in the present context, but I do think that the unexpected complexity in tectal efferent organisation clearly requires acknowledgement by some term more weighty than 'reflex pathways'. Moreover, I will try to show that 'choice', at least in an important rudimentary sense, is real in the situation described and, further, that the tentative use of the term in the present context helps us to understand its meanings in more general usage.

An initial concern is that many readers are likely to be most comfortable using the term 'choice' for situations in which, for a given input, there is variation in the motor output of an *organism*, and no variation in the motor output of a frog in response to a stimulus at a given location has been asserted so far (although it will be in the following). All that has been claimed is that there is a degree of indeterminacy in the output associated with activation of a given superficial tectal locus. Frogs, of course, have two eyes and overlapping visual fields (cf. Grobstein *et al.*, 1980), and one might reasonably expect the indeterminacy to disappear if one considers the input from both eyes rather than from only one. It does not in fact, but, even putting this temporarily aside, an important point is being missed if one considers the matter from the perspective of binocular convergence (or the whole organism) rather than from the perspective of one eye. Each retina is two-dimensional, as is its projection to the tectum, in so far as this is organized to represent information about stimulus location. Hence, each location in the plane of the two-dimensional superficial tectum must project in such a way as to trigger any of a variety of movements. Convergence of a signal from the other eye may provide a way to gate this divergent circuitry, but the possibility does not vitiate the argument for its existence.

What all this suggests as an important generalisation is that 'choice' is frequently a matter of perspective. From the vantage point of a location on the retina or in superficial tectum, one is dealing with an activity-gated divergent circuit. If one stands outside the animal, however, then one might be dealing not with activity-gated divergence but simply with two input channels whose combined activity determines the output. 'Choice' seems to have disappeared. This raises the issue of whether 'activity-gated divergence' is really a distinctive concept as opposed to being a fancy new name for what most neurophysiologists presume about the nervous system anyhow: that outputs typically reflect the interaction of signals

on several input channels. The answer is a little bit of both, with no apologies for the latter; it all depends on perspective. From the point of view of an observer sitting at a particular point on the retina, or at the corresponding terminals in the optic tectum, the output resulting from activity at that location differs from occasion to occasion and clearly reflects a process of choice. Neurobiologists often work from local vantage points of this kind, only to find subsequent circuitry more complex than they expected it to be. Only later do they realise that the information processing going on from that point necessarily involves the kind of convergence of additional sensory information which constitutes the choice process (Grobstein, 1988a, 1990a). That hypothetical mechanisms underlying such a capability exist within the imagination of neurobiologists ought not to be allowed to detract from the recognition that particular circuits are indeed structured for this purpose.

Indeed the presence of 'choice' at one level of organisation, and its disappearance at a second, seems to me not so much an embarrassment as an instructive realisation. If one is looking at any given system or subsystem and it displays variation in outputs for a given known input, then that system or subsystem is organised to support the capability for choice. That a larger system, of which the system or subsystem being analysed is a component, is more predictable in terms of *its* output relationships this may be significant for understanding the larger system, but may equally be irrelevant for characterising the smaller. Components with variable response characteristics are not infrequently combined so as to yield apparently more stereotyped input/output relations at a higher level of complexity (Oyama, 1985; Grobstein, 1990a). What this highlights is that 'choice' (or something very like it) is not a phenomenon which appears only with increasing complexity. It is a property of components at a variety of levels of organisation, a phenomenon which sends roots 'down to the simplest basal functions of the CNS'.

The concept of 'activity-gated divergence' not only recognises a known capability of neural nets with regard to 'choice', but also distinguishes one of several different general ways in which the nervous system is organised so as to yield the phenomenon of different outputs associated with a given input. Use-dependent synaptic lability has been well established as a mechanism of this sort (cf. Carew and Sahley, 1986), and recently it has become clear that relatively diffusely acting pharmacological agents can influence both synaptic events and intrinsic cell properties in such a way as to produce substantial changes in the responses of networks to particular inputs (cf. Getting, 1989; Harris-Warwick *et al.*, 1990). Activity-gated divergence differs from the former in that it provides a kind of variation which neither reflects nor depends on cellular changes produced by prior patterns of activation of the network. Perhaps more fundamentally, activity-gated divergence differs from both use-dependent

synaptic lability and the effects of diffusely acting pharmacological agents in that different input/output states occur with no changes whatsoever in either synaptic or intrinsic cellular properties; they reflect instead transient activity patterns. This has interesting methodological implications, in that potential variability is unobservable by studies aimed at detecting changes of intrinsic cellular and synaptic properties. It also probably means that activity-gated divergence represents the most rapidly achieved and labile form of input/output variation, since the need for a coupling of neuronal activity to metabolic processes is obviated. Indeed, it seems likely that this rather simple form of functional lability may be the most common (cf. Forssberg *et al.*, 1975; Fukson *et al.*, 1980; Hoy and Nolen, 1987). One need only reflect on how frequently one's own behavior is altered by a given experience (or a given thought) so rapidly and specifically that neither changes in synaptic strengths nor diffusely acting pharmacological agents are likely to be involved. As noted by Lashley many years ago, 'input is never into a quiescent or static system, but always into a system which is already excited and organized ... behavior is the result of interaction of this background of excitation with input from any designated stimulus' (Lashley, 1951). This background of excitation is a significant information store for the functioning nervous system (Grobstein, 1990a), and its variations almost certainly provide a major source of input/output variability.

My hope is that the discussion so far not only contributes to an understanding of the potential for 'choice' in stable networks with stable neuronal properties, but also illustrates what seems to me a natural and useful logic for further analysing some of the multiple meanings inherent in this term as it is generally used. I have argued that a minimal criterion of 'choice' is that a system exhibits several possible outputs for a particular input, and that this same criterion may be applied whether one is speaking of an organism or a part of an organism (a particular neural circuit). What this calls attention to is the need for careful definition of both system and input, together with a willingness to let 'choice' come and go depending on one's perspective and the outcome of particular lines of investigation.

