Doublesided Rose F-2

Learned topography: the eye instructs the ear

A unified experience of the external world may depend on the neural alignment of different sensory modalities. Why else would the nervous system bring together input from several senses and align them? In the optic tectum, visual, auditory, somatosensory[1,2], infrared[3] (in certain snakes), and electrosensory[4] (in electric fish) maps of space are superimposed. A recording electrode passing perpendicularly through the tectal cortex will encounter units of several modalities, each registering information from similar external locations. The alignment of sensory maps may be viewed from a motor rather than a perceptual frame of reference. For example, in mice somatosensory neurons carrying information about what is happening at the tip of a particular whisker project to the same tectal coordinate as the retinal neurons that see the tip of that whisker[1]. Stimulation of this part of the tectum by either modality or by an experimental electrode will cause the animal to orient to the real or virtual stimulus. Many tectal units are even multimodal, responding only when a particular combination of senses is conjointly stimulated from a particular event in the external world.

The most intriguing spatial map of sensory information must surely be the auditory one, for the one-dimensional, tonotopical organization of the cochlear sensory apparatus seems ill-suited to relay the information necessary to construct a two-dimensional map of exterior space. Neurons encoding the time and intensity differences of sound waves at the two ears – information needed for the formation of such a spatial map – have been discovered[6,7], and the neural mechanics of auditory localization are under active investigation. It is certainly clear from work in a number of species that auditory maps of space do exist, and that in the tectum they are in register with the overlying visual maps[1,8]. Nowhere has this demonstration been clearer than in the owl (Fig. 1), whose nocturnal predatory habits have undoubtedly put heavy selective pressure on auditory acuity[9,10].

The alignment of sensory maps in the tectum leads to the question of how the proper registration is initially constructed and thereafter refined[2]. A number of laboratories have begun to address these questions by experimentally misaligning the maps. Eye rotation is one way to do this. In the first such study, two visual projections to the frog tectum were misaligned[11], one a direct projection from the contralateral retina, and the other an indirect projection through the nucleus isthmus, originating from the contralateral eye[12]. During the weeks following the eye rotation, the two maps realigned through a reorganization of the isthmotectal projection[11,13,14]. Interestingly, the realignment only occurs in young premetamorphic frogs, and in these animals visual experience is essential for this process. Thus experimentally misaligned frogs kept in the dark do not re-register their disparate maps[11,15]. In other studies using salamanders[16] the visual and somatosensory maps were taken out of alignment before either map had even formed, by the rotation of an eye primordium. In this case there was no apparent alignment between the maps, suggesting that the tectal maps for the different modalities are established independently. Eye removal from a neonatal hamster suggested only a minor interaction between the visual and somatosensory systems in the tectum[17]. Similarly, it has been found that auditory–visual misalignment caused by an 180° eye rotation in a neonatal ferret is not resolved with time[18].

In a series of recent experiments using smaller misalignments, Knudsen and colleagues have shown that the auditory and visual maps in the owl tectum do interact. If one ear is plugged in an adult owl, the sound coming through that ear is delayed and attenuated. The result is that any sound in the environment appears to the owl to originate closer to the side of the unplugged ear than it actually is[19]. This is expected from the neurons that compute the spatial location of a sound by comparing interaural timing and intensity. Such experimental owls make predictable orientation mistakes of about 10° in auditory localization experiments. If one records from bimodal units in the tectum of such an animal, one finds the expected mis-

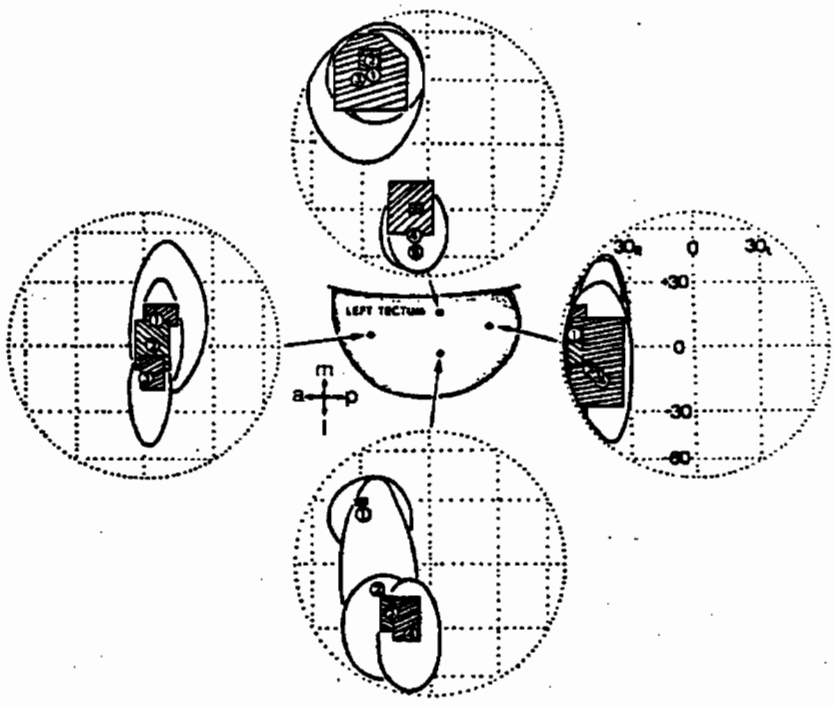

Fig. 1. *Visual and auditory receptive fields of sequentially recorded, bimodal units from four separate electrode penetrations in the left optic tectum. The penetrations were made at the locations indicated by the solid circles on the dorsal view of the tectum (center). The visual receptive fields are hatched; the auditory receptive fields are oblongs; the centers of auditory best areas are numbered. The numbers represent the order in which the units were encountered during each dorsoventral penetration. The receptive fields from the most medial penetration (top center) jumped from high to low. This is because the tectum curves around underneath, causing such medial penetrations to intersect both the dorsomedial (high fields) and ventromedial (low fields) edges of the tectum at two discontinuous portions of the track. a, anterior, p, posterior, m, medial, l, lateral.* (Taken from Ref. 10.)