My definition of choice, albeit rudimentary, is actually more demanding than one might prefer in some contexts. Organisms generally exhibit a variety of outputs and one can reasonably ask how they 'choose' among them with no preconceptions whatsoever about the determinants of the choice. The parallel reflex model with which I began this chapter would be a perfectly reasonable outcome of such an investigation. Prey items at different locations in space represent different inputs to the nervous system (because of the optics of the eye), and the act of 'choice' involved in selecting the right output for each stimulus presentation is materialised as a series of parallel reflex paths associating each retinal locus with a

distinctive movement. Examples of choice in this sense are quite real and behaviourally significant (for both some examples and some subsequently recognised complexities see Wine, 1984; Stein, 1986; and Newland and Neil, 1990). At the same time they do not involve an underlying circuitry which associates several different outputs with a particular input; they instead associate each of a set of different outputs with each of a set of different inputs. For this reason, they lack something of the drama of what is meant by 'choice' in general usage.

The activity-gated divergent network linking a retinal and tectal locus with movement clearly does have the property of associating several different outputs with a particular input, so long as one keeps in mind that by input one means the signal originating in one eye, rather than in two. Such circuits are thus not only neurobiologically interesting, but represent something closer to what comes to most people's minds when one uses the word 'choice'. However, if one thinks of the input as occurring not on one channel but on two, as in the organism as a whole, then, as already noted, one could be dealing not with a system which associates a given input with several outputs, but rather with one that combines several inputs and associates with each combination a particular output. That the output associated with a given input is influenced by other inputs seems to me to reflect more of what is generally meant by 'choice', but an important something seems still to be missing and I expect readers will agree. The missing something, I suggest, is an answer to the question of whether a knowledge of all input signals would suffice to predict the movement, or whether something else is involved. If the latter, then one is still closer to what is generally meant by 'choice'.

At this point it becomes relevant that binocular convergence is not necessary for a frog's variation of movement with variation in stimulus distance. Frogs show such variations for stimuli in areas of the visual field seen by only one eye, and continue to vary their movements appropriately with variations in stimulus distance for stimuli in the binocular visual field even after interruption of one optic nerve (Ingle, 1972; Grobstein *et al.*, 1985). Frogs can use binocular convergence as a distance cue (Collett and Harkness, 1982) but, like most animals, have a number of other cues at their disposal (a point to which I will return in the following section). Among these cues, one which is particularly germane to the present discussion is accommodative state (Jordan *et al.*, 1980; Douglas *et al.*, 1986). Stimuli at different distances require different lens settings for their images to be sharply focused on the retina. Definitive experiments have not as yet been done, but it seems likely that what gates the divergent network from the tectum in this situation is not an afferent signal but rather a corollary discharge signal related to the motor output to the ciliary muscles (Douglas *et al.*, 1986). If this is so, then a knowledge of activity in all of the sensory pathways of the nervous system

would still not suffice to predict a frog's movement in response to a stimulus at a given location. For different object distances a feedback mechanism will adjust the power of the lens, but once this has been accomplished all afferent signals to the nervous system will be the same, and still the resulting output will differ. The gating signal would thus not be an afferent signal at all, but rather one internal to the nervous system.

While still hypothetical in the case of the frog, the reality of different responses to the same input signal resulting from differences in ongoing activity in the nervous system rather than to other afferent signals is well documented in other systems (Sperry, 1950; von Holst and Mittelstaedt, 1950; Kovac and Davis, 1980, and more recently Moore-Ede *et al.*, 1982; Sparks, 1986; Huang and Satterlie, 1990; and Posner and Petterson, 1990). This, it seems to me, adds an important further level of sophistication to the potential display of choice by neuronal networks which are stable anatomically, synaptically, and in terms of intrinsic cell properties. Parallel systems can account for different outputs resulting from different inputs. Activity-gated divergent systems can account for different outputs resulting from a particular input and can do so by two important mechanisms: one involving additional significant afferent signals and the other involving internal changes in neuronal activity.

This breakdown, in neural terms, of the concept 'choice' seems to me useful not only in specifying some of the multiple meanings of the general concept, but also in identifying what additional features remain to be accounted for. Two are likely to occur to most readers: the sense of oneself having picked between alternatives, and the feeling that one is free to choose, that is that there is something more going on than simply responding to the environment. The latter is to some extent dealt with by the recognition that internally generated signals may determine the responses of activity-gated divergent circuitry, but the situation remains more deterministic than one might like. I will return to this issue, and briefly to the sense of oneself as an agent of choice, in the last two sections of this chapter. A useful breakdown of 'choice' in neural terms ought also to be helpful in providing a defining paradigm for posing novel experimental questions about neuronal organisation itself. Here too an aspect of frog orienting briefly mentioned earlier is illustrative. Even for a fixed stimulus location, the movement exhibited by a frog is not stereotyped, but rather displays significant variation. Two fairly obvious forms of this variation are relevant here, and I will describe a third later.

The visual field of each eye in the frog includes in excess of 225 degrees on the horizontal plane, meaning that a frog can not only see behind itself but can do so with both eyes (Grobstein *et al.*, 1980). Stimuli directly behind a frog trigger an orienting turn of 180°. This turn could in principal be either clockwise or counterclockwise. It is, in fact, either, with roughly equal probability (Kostyk and Grobstein, 1987a). Since the target

is seen by both eyes, one might entertain the possibility that the clockwise/counterclockwise 'choice' relates to which of the two eyes is more effectively activated, and thus has a parallel pathway character to it. This hypothesis was tested by optic nerve section and it was found that both clockwise and counterclockwise turns persist (Kostyk and Grobstein, 1987a). The implication is that one is dealing with an activity-gated divergent circuit, and that the gating, or 'choice', must be occurring at some location central to the retina. Corresponding findings of persistent variation following unilateral tectal lobe lesions, and unilateral interruption of descending tectofugal pathways, imply an activity-gated divergent circuit subsequent to both of these locations, suggesting that the 'choice' is actually being made in the spinal cord. Some additional evidence identifying spinal cord as an important locus of motor choices in the frog will be given in the following section. My major point here is that one can fairly readily design experiments which not only help to specify the nature of a particular 'choice' along the lines discussed, but also yield information about its anatomical location.

A second documented variability in the movements made by frogs in response to stimuli at particular locations relates to the fact that frogs use different motor patterns for stimuli at different distances (Ingle, 1970; Comer and Grobstein, 1981; Grobstein *et al.*, 1985; Grobstein, 1988b). For nearer stimuli, what is involved is a 'snap' involving a lunge and a tongue flick. Over the range where it is used, the amplitude of this movement increases linearly with increasing stimulus distance. For more distant stimuli, the response is a 'hop', a reorienting movement which differs in a number of ways, including the absence of both lungeing and the tongue flicking. Frogs switch rather abruptly from one motor pattern to another at a characteristic distance, termed the 'snap/hop border' (the basis of this motor 'choice' will be discussed in the following section). Around this distance, however, there is a small zone of ambiguity where stimuli may elicit on any given trial either a snap or a hop. Since the snap/hop choice is in general related to stimulus distance, one might well entertain the hypothesis that the variation in movement within the zone of ambiguity reflects variation in the distance signal. An analysis of snap amplitudes, however, shows this not to be the case (Grobstein *et al.*, 1985). Snap amplitudes increase with stimulus distance throughout the zone of ambiguity, indicating that the distance signal does not in fact vary in such a way as to account for particular snap/hop choices. The distance signal must therefore be the input to a subsequent activity-gated divergent circuit, with some additional signal responsible for the actual motor choice. While the logic here is similar to that in the previous case of clockwise and counterclockwise turning, the situation is interestingly different in representing a distinctly more abstract analysis. For reasons discussed in the following section, the distance signal is unlikely to

have any simple relation to a particular sensory input pathway, and to be instead an abstraction constructed at some as yet unknown central nervous system location. In short, what the present form of analysis allows is not only a characterisation of choice with regard to inputs and known pathways, but also a formal characterisation which can be used to predict the existence of abstract forms of organisation for use in locating and identifying particular central nervous system structures and signals.

I have not discussed the nature of the gating signal for either the snap/hop choice within the zone of ambiguity or the clockwise/counterclockwise choice. We do not in fact have any information on this matter in either case, but it is not difficult to imagine appropriate experiments to provide such information. The gating signal could be a second sensory signal, one related to posture, for example. It could also be a deterministic internal signal of the kind mentioned already, perhaps a corollary discharge signal or one related to motivational state. However, both examples, particularly that of clockwise/counterclockwise turning, have an air of 'what difference does it make?' This raises the possibility that one may be dealing with a non-deterministic internal gating signal, something equivalent to a coin toss (Grobstein, 1988c). The existence and possible usefulness of such a signal will be considered further in the final sections of this chapter.

13.3. An intermediate spatial representation: gestalts and choices

In the preceding sections I have been concerned with the overall character of the neuronal organisation which links sensory maps with output pattern generating circuitry in the case of anuran orienting behaviour, and with the contributions that an appreciation of this organisation can make to an understanding of the concept of 'choice'. An additional perspective on phenomena of 'choice' and, in particular, their relation to other 'higher order gestalts' comes from studies that reveal something of the details of the individual information processing steps which together yield the overall organisation of the anuran sensorimotor interface. Of particular importance in the present context are a series of observations suggesting that there exists in the interface a generalised, non-sensory, non-motor, three-dimensional representation of stimulus location.

The relevant studies (Kostyk and Grobstein, 1982, 1987a,b,c; Masino and Grobstein, 1989a,b; Grobstein *et al.*, 1988; Grobstein and Staradub, 1989) largely involve observations of behaviour following selected central nervous system lesions, a form of analysis whose validity, logic, and distinctive appropriateness for investigations of central nervous organisation in relation to behaviour have been discussed elsewhere (Grobstein, 1990a,b). The particular form of spatial representation observed appears not to be idiosyncratic to the frog but instead to be common to a wide

MIDBRAIN

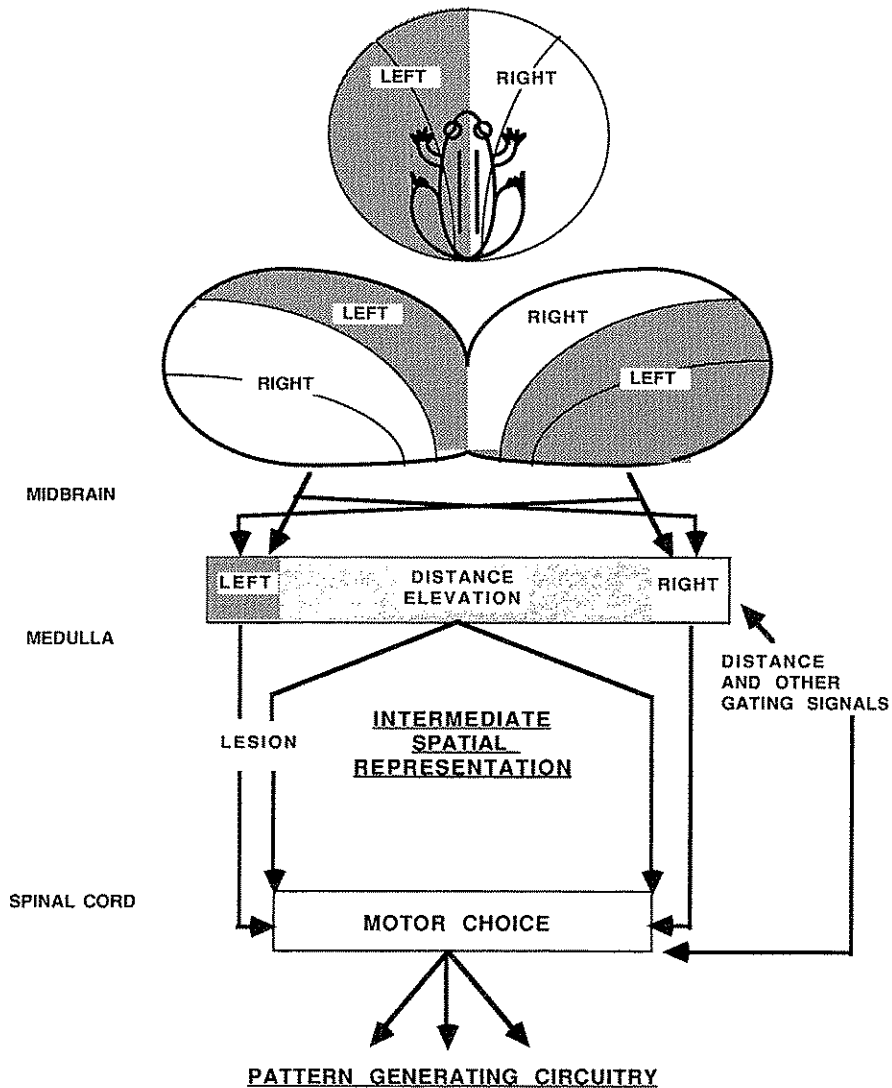MEDULLA

SPINAL CORD

PATTERN GENERATING CIRCUITRY

Fig. 13.3. Schematic illustration of a still more realistic model of the linkage between tectum and motor output in the case of frog orienting behaviour. The visual world of a frog and its representation on the two lobes of the optic tectum is shown in the top diagram. The frog should be imagined as centred in a hemispherical dome, on which the left visual hemifield is shaded and the edges of the visual fields of the two eyes (LFL, RFL) are indicated with curved lines. As illustrated, the visual field of each eye includes a full hemifield and extends across