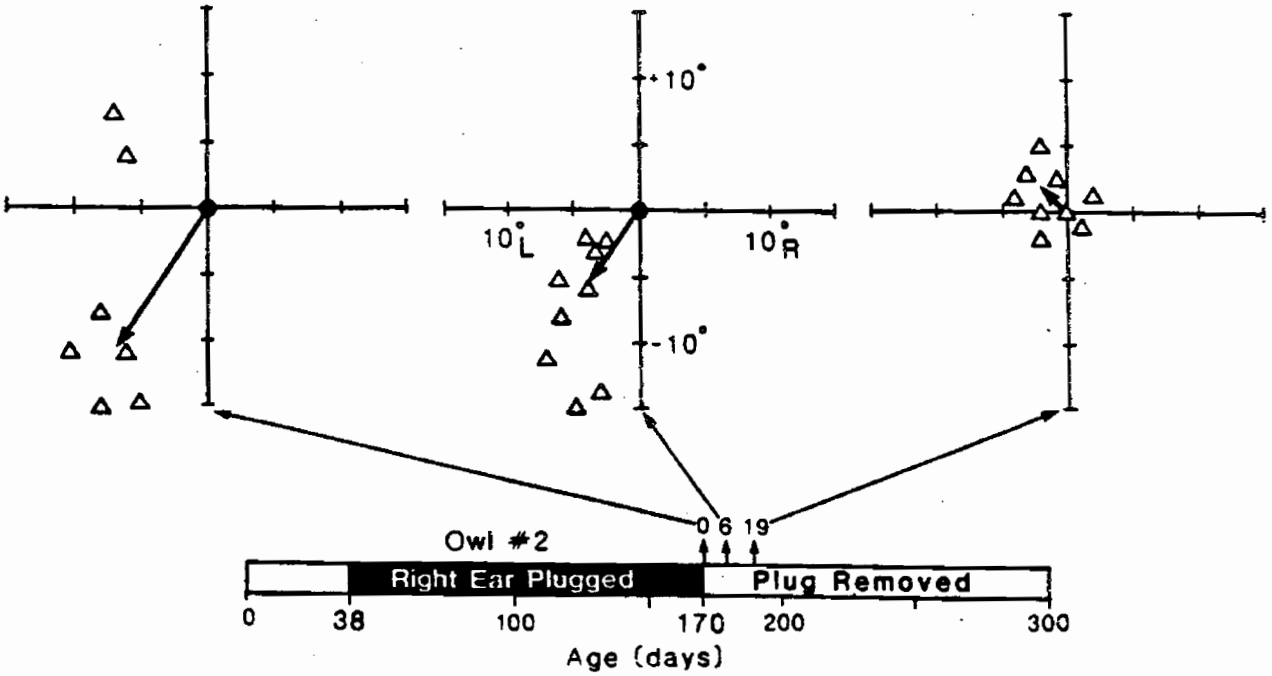

Fig. 2. *Progressive realignment of auditory spatial tuning with visual receptive fields over time in an owl that had earplugs removed at 170 days of age. The locations of auditory best area centers are plotted relative to the locations of visual receptive field centers for all bimodal units in the rostral tectum recorded on the day indicated. The vectors represent the median auditory–visual misalignments for these samples.* (Taken from Ref. 23.)

alignment of the visual and auditory receptive fields in a singe cell. This is not an example of neuronal plasticity since it is the result that would be expected if there were no changes in neural circuitry. Yet electrophysiological and behavioral studies of young owls, after many weeks of wearing an earplug, reveal that the auditory map becomes aligned with the visual one, implying an adjustment of the auditory map[20–22]. If the earplug is removed from a young owl who has adjusted to it, a new misalignment is introduced in the reverse direction, and this too readjusts over the next several weeks. The course of this topographic plasticity can be followed both electrophysiologically and behaviorally[23,24] (Fig. 2). As with the isthmotectal

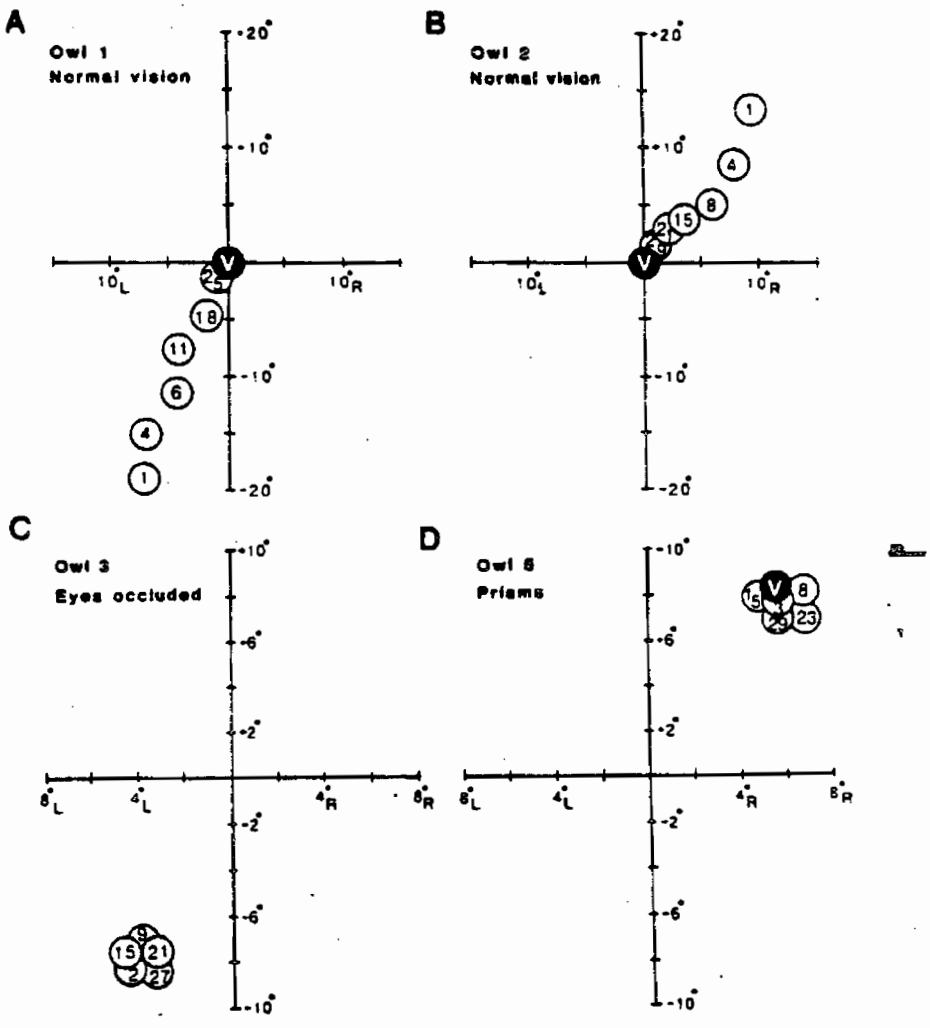

Fig. 3. *Auditory localization errors following earplug removal in four barn owls that had been raised with one ear plugged. The origin of each coordinate system was defined by the mean of more than 100 responses by the owl to the visual stimulus measured without opaque occluders or prisms in the spectacle frames. Each open circle represents the mean of 15 to 25 responses of the owl to the auditory stimulus; the number indicates the number of days after earplug removal on which the data were gathered. Standard deviations of the auditory responses ranged from 0.8° to 3.8°, but were typically between 1.0° and 2.5°. The owls were tested every 2 to 3 days, but because the data overlapped extensively, only a few representative points are shown. Circled Vs indicate the visual error attributable to the prism.* (Taken from Ref. 24.)

system discussed above, the realignment is only possible in young owls, because if the earplug is removed from an adult owl who received it neonatally, the behavioral error and neural misalignment induced by the plug seems to be permanent[23]. Knudsen and Knudsen[24] have also shown that recovery of sound localization accuracy requires visual experience. Young owls that are prevented from seeing after earplug removal persist in making auditory errors in behavioral tests[24] (Fig. 3). It is as if the visual input plays an instructive role in directing the proper neural alignment of auditory space. This idea is strengthened by experiments with young owls wearing prism glasses that, for example, deviate vision 10° to the right. Within a month such an owl adjusts his auditory response so that it matches the visual error induced by the prism. Thus, the owl would orient 10° to the right of a purely acoustic stimulus[25]. Similarly, if a visual error is introduced by prisms to match the auditory error induced by an earplug, there is no correction when the earplug is removed[24] (Fig. 3). This proves that accurate auditory spatial localization can, in a sense, be learned by comparing sounds with sights.

Experience-dependent changes in neural connectivity are usually considered a form of learning. In this case the learning seems special, for it may involve the shifting of a large population of afferents so as to bring an entire misaligned map into register. Readjustments of the auditory map may actually occur at an earlier level of auditory processing than the tectum, since neuroanatomical studies of earplugged animals show no evidence for a remapping of the auditory projection from the inferior colliculus to the tectum[23]. Thus, it could be that the neurons that compute interaural time and intensity differences are being retuned in these experimental animals. If so, the visual input may refine the auditory map simply by providing a directional error signal. This could be similar to the way retinal slip provides the error signal necessary for changing the gain on the vestibulo-ocular reflex[26,27]. Of course, this line of reasoning brings with it the possibility that a cerebellar pathway is involved, an issue which the Knudsens and colleagues are considering. Clearly, the neural mechanisms allowing intermodal transfer of spatial information to rewire the brain are of great interest to students of neural adaptation and learning.

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Doublesided Rose F2

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The Generation and Subtraction of Sensory Expectations within Cerebellum-Like Structures

Abstract

The generation of expectations about sensory input and the subtraction of such expectations from actual input appear to be important features of sensory processing. This paper describes the generation of sensory expectations within cerebellum-like structures of four distinct groups of fishes: Mormyridae; Rajidae; Scorpaenidae; and Apteronotidae. These structures consist of a sheet-like array of principal cells. Apical dendrites of the principal cells extend out into a molecular layer where they are contacted by parallel fibers. The basilar regions of the arrays receive primary afferent input from octavolateral endorgans, i.e., electroreceptors, mechanical lateral line neuromasts, or eighth nerve endorgans. The parallel fibers in the molecular layer convey various types of information, including corollary discharge signals associated with motor commands, sensory information from other modalities such as proprioception, and descending input from higher stages of the sensory modality that is processed by the structure. Associations between the signals conveyed by the parallel fibers and particular patterns of sensory input to the basal layers lead to the generation of a negative image of expected sensory input within the principal cell array. Addition of this negative image to actual sensory input results in the subtraction of expected from actual input, allowing the unexpected or novel input to stand out more clearly. Intracellular recording indicates that the negative image is probably generated by means of anti-Hebbian synaptic plasticity at the parallel fiber to principal cell synapse. The results are remarkably similar in the different fishes and may generalize to cerebellum-like structures in other sensory systems and taxa.

Key Words
Expectation
Cerebellum
Plasticity
Octavolateral
Fish
Teleosts
Elasmobranchs
Long-term depression

Introduction

Many aspects of sensory processing may be understood as the generation of expectations or predictions about sensory input and the removal of such expectations from the current sensory inflow [Bullock, 1988; Barlow, 1990]. Removing what is expected allows the unexpected or novel sensory input to stand out more clearly, and it is this novel input that conveys new information and is critical for the animal's survival. This review describes the generation of expectations in different cerebellum-like structures of fish and places this work in the context of general issues in sensory processing.

In an information-theoretic sense, the amount of information in a signal is reduced in proportion to its predictability and a completely predictable signal conveys no

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Abbreviations

AM	amplitude modulations
CB	cerebellum
CC	cerebellar crest
DON	dorsal octavolateral nucleus
DCN	dorsal cochlear nucleus
DGR	dorsal granular ridge
E-cells	receptive field centers excited by stimuli that excite afferents
EG	eminentia granularis
Egp	eminentia granularis posterior
ELL	electrosensory lateral line lobe
EOD	electric organ discharge
FL	fin lift
I-cells	receptive field centers inhibited by stimuli that excite afferents
I-inj	intracellular current injections
LG	lateral granular area
LTD	long term depression
MON	medial octavolateral nucleus
nAll	anterior lateral line nerve
nVIII	eighth nerve
VCN	ventral cochlear nucleus

information at all [Shannon and Weaver, 1949]. Thus, removal of what is predictable or redundant in a sensory message results in a greater density of information in the signal and greater efficiency in the use of central circuits for processing and storing the information. In a similar manner, computer science has developed encoding methods to remove redundancy from digital data to allow for greater efficiency in the transmission, analysis, and storage of such data.