array of vertebrate and perhaps invertebrate organisms (Grobstein, 1988b, 1989, 1990b), suggesting the existence of some important generalities about the neuronal organisation underlying directed movement and raising interesting questions as to why a rather diverse set of problems are solved in such similar ways (Grobstein, 1988c, 1990b). The observed spatial representation also appears to be distributed and fundamentally dependent on activity coding (Grobstein and Staradub, 1989; Masino and Grobstein, 1989a,b, 1990; Grobstein, 1991), suggesting that the map-like representations of spatial information seen near the nervous system periphery may not be a good model for more central representations of such information. While of interest in their own right, neither of these matters is directly germane to the present discussion, and I will confine myself to a description of those observations which bear most immediately on 'gestalts' and 'choices' (see Ewert, 1987, for a discussion in a different context of 'gestalt' phenomena in anuran prey orienting behaviour).

Figure 13.3 provides a schematic summary of our current understanding of the sensorimotor interface with an emphasis on the intermediate representation of stimulus location and its relation to the determination of motor output patterns. The key observation on which this figure is based is the finding that unilateral lesions of a defined fibre tract at locations between the midbrain and the spinal cord (Kostyk and Grobstein, 1987b; Masino and Grobstein, 1989a) produce a deficit whose character implies a disturbance in neuronal processing at some level between initial sensory analysis and motor choice. Frogs with such lesions do not fail to respond to prey items. Orienting movements are triggered by stimuli

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the midsagittal plane to include a portion of the opposite hemifield. Each eye projects in its entirety to the opposite tectal lobe, so that, as illustrated, the midsagittal plane (upper curved line ML) and portions of visual space seen by both eyes (to lower curved line LFL, RFL) are represented in both tectal lobes.

Within the midbrain, but after the tectum, information about target location is transformed (arrows from tectum and box immediately below it) into an 'intermediate spatial representation,' as discussed in the text. Information about the horizontal eccentricity of a stimulus in the left and right hemifields is carried through the medulla along descending axons on the left and right sides of the brain respectively (arrows descending from left and right sides of box). Information about the distance and elevation of such stimuli is carried on a separate bilaterally descending pathway or set of pathways (arrows descending from middle of box). In consequence, a left sided 'lesion' prevents leftward turning, but spares other components of responses to stimuli on the left and has no effect on responses to stimuli on the right. Horizontal eccentricity and distance signals remain separate until the spinal cord. It is not until they converge that a 'motor choice' occurs and pattern generating circuitry can be appropriately activated. 'Distance and other gating signals' may be involved both in creating the central spatial representation, and in motor choice, as shown to the right.

presented at all locations in visual space. For stimuli in the hemifield contralateral to the lesion (clear area in Fig. 13.3), the orienting movements themselves are normal, and vary normally with variations in stimulus location in all three spatial dimensions. For stimuli in the hemifield ipsilateral to the lesion (shaded area in Fig. 13.3), however, the movements are abnormal, in a way which relates quite specifically to one of the three dimensions of stimulus location. The lesioned frogs show no variation in their orienting movements associated with variations in stimulus angle on the horizontal plane (horizontal eccentricity). The orienting movements are forwardly directed, regardless of the angle of stimulus presentation. Even more significantly, these orienting movements, while not varying with horizontal eccentricity, continue to vary appropriately with the elevation and distance of stimuli in the affected hemifield.

In addition to their continued responsiveness, two other features of the behaviour of the lesioned frogs indicate a disturbance which is subsequent to the initial stages of sensory processing. Unilateral lesions of the optic tectum, the locus of initial sensory processing, produce deficits in response to stimuli in regions of space defined by the borders of the visual fields of the eyes, instead of by the midsagittal plane as in the hemifield deficit described previously (Kostyk and Grobstein, 1982, 1987a). The difference is about 45° of visual angle (see Fig. 13.3), easily measured and quite significant. The hemifield deficit indicates disturbance of a process in which spatial information is represented in a head or body coordinate frame, rather than in the retinocentric coordinate frame of the eye and its projection to the tectum. The other aspect of the deficit in lesioned frogs which distinguishes it from a primary sensory disturbance is that the deficit is related specifically to one dimension of the three dimensions of stimulus location. In the retinotectal projection, each location codes simultaneously two dimensions of stimulus location, one of which is horizontal eccentricity (or something related to it). There is no way in which a tectal lesion could selectively affect only one dimension of stimulus location. One is dealing with a process in which components of a three-dimensional representation of spatial location exist independently of one another (lines carrying separate signals in the 'intermediate spatial representation' of Fig. 13.3), rather than being corepresented as in the initial retinotectal projection. Consistent with these two lines of evidence for a post-tectal process is a related series of findings suggesting that what is damaged by the lesions is a descending, indirect tectofugal projection containing axons of tegmental neurones which themselves receive tectal input, and it is presumably in the tecto-tegmental relay (upper box in Fig. 13.3) that the non-retinotopic representation of spatial information is created (Masino and Grobstein, 1989b, 1990).

That the deficit in lesioned frogs reflects a disturbance of neural pro-

cessing at some level prior to motor choice is less obvious. Our initial hypothesis was that the deficit reflected the existence of distinct sets of pattern-generating circuitry, and of distinct pathways linking them with the tectum (Kostyk and Grobstein, 1982, 1987a). The failure of lesioned frogs to turn towards stimuli in one hemifield seemed straightforwardly understandable as a selective interruption of a pathway responsible specifically for activation of pattern-generating circuitry for horizontal turning in one direction, and the persistence of other movements and movement components was presumed to reflect sparing of additional, distinct pathways responsible for activation of turns in the opposite direction, as well as of movement components related to stimulus elevation and distance. The organisation of the descending pathways in Fig. 13.3 is consistent with this interpretation, except for the fact that they converge at a motor choice step rather than on distinct sets of pattern-generating circuitry. The reason for this additional feature is that the simpler motor hypothesis predicts that the movements of lesioned frogs in response to stimuli in the affected hemifield should be identical to those of normal frogs except for the missing horizontal turn component. More careful examination of the behaviour of lesioned frogs showed that this was not in fact the case: the lesions affected not movement *per se*, but rather motor pattern choice.