In addition, the input to some sensory systems can not even be interpreted or used unless some of the predictable components of that input are accounted for or removed. This is certainly true for those systems with movable sensory surfaces. The location and the movement of the sensory surface must be accounted for if the input to the surface is to be correctly interpreted and if movements of the sensory surface are to be distinguished from movements in the external world. Changes in the orientation of the head, for example, will have predictable effects on retinal, auditory and vestibular input and these effects must be accounted for if the input signals are to inform the animal about its own location or the location of external stimulus sources.

Finally, perception itself may be viewed as the active generation by the organism of an interpretation or model of the stimulus source [Helmholtz, 1925; Mackay, 1951; Barlow, 1990]. The model may be derived from a small set of sensory cues and then tested by comparing the sensory predictions of the model against additional sensory cues. If the match is a good one then the model is confirmed. If the match is not so good then a variation on the model is generated and tested, or new knowledge of a new object is created. The overall process is one of generating hypotheses or expectations about sensory input and comparing those expectations with actual input, perhaps by a subtractive process.

There are three general sources of information on which to base expectations or predictions about sensory input: (1) regularities or associations within the sensory modality being processed; (2) regularities or associations between other sensory modalities and the modality being processed; (3) regularities or associations between motor commands and the sensory input that is evoked by the motor commanded motor act ('reafferent' input in the nomenclature of von Holst and Mittelstaedt [1950]). Most discussions of redundancy and encoding to reduce such redundancy are restricted to the first of these sources, predictive information within a single modality, but all three sources are discussed in this review.

Some associations are so consistent or so universal that expectations can be generated and subtracted from the sensory inflow by hard-wired processes that do not involve memory. For example, temporal adaptation to a maintained stimulus, whether it occurs peripherally or centrally, can be understood as the subtraction of an expected mean level based on the input of the immediate past. Similarly, in the spatial domain, lateral inhibitory processes mediate the subtraction of an expected level derived from a spatial average. A few additional examples of the hard-wired generation and subtraction of expectations are provided in subsequent sections of this review.

However, both animals and their environments are variable and complex. Associations appear, change, and disappear over time. Memory-like processes will in general be required for animals to take advantage of all the associations that occur within modalities, between modalities, or between motor commands and reafferent input.

This review describes memory-based expectations about sensory input and their subtraction from actual sensory input in the cerebellum-like structures of fishes from four well-separated taxa. The fishes to be discussed are an electric teleost of the family Mormyridae (*Gnathonemus petersii*), a skate of the family Rajidae (*Raja erinacea*), a marine teleost of the family Scorpaenidae (*Scorpaena papillosus*), and a second electric teleost of the family Apteronotidae

(Apteronotus leptorhynchus). The next section of this review describes the anatomy of different cerebellum-like structures associated with octavolateral endorgans. Subsequent sections describe the expectation-like phenomena that are observed in the four different fish systems. The two final sections present an overview of the different fish systems and speculate on the significance of the findings for other structures with similar histology including the cerebellum itself.

Cerebellum-Like Structures Associated with Octavolateral Sensory Systems

Cerebellum-like structures that receive primary afferents from octavolateral endorgans are found in the medullae of fish, amphibians and mammals (fig. 1; Montgomery et al. [1995]). These structures include the dorsal cochlear nucleus (DCN) of mammals which receives primary afferents from the cochlea, the dorsal octavolateral nucleus (DON) of many nonteleost fishes and some amphibians which receives primary afferents from electroreceptors, the electrosensory lateral line lobe (ELL) of electroreceptive teleosts which also receives primary afferents from electroreceptors, and the medial octavolateral nucleus (MON) in most fishes and some amphibians which receives primary afferents from mechanical lateral line endorgans and in some cases from eighth nerve endorgans. Only a brief summary is given here. The paper by Montgomery et al. [1995] should be consulted for a more complete description of the histology and connectivity of these different structures and for additional references.

The cerebellum-like structures are composed of a sheet-like array of principal cells in which the primary afferent input maps onto the basilar regions of the array (fig. 2). The mapping of electroreceptor input to DON and ELL is somatotopically organized: the mapping of auditory input onto DCN is tonotopic. In the ELL of teleost fishes, the receptive field centers of some principal cells are excited by the same stimuli that excite afferents (E-cells), whereas the receptive field centers of other principal cells are inhibited by such stimuli (I-cells; Bastian [1981], Bell and Grant [1992], McCreery [1977]). In gymnotid fishes, the E-cells have been shown to be contacted directly by the afferents and I-cells to be affected indirectly via inhibitory interneurons [Saunders and Bastian, 1984]. The E- and I-cells have been identified so far only in the ELL of teleosts and may not exist in other cerebellum-like octavolateral structures.

Axons of projection neurons in these structures convey the output to higher, mesencephalic stages of processing. Most if not all principal cells are projection neurons in the DON of elasmobranchs and the ELL of gymnotid fishes. In the ELL of mormyrids, however, most of the principal cells are inhibitory neurons that terminate locally on those principal cells that are projection neurons [Meek, 1993]. The ELL of mormyrids is similar in this respect to the histological pattern of the cerebellum of teleosts where Purkinje cells terminate locally within the cortex on projection neurons known as eurydendroid cells [Nieuwenhuys et al., 1974; Meek and Nieuwenhuys, 1991; Mugnaini and Maler, 1993].

The apical dendrites of the principal cells are densely covered with spines and extend into the overlying molecular layer where the spines are contacted by parallel fibers. In fishes and amphibians, the parallel fibers arise from the granule cells of an external granule cell mass that is generally known as the eminentia granularis (EG), although in elasmobranch fishes the terms dorsal granular ridge (DGR) and lateral granular area (LG) have been given to the granule cell populations supplying parallel fibers to the DON and MON, respectively. In the DCN, the parallel fibers arise from granule cells that are located both below and at the edges of the principal cell array. Stellate-like inhibitory interneurons are also present in the molecular layer of all of these structures as shown in figure 2. Additional inhibitory interneurons are present in the deeper layers which influence the center-surround structure of receptive fields and the temporal pattern of sensory responses in principal cells. Other interneurons mediate commissural inhibition of the contralateral side [Bastian et al., 1993; New and Bodznick, 1990].