In the preceding section, I briefly described a snap/hop motor pattern choice which occurs with increasing stimulus distance, and it is this choice which is most dramatically altered, in a quite reliable way, by the lesions under discussion here. The switch between one motor pattern and the other normally occurs at a distance of two body lengths for stimuli in front of the frog on the midsagittal plane, and at one body length for stimuli at 90° of horizontal eccentricity. If the misdirected movements of lesioned frogs were normal except for the missing turn component, they should have consisted of forwardly directed snaps in response to lateral stimuli at distances up to one body length and of forwardly directed hops for stimuli at greater distances. What was actually observed was a snap/hop motor choice occurring at a distance of two body lengths, the same distance at which it occurs for frontal stimuli (Kostyk and Grobstein, 1987a; Masino and Grobstein, 1989a). In short, the abnormality in lesioned animals consists not only of responding with forwardly directed movements rather than turns, but also in making qualitative motor pattern choices which are appropriate for frontally rather than for laterally located stimuli.

The fact that lesioned animals snap for stimuli at locations where normal animals hop clearly indicates that the disturbance has altered the process of motor choice, and hence that the lesion must be disturbing something at this stage or prior to it, rather than something involved in the elaboration of particular motor output patterns. This something

is most reasonably interpreted as a signal representing the horizontal eccentricity of the stimulus. Such a signal must be combined with one related to stimulus distance before the decision as to what movement to make is accomplished. The absence of a signal in the horizontal eccentricity pathway is apparently interpreted as indicating zero degrees of horizontal eccentricity (a frontal stimulus) and so the motor choices are those appropriate for frontal stimuli. This has several implications, one of which was briefly alluded to in an earlier section. The tegmental axons of the critical tract run all the way to the spinal cord, and the same behavioural deficits result from interrupting them at the junction of midbrain and medulla, or at the junction of medulla and spinal cord. The latter implies that the process of motor choice has not in fact occurred by the time signals leave the medulla, and hence that this process (and the associated box of Fig. 13.3) must be in the spinal cord.

The other, and perhaps more general, implication of the findings described is that this body-centred, distributed, three-dimensional form of spatial representation is, in reality, an intermediate spatial representation in the sense that its character is intrinsic to itself, reflecting organisational features of neither the sensory nor the motor sides of the nervous system. This is true not only in detail but also in a broad sense. As I have briefly discussed elsewhere (Grobstein, 1988b, 1989, 1990b), there is no obvious reason why a specifically three-dimensional representation of target location should exist at all. Associated with a stimulus at a given location in space are a large number of potentially independent input signals, certainly more than three, and similarly a large number of independent output signals, again certainly greater than three. I will here elaborate on this, since I think it not only sharpens the question of why the intermediate spatial framework exists but also sheds some further light on 'choice' and 'higher functional gestalts', which in turn helps to define some interesting neurobiological problems. What I want to suggest is that sensory 'gestalts' emerge as a consequence of going from neuronal signals of higher dimensionality to signals of lower dimensionality, that 'choice' and motor 'gestalts' are phenomena associated with going from lower dimensionality to higher dimensionality, and that both sorts of transition may require rather elaborate neuronal circuitry.

While the three-dimensional description of a given stimulus location may be obvious to the experimental observer, it is not apparent in the sensory pathways to the central nervous system. In the simple case of binocular vision, the input signal is not actually three-dimensional but rather four-dimensional, corresponding to a two-dimensional input signal from each eye. The situation is, however, even more complicated than this. As alluded to earlier, frogs may use binocular vision to extract a distance signal, but have additional cues available as well: monitoring of accommodative state and at least one or two others (Jordan *et al.*, 1980;

Collett and Harkness, 1982; Grobstein *et al.*, 1985; Douglas *et al.*, 1986; Collett and Udin, 1988). There is also reason to believe that a frog's visual localisation abilities take account of its own body size as well as its posture (Reyes and Grobstein, 1984; Grobstein *et al.*, 1985), so that the number of input variables involved in the production of a directed movement must be nine or greater. In addition, frogs can localise, in three dimensions (Comer and Grobstein, 1981) using tactile stimuli, suggesting that cutaneous input (in at least two dimensions) and some distance variable related to limb position (Grobstein *et al.*, 1988) may also need to be included in thinking about input dimensionality.

My point in all this is that stimulus location in three-dimensional space is not a sensory reality but rather an abstraction, something very close to a 'higher order functional Gestalt'. A given signal in the intermediate spatial representation is presumably not associated with any particular set of input signals but rather with any of a wide array of sets of input signals all corresponding to the same three-dimensional spatial location (what I have called elsewhere a 'bounded variance'; Grobstein, 1988c). Furthermore, these bounded variant sets are not continuous in any mathematical sense. Nearby distances may reflect similar binocular signals, or instead a given binocular signal in comparison with a particular accommodative signal. Nearby horizontal angles may reflect similar retinal eccentricities, or a given retinal eccentricity in comparison with a particular somatosensory signal. Consistent with this gestalt interpretation of the intermediate spatial representation in the frog is that lesions altering visually triggered turn angles produce qualitatively and quantitatively similar effects on turn angles triggered tactually (Grobstein *et al.*, 1988). Recently we have also found that damage to tracts carrying distance information produces similar effects on responses to stimuli in binocular and monocular visual fields (Grobstein and Staradub, 1989).

Two points follow from this, one having to do with the notion of gestalts, the other with its implications for studies of the nervous system. The first is that sensory 'gestalts' can be thought of as a consequence of reducing input dimensionality, of creating an internal signal of low dimensionality which corresponds to a bounded-variant set of a large number of input signals that exist in a higher dimensional space. The second is that describing the neuronal circuitry which underlies such a process is a non-trivial problem. Simple convergence of inputs will not do. What is needed is a form of neuronal organisation that will yield a given output for an array of quite different inputs, and which is further capable of using or ignoring signals along one input pathway depending on the presence or absence of input signals along another. The characterisation of such circuitry, even at a hypothetical level, is a significant challenge for neurobiology.