The granule cell masses that give rise to the parallel fibers receive their inputs from a rich variety of sources: (1) descending input from higher stages of the modality being processed; (2) input from other sensory modalities, such as proprioception, and (3) corollary discharge signals associated with motor commands. These inputs have been identified by both anatomical and physiological means. The EG of mormyrids and the DGR of elasmobranchs have been shown to receive all three types of input, and the EG of gymnotids has been shown to receive both descending electrosensory and proprioceptive input. The different inputs to the granule cells are labeled as 'Predictive Inputs' in figure 2. Note that these inputs include all three sources of information that were referred to in the Introduction as potentially associated with current sensory input and thus potentially capable of predicting it.

The general hypothesis regarding these various structures is that the occurrence of a temporal association between parallel fiber inputs and sensory input to the deeper

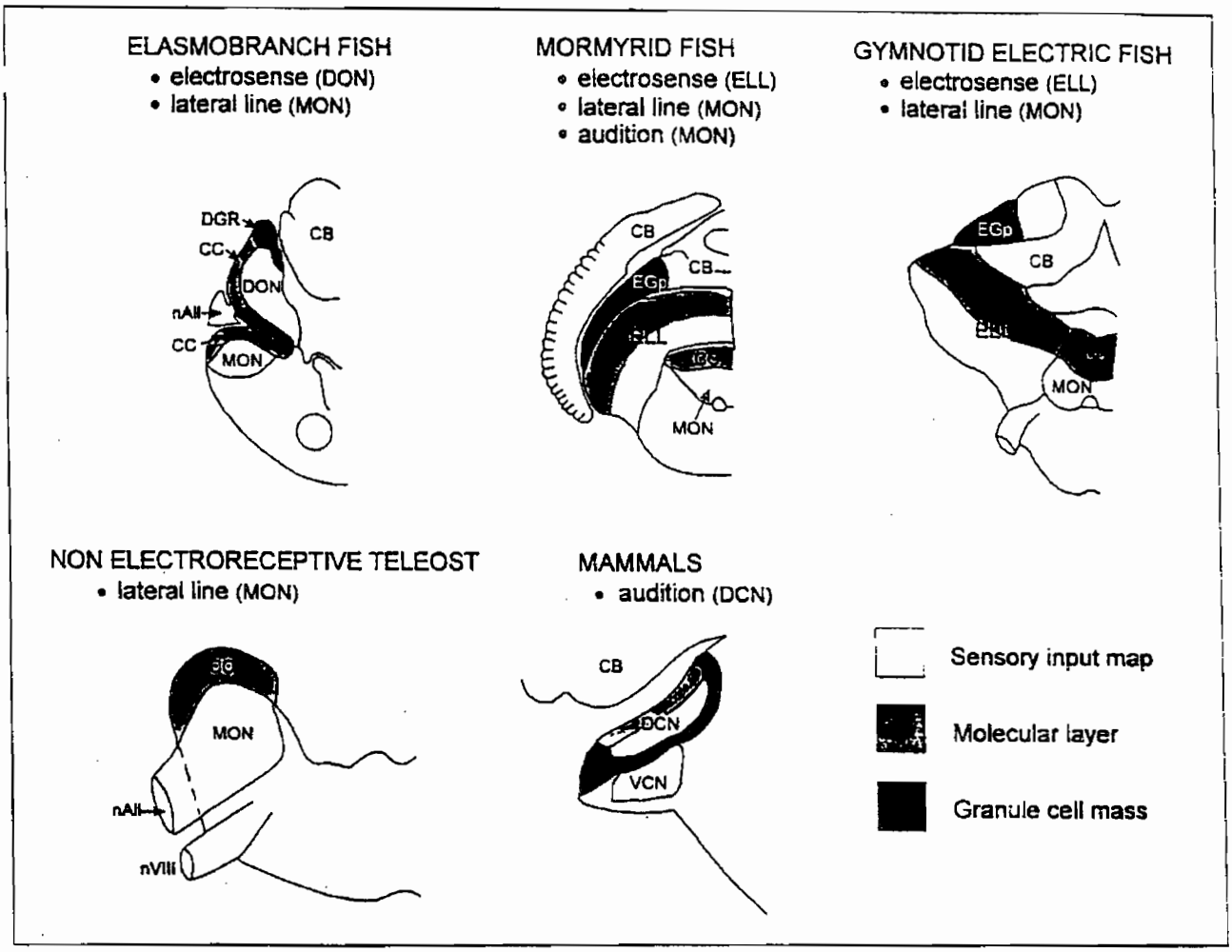

Fig. 1. Cerebellum-like structures associated with octavolateral sensory systems. The sensory input map, molecular layer and granule cell mass of the different structures are shown with different types of shading, as indicated at the lower right. Bullet marks below the name of the taxon indicate the sensory systems and associated structures in each group. CB = Cerebellum; CC = cerebellar crest; DCN = dorsal cochlear nucleus; DGR = dorsal granular ridge; DON = dorsal octavolateral nucleus; EGp = eminentia granularis posterior; ELL = electrosensory lateral line lobe; MON = medial octavolateral nucleus; nALL = anterior lateral line nerve; nVIII = eighth nerve. [Adapted from Montgomery et al., 1995.]

layers leads to the generation of a negative image of predicted or expected input within the principal cells. The proposed mechanism is that of anti-Hebbian synaptic plasticity at the parallel fiber to principal cell synapse. Anti-Hebbian plasticity means that the pairing of parallel fiber input with depolarization of the principal cell by sensory input results in a reduced efficacy at the paired parallel fiber synapse. Unpaired parallel fiber inputs are either unaffected or possibly enhanced in efficacy (see below). Reduction in the excitatory effect of paired parallel fiber input relative to unpaired inputs results in a hyperpolarization when the previously paired parallel fibers are active. Plasticity leading to enhanced efficacy at paired inhibitory synapses could contribute to such a hyperpolarization (see below). The result is a negative image of expected sensory input that is generated in the principal cell array by the predictive parallel