The dimensionality of neuronal signalling is higher not only on the

input side of the intermediate spatial representation but also on its output side. Here too the actual number of independent variables is unknown but certainly greater than three. Frog orienting movements involve, at a minimum, displacement in three dimensions together with three degrees of rotational freedom, yielding at least six dimensions. Depending on the organisation of the underlying pattern-generating circuitry, the output dimensionality may be much higher (Grobstein, 1990b). What this suggests is that just as a bounded variant set of input combinations is associated with a given three-dimensional localisation signal, so too may it be the case that a given three-dimensional localisation signal is associated with a bounded variant set of outputs. We have recently begun to acquire evidence that this is indeed the case not only for turn direction, as described earlier, but quite generally (Grobstein *et al.*, 1990). A close analysis of frog orienting movements shows that an accurate turn towards a stimulus at a fixed location involves not only a rotation but also a two-dimensional displacement of the body, with the two components covarying so as to yield in a variety of different ways an accurate turn (Fig. 13.4; see Collett and Land, 1974, for a related phenomenon in a quite different organism). In short, an 'accurate' turn is itself an abstraction, a motor 'gestalt' whose origin is the association of a given central spatial representation signal with a bounded variant set of possible movements. Here, too, one encounters some quite challenging neurobiological problems: for example, what kind of neuronal circuitry produces an association between a given spatial signal and a bounded-variant set of movements? In addition, one re-encounters the problem of 'choice', of what is responsible for the particular movement exhibited on a particular occasion. I will return to this question in the next section of this chapter.

The central spatial representation not only provides a second example of 'higher behavioral theory' with roots deep in the 'simplest basal functions of the CNS', but also raises an intriguing question about 'functional Gestalts' in general: why do they exist? I have argued that there is no obvious explanation on either the sensory or motor sides of the nervous system for a specifically three-dimensional central spatial representation. The frog might in principle have been organised in some parallel reflex fashion, with each of the possible ensembles of inputs corresponding to a given location in space linked independently and appropriately to pattern-generating circuitry. Instead, one has a convergence from many input dimensions to three dimensions and then a divergence from three to many output dimensions, a bottleneck so to speak. It is not impossible that a key to the question of why this bottleneck exists will be found in general rules of information acquisition and processing (Grobstein, 1988c), that is, in some sense, the optimal solution to the problem of relating large numbers of different kinds of information defined in dif-
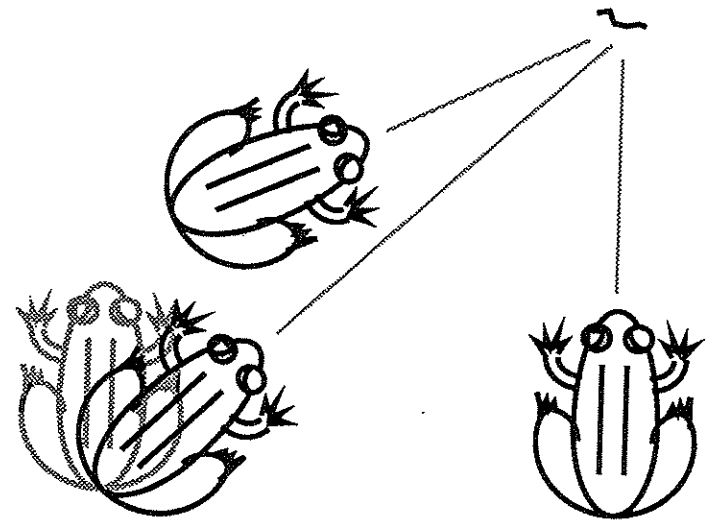
Fig. 13.4. Schematic diagram to illustrate one kind of variability in the responses of frogs to stimuli at a fixed target location. The end points of three different movements from a single starting position (lighter frog) are shown. The movement represented to the lower left involves a pure rotation of the body, that to the lower right a pure translation of the body with no rotation, and that above a combination of body rotation and translation. Note that, in all three cases, the frog achieves the objective of aligning its midsagittal plane with the stimulus (worm to upper right). An infinite number of other combinations of rotation and translation would similarly satisfy the objective. The variability normally observed for a target at the location shown is within this set of correlated rotations and translations. Pure translation is uncommon under the circumstances studied.

ferent coordinate frames (Grobstein, 1989, 1990b). It would be interesting if this were in some formal sense true of 'gestalts' in general.

13.4. Motor equivalence and internal feedback: on the road to free will?

The models illustrated Figs 13.2 and 13.3 represent a degree of sophistication in neuronal circuitry substantially greater than that of the model in Fig. 13.1, reflecting, as I have argued is necessary, aspects of both choice and higher order gestalt representations. At the same time they share with the model of Fig. 13.1, and indeed with many — perhaps most — models of neuronal organisation, a peculiar flavour of being somehow less than what most people feel behaviour to be. To call a nervous system organised like that in Fig. 13.3 a reflex machine is to miss the point of the

intermediate spatial representation and of activity-gated divergence; but, at the same time, a nervous system like that in Fig. 13.3 seems to lack both purpose and playfulness. Given a knowledge of all inputs, and the value of some internal signals, one can reasonably expect to be able to predict the output of the system, and this output can reasonably be expected to occur whether or not it achieves any desired objective in a given context. In this section I want to review two quite new and still somewhat preliminary findings which suggest that the model of Fig. 13.3 will need further supplementation to approximate the actual neuronal organisation underlying anuran orienting, precisely because of its lack of elements which would yield a sense of purpose and playfulness. As in previous sections, my hope is both to use these general terms to help illuminate nervous system organisation and to use the nervous system to better understand the general terms, together with the related concept of free will.

One of the two sets of relevant new observations has already been mentioned: the finding that frogs can and do achieve accurate orienting turns in a variety of different ways. This is a novel finding in the context of frog orienting behaviour, but not in the context of motor control generally. A variety of workers in a variety of systems have noticed a similar variance in the actual motor output patterns underlying a series of apparently equally successful movements (Lashley, 1930; Bernstein, 1967; see also Möhl, 1989, Stein, 1989, for recent examples). The phenomenon has been termed 'motor equivalence', and variously perceived as a more or less biologically irrelevant but computationally interesting problem associated with going from low-dimensional to high-dimensional signals (Hogan, 1985; Pellionisz, 1985), or as evidence for successive translations from higher level to lower level motor commands (Lacquaniti and Soechting, 1982; Soechting, 1984), or as an indication of a desirable capability to adjust movements during their execution based on afferent or reafferent signals (Berkinblitt *et al.*, 1986; Abbs and Cole, 1987). In the frog, elements of the first two of these views of motor equivalence are clearly present. The intermediate spatial representation can certainly be regarded as a higher level motor command signal. Going from this three-dimensional signal to a motor output signal of greater dimensionality does mean that any of a number of different movements are potentially associated with a given localisation signal, and hence does raise what might be regarded as computational problems. My own inclination though, consistent with the entire direction of this chapter, is to regard such matters as problems of 'choice', and so to focus on the nature of the additional signals which gate the divergent circuitry linking the intermediate spatial signal with movement.