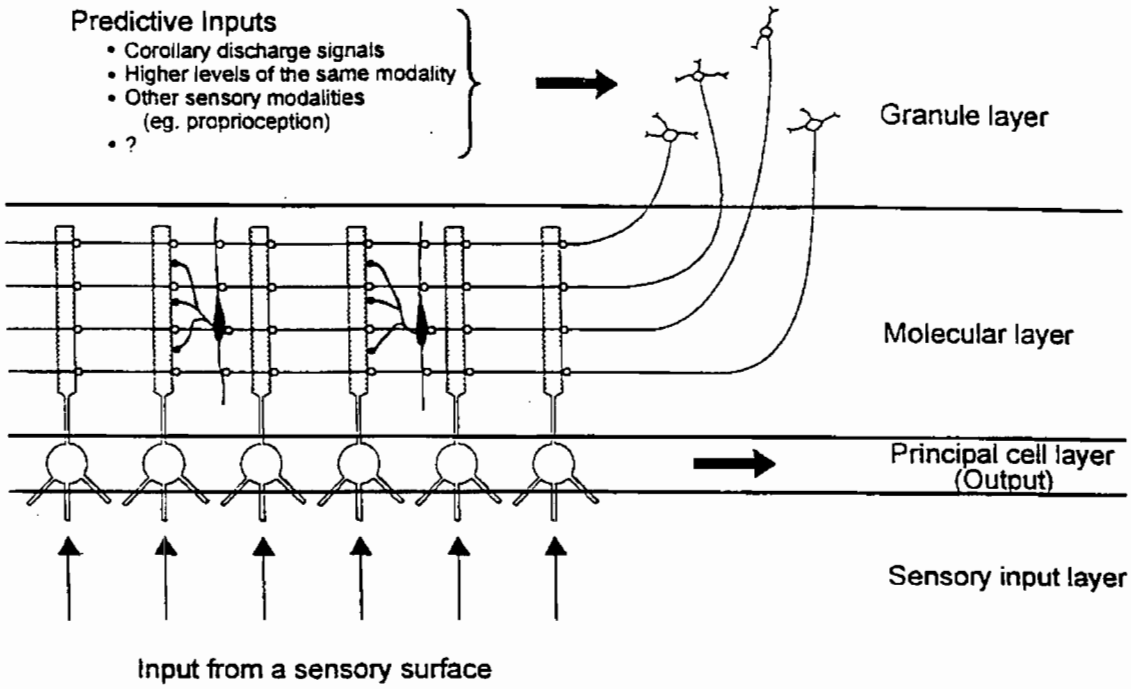

Fig. 2. Schematic drawing showing major features of cerebellum-like octavolateral structures. Inhibitory stellate cells of the molecular layer are shown in black. See text and Montgomery et al. [1995] for additional information.

fiber inputs. Addition of the negative image of expected input with the current input results in the continuous subtraction of expected from current input. Evidence for such a process in the different fish systems is presented in the following sections.

Mormyrid Electrosensory Lobe

Evidence for the generation of a negative image of expected input was first obtained in the ELL of mormyrid electric fish [Bell, 1982]. Corollary discharge signals associated with the motor command that elicits the electric organ discharge (EOD) are prominent in the mormyrid ELL and have strong effects on the processing of reafferent sensory input that is evoked by the EOD. Experiments are done in curarized fish in which the normal EOD is blocked but in which the EOD motor command continues to be emitted ('fictive discharging') and in which the electrosensory input is controlled by the experimenter.

Some of the corollary discharge effects are fixed and do not change during many hours of recording in spite of long periods of association with sensory stimuli. These fixed effects are inhibitory for one class of electroreceptor afferents where they provide an example of the generation and subtraction of a hard-wired motor command-driven expectation about sensory input [Bell and Grant, 1989]. A hard-wired inhibitory process is effective here because the reafferent response for this class of electroreceptors is very brief and does not vary.

Other effects of the corollary discharge are plastic, however, and are strongly affected by the pattern of reafferent electrosensory input that has followed EOD motor commands in the recent past [Bell, 1982]. Pairing an excitatory sensory stimulus with the EOD command for a few minutes leads to an inhibitory corollary discharge effect at the same latency as the paired excitatory sensory stimulus. Pairing with an inhibitory sensory stimulus leads to an excitatory corollary discharge effect (fig. 3). The altered corollary discharge effects are observed by simply turning off

the sensory stimulus and looking at the effect of the EOD command by itself. No change occurs if the stimulus is given at the same temporal frequency but with no association to the command. The modifiable corollary discharge effect is temporally specific in that it matches the delay of the paired sensory stimulus out to delays of about 100 msec. The effect is spatially specific in that sensory stimuli must be in the cell's receptive field, i.e. they must affect the cell, for the pairing to result in a modification. Thus, the corollary discharge elicits a temporally and spatially specific negative image of the afferent input that has followed the command in the recent past.

The modified corollary discharge effect disappears within a few minutes when the paired sensory stimulus is turned off (fig. 3). This decline does not appear to be a simple passive decay of a stored image, however, but rather an active rematching of the (unchanging) afferent input that now follows the command after turning off the sensory stimulus. This was shown by silencing the command after pairing by means of lidocaine in the command nucleus and noting that a response was still present when the command was allowed to occur again 30 min later [Bell, 1986]. Thus the altered responsiveness to the corollary discharge appears to last at least 30 min when updating by the continued occurence of the corollary discharge is prevented.

The question immediately arises as to whether the altered corollary discharge effect is due to a change in the corollary discharge driven activity of fibers that terminate on the principal cell or to an altered response of the cell to an unchanging corollary discharge input. In the former case the modification or plasticity in the corollary discharge response would be occurring outside the ELL. In the latter case, the modification would be occurring within the ELL at the synapses onto principal cells. These two alternatives were tested by intracellular recording from principal cells and pairing the corollary discharge with an intracellular injection of depolarizing current to a single cell (instead of with a sensory stimulus that affects many cells [Bell et al., 1993]). Such pairing was effective in generating a hyperpolarizing response at the delay of the paired current injection (fig. 4). A broad spike, presumed to be a dendritic spike in the apical dendrites, appeared to be critical for the plasticity. The fact that pairing with intracellular stimulation of a single cell was effective and that the critical postsynaptic event (a dendritic spike) appeared to be restricted to a single principal cell strongly sugests that plasticity took place at synapses onto the principal cell.