The possibility remains that the motor equivalence phenomenon in the frog is a reflection of afferent or reafferent-based adaptive adjustment of

movements during their occurrence. However, for several reasons, I am inclined to suspect a different explanation for the observed motor variation, and a different biologically meaningful significance. We have as yet been unable to correlate the variation with other likely phenomena which might require movement adjustment, and frog movements are in general rather ballistic, with relatively little influence of afferent and reafferent signals during their execution. Moreover, the variation described, like those mentioned earlier, has, under the circumstances in which it was observed, a 'what difference does it make?' character. The movements of a given frog differ from trial to trial in a way that seems to have no pattern and appear almost random, but this makes no difference to their achieving their object.

I have noted elsewhere that an element of randomness may be a general feature of biological systems, and that such elements can, without difficulty, be conceived as concrete, material realities (Grobstein, 1988c). In the present case, a neurone or group of neurones with a truly random or quasi-random firing pattern could provide the relevant gating signal. For reasons I will come to in a moment, an element of this kind could play a quite significant biological role. It also adds a sense of playfulness to models of the neuronal organisation underlying orienting, bringing them more in accord with one's impression of frogs and of nervous systems generally. The model of Fig. 13.5 incorporates such an element as a testable hypothesis. In so doing, it also raises some intriguing new neurobiological questions. What kind of circuitry, for example, would allow a gating signal to act to generate a choice which is random but at the same time constrained to some outcome within a defined set of movements (those which successfully point the frog towards the target; the phenomenon, previously alluded to, of bounded variance, but with the added twist of an element of randomness).

The model of Fig. 13.5 differs from that of Fig. 13.3 in two additional ways, reflecting the second set of recent observations mentioned at the outset of this section. For years we have restricted our observations on anuran orienting behaviour to the initial movement triggered by a stimulus, since we were interested in the coupling between sensory maps and pattern-generating circuitry and did not want our interpretations confused by the possibility of afferent-dependent corrective movements. Over the past year we have begun to look not only at the first movement but at subsequent ones as well, particularly in those lesioned animals, described earlier, which fail to turn towards stimuli in one visual hemifield and whose initial movement is forwardly directed. As in normal frogs, however, the forwardly directed movements are not invariant, and may include small components of body rotation. What we have recently found is that such frogs may, by a sequence of small movements, end up pointing towards the target location even under conditions where the
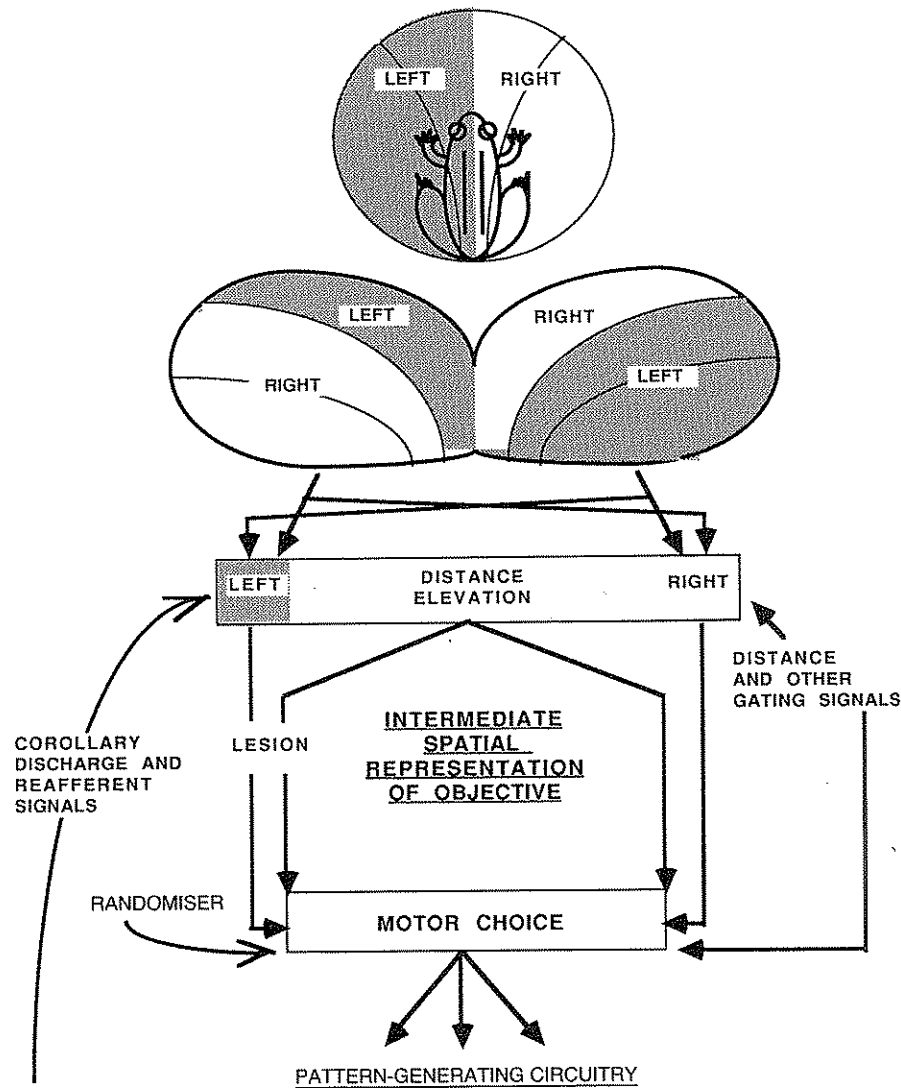
Fig. 13.5. Schematic illustration to show new directions in understanding the neuronal organisation underlying prey orienting movements in the frog. The model shown is identical to that of Fig. 13.3, with one slight modification ('intermediate spatial representation *of objective*') and two additions (to left). First, the output of the motor choice box is not determined by the central spatial representation but involves in addition a 'randomiser' input. Secondly, 'corollary discharge and reafferent signals' are used to determine whether a particular objective defined by the central spatial representation was in fact achieved. If not, a new movement (again with an element of randomness) is generated. Such a system, as discussed in the text, has the capacity to create novel, successful, motor pattern sequences.

target was removed subsequent to their first movement (Grobstein *et al.*, 1990).