For many years, the mormyrid results appeared to be an isolated example of plasticity in a cerebellum-like octavolateral structure. Recent and surprisingly similar results in three quite different systems show, however, that the phenomenon is much more general.

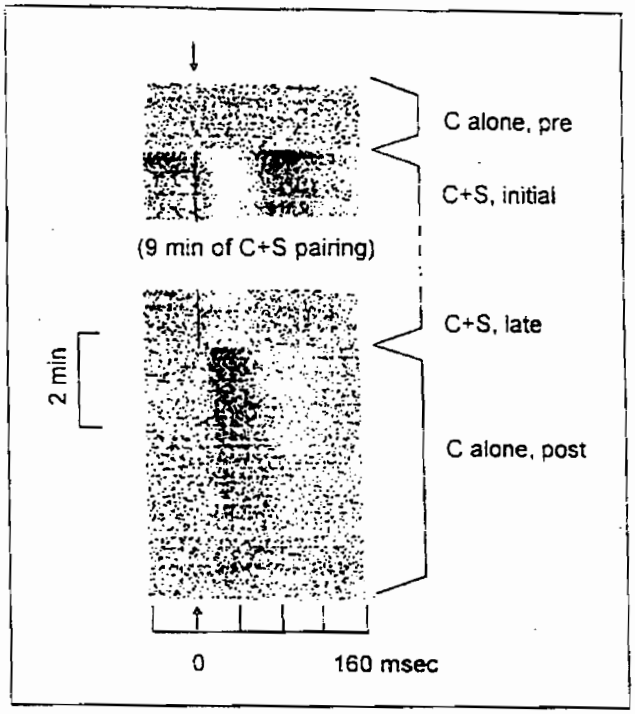

Fig. 3. Principal cell in the mormyrid ELL showing plasticity in the response to corollary discharge of EOD motor command due to pairing with a sensory stimulus. Each dot represents a spike. The EOD motor command occurs at time 0 (vertical arrows). The EOD itself has been silenced by curare. Initially the command alone (C alone, pre) has little effect on the cell. An electrosensory stimulus that inhibits the cell is then paired with the command (C+S, initial). The time of the stimulus is indicated by the vertical black line. The effect of the stimulus is reduced after 10 min of pairing (C+S, late). This reduction is due to the development of a response to the command that is opposite to the response to the sensory stimulus, as shown by turning of the stimulus (C alone, post). The newly developed response to the command disappears within a few minutes in the absence of stimulation [from Bell, 1986].

The Dorsal Octavolateral Nucleus of Elasmobranchs

In elasmobranch fishes, an electrical current flow between the gills and the rest of the body is modulated by the animal's respiratory movements. Electroreceptors in the skin are affected by this current, and the primary afferent activity is strongly modulated during respiration [Bodznick

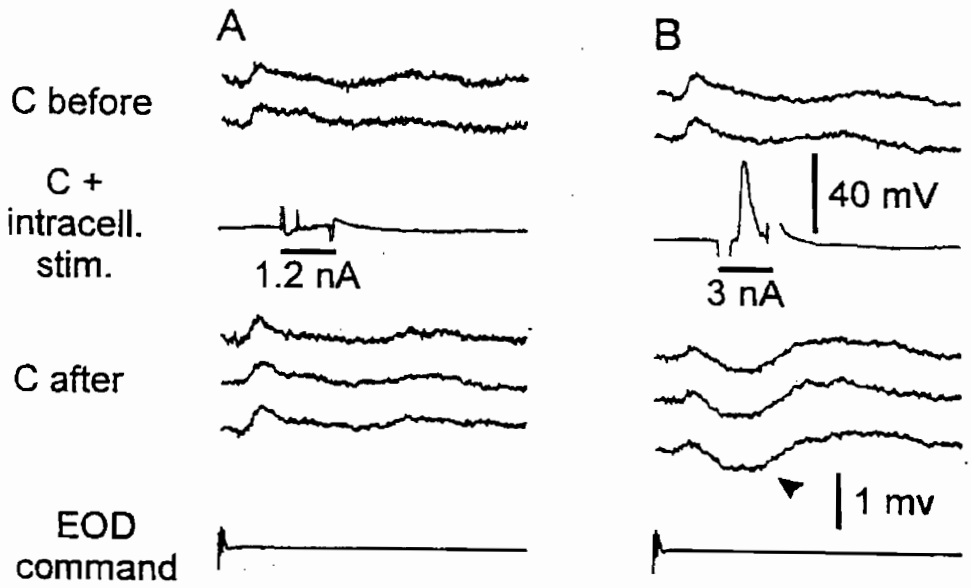

Fig. 4. Principal cell in mormyrid ELL showing plasticity in response to corollary discharge of EOD motor command due to pairing with an intracellular current pulse. All traces are triggered by the EOD motor command as indicated in the bottom trace of each column. High gain traces before (C before) and after (C after) pairing are averages of 15 sweeps taken at 15 second intervals. A single sweep at low gain shows the effect of the intracellular current pulses during pairing. **A** Effect of pairing with a low intensity current pulse that evokes only a small narrow spike (probably a somatic or axonal spike). Pairing has little effect on the response to the EOD motor command. **B** Effect of pairing with a stronger current pulse that evokes a large broad spike (probably a dendritic spike). Pairing now leads to the development of a hyperpolarizing response to the command that is centered on the time of the previously paired broad spike [from Bell et al., 1993].

et al., 1992; New and Bodznick, 1990], but the principal cells of the DON, on which the primary afferents terminate, are either unaffected or only weakly modulated during respiration. How is this possible? The absence of responsiveness in principal cells to respiratory movements was initially thought to be due entirely to a common mode rejection mechanism [Montgomery, 1984; New and Bodznick, 1990; Bodznick et al., 1992]. The receptive fields of principal cells include both an excitatory and an inhibitory region. Afferents from each of these regions are modulated by respiration. If excitation and inhibition are balanced, then the cell as a whole would be only minimally affected by respiration. This mechanism certainly contributes to the unresponsiveness of principal cells and provides another example of a hard-wired mechanism for removing a highly predictable and unwanted reafferent input.