These observations suggest that the spatial localisation signal, rather than being conceived simply as an intermediate signal generated transiently and then disappearing once transmitted to the spinal cord, might instead be better understood as a signal defining an objective to be accomplished, a signal which potentially can remain present for an extended period of time ('intermediate spatial representation of objective' in Fig. 13.5). They also suggest the existence of an internal feedback loop, making possible a comparison between the objective signal and signals indicating the actual movement accomplished. Once a motor choice is made, based on the objective signal, corollary discharge signals indicating the particular choice and reafferent signals indicating the actual effects of the motor pattern selected (to left in Fig. 13.5) could be compared with the objective signal itself. If the two match (as in much of normal behaviour), the objective signal is cancelled. If they fail to match, an objective signal persists and a new motor choice and movement occur, with the process potentially generating an extended sequence of movements that ultimately achieve the defined objective.

Feedback loops provide a well understood basis for endowing biological (or other) systems with properties that correspond to purpose, in the sense of displaying capabilities to adjust for unpredictable perturbing events. Internal feedbacks loops, of the kind illustrated in Fig. 13.5, were in fact a prominent characteristic of models developed by von Holst and Mittelstaedt forty years ago to account for directed movement (von Holst and Mittelstaedt, 1950). These models, however, differed in two important respects from the present one. First, the internal feedbacks and associated comparators were developed to account for the organisation of a given movement pattern, rather than for successive movements. More importantly, the earlier models contained no randomising element, and the combination of purposiveness and playfulness in the present model gives it a special flavour. The deterministic model of Fig. 13.3 will yield a particular motor output for each input, but will display no capability to correct with successive movements for unpredictable variations either in the organism or in the environment. The model of Fig. 13.5 will be capable not only of corrective movements but also of the generation of novel sequences of corrective movements, enabling the frog to explore and find new effective sequences regardless of the particular challenge. In short, it is capable of behaviour which is not only purposeful but also creative. An observer would be totally incapable of predicting the effective solution which will be generated in response to a problem. The combination of internal feedback and a randomising element seems to me to take one a long way along the road to what is generally meant by 'free will'. Exactly how far along that road I will consider in the final section of this chapter.

13.5. Epilogue: the frog and beyond

I began this chapter with an excerpt from a classic paper by von Holst and Mittelstaedt. There are substantial and historically interesting coincidences between that paper and a quite different but equally important paper published in the following year by Karl Lashley (Lashley, 1951), who wrote 'I am coming more and more to the conviction that the rudiments of every behavioral mechanism will be found far down in the evolutionary scale and also represented even in primitive activities of the nervous system.' What is common to both papers is a sense of connectedness among phenomena at quite different levels of organisation, a concern that the reflex perspective was standing in the way of recognising that connectedness, and a conviction that analysis of the nervous system should both contribute to and take account of a concern for higher order behavioural phenomena. My objective in this paper has been to try to show that recent research on the frog is consistent with this prospectus. The problem of motor choice in the frog is not reducible to a parallel series of reflex pathways (see Altman and Kien, 1987, 1989, and Kien and Altman, Chapter 9 of this volume, for similar conclusions with regard to other systems). Efforts to generate more realistic models of the underlying neuronal organisation have successfully made use of such higher order behavioural concepts as 'choice' and 'gestalt' and at the same time are useful in dissecting the multiple meanings inherent in such terms. Moreover, what has emerged is that much of the richness of behavioural phenomenology which many presume to be the exclusive province of the most elaborate nervous systems is present in the less elaborate nervous system of the frog, as both Lashley, and von Holst and Mittelstaedt, suspected.

There remain, however, some deferred issues with regard to both 'choice' and 'free will' which might be brought into the framework of the present discussion. I believe that they can, and that while the frog may well prove not to be an organism in which they can be further explored experimentally, it is none the less useful for the conceptual analysis. I have argued that the frog displays a fairly sophisticated level of 'choice', with mechanisms to associate a given input with one of a number of possible outputs in a way which cannot be predicted from a knowledge of the activity in all input pathways. I have also argued that it displays elements of 'free will', at least to the extent of being capable of generating truly creative solutions to problems. What is noteworthy is that it does this in the absence of any semblance of a developed neocortex, the structure so prominent in more elaborate brains. This suggests that an identity may exist between the basic functions of neocortex, and those last troubling bits of the concepts of both choice and of free will.

What was put aside for latter consideration in the case of 'choice' was

'the sense of oneself having picked between alternatives, and the feeling that one is free to choose', and I think most readers would include these characteristics, in addition to the ability to generate novel solutions, as ingredients of 'free will'. Significantly, there are various reasons to believe these may indeed be cortical functions. Cortical activity in humans, at least as measured by encephalography, is quite similar in the waking state and during periods of dreaming, both of which are characterised by a fairly active sense of oneself, and differs in states such as quiet sleep in which a sense of self is absent. Furthermore, it has become increasingly clear in recent years that a not infrequent sequela to cortical damage is persistence of behaviour in the absence of a sense of things happening to oneself (cf. Weiskrantz, 1986). Finally, it has long been known that the cortex exerts substantial inhibitory control over subcortical circuitry.

What the studies on the frog imply is that there is a quite sophisticated information processing capability in subcortical circuitry. Cortex, and its associated afferent and efferent projections, represent a parallel input/output system with respect to the external world, but it is also capable of functioning relatively independently of that world (as during dreaming). A second 'world' with which the cortical system has input/output relations is subcortical circuitry. It seems to me not unreasonable to suggest that a sense of self emerges from the monitoring of subcortical circuitry by the cortex, and that a sense of choice arises from the capability of the cortex to exercise an executive control on the potential outputs of that subcortical circuitry. If there is indeed a capability to generate novel outputs, and an oversight function capable of approving or vetoing particular outputs that are generated, then one is indeed picking among alternatives and free to choose, in a quite full and meaningful sense. There is something satisfying in that, whether or not it is a capability which the frog has as well.

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