Recent work has shown, however, that an adaptive memory-based mechanism also makes an important contribution to the reduction in reafferent responses of principal cells [Bodznick, 1993; Montgomery and Bodznick, 1994]. The experiments were done by recording from a principal cell in DON and giving an extra electrosensory stimulus at a fixed phase of the respiratory cycle (fig. 5). The response to this extra excitatory sensory stimulus is progressively reduced over several minutes. When the stimulus is turned off after several minutes of pairing, a pause is present at the same phase of the respiratory rhythm as the previously paired excitation. Similarly, pairing with an inhibitory stimulus leads to a progressive decline in the inhibition, and turning off the stimulus reveals a burst at the time of the previously paired inhibition. Control experiments show that in most cases there is no decline to repeated stimuli in the absence of an association to the respiratory rhythm. Thus, in elasmobranchs as in mormyrids, a highly specific negative image of expected reafferent input has been generated and added to the actual input.

Granule cells of the DGR give rise to the parallel fibers and are known to receive three types of information which

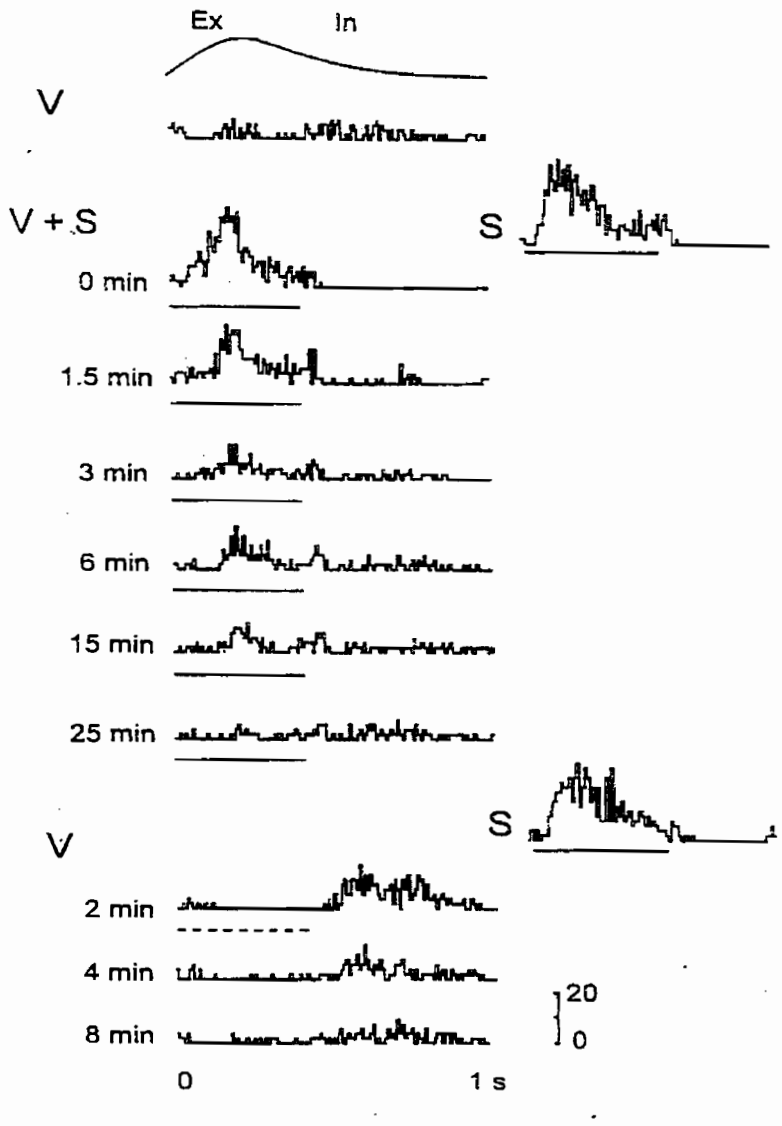

Fig. 5. Principal cell in a skate dorsal octavolateral nucleus showing plasticity in the response to the fish's ventilatory movements due to pairing with an electrosensory stimulus. Each histogram shows the summed effects of 50 trials. The top trace shows the ventilatory movement. Records were taken in the order shown. The top histogram labeled 'V' shows the response to ventilatory movement before pairing. The traces labeled 'V+S' show the responses of the cell when a 2 μV dc step dipole stimulus is coupled to the animal's ventilatory movements. The time of the stimulus is indicated by a bar below the histograms. Note that the response to the stimulus coupled to ventilatory movements shows a gradual decline over the 25 min of presentation. When the stimulus is abruptly turned off the neuron's activity during ventilation is a negative image of the previous reafference (histograms labeled 'V' at the bottom). Responses to the same dipole presented uncoupled from ventilation but at about the same rate of 0.5 Hz are not affected by the period of coupling (histograms labeled 'S' at right) [from Montgomery and Bodznick, 1994].

could provide the necessary signals for generating an image of expected reafference: (1) electrosensory input from higher electrosensory centers that is also modulated by respiration; (2) proprioceptive input signaling respiratory movements, and (3) corollary discharge input associated with the motor commands to respiratory muscles [Hjelmstad et al., 1993; Conley and Bodznick, 1994]. Experiments have been done to determine which of these signals are used in the generation of the negative image, and a report is in preparation [D. Bodznick, J. Montgomery and A. Pachynski, unpubl. observ.].

The clearest results were obtained with proprioceptive stimuli as illustrated in figure 6. The fin of the ray was raised and lowered passively in a cyclic manner and a local electrosensory stimulus affecting the principal cell was given at a fixed phase of the movement. Once again, the effect of the local electrosensory stimulus diminished over time, and a pause in the cell's firing was observed after turning off the electrosensory pause. The time of the pause with respect to the proprioceptive stimulus was the same as that of the previously paired stimulus, illustrating again the temporal specificity of the negative image. The pairing with

a proprioceptive stimulus affected only a small proportion of principal cells, whereas the pairing with the self-generated respiratory movements resulted in a diminished response in the majority of principal cells.

Pairing a local electrosensory stimulus with a large field electrosensory stimulus that affected the whole body or with the isolated respiratory motor commands (recorded as motoneuron activity from the facial nerve of a curarized fish) were less effective than pairing with proprioceptive stimuli. Some cells appeared to be marginally affected by pairing with the whole field electrosensory stimulus but no cells were observed to change as a result of pairing with the respiratory corollary discharge signals alone.

The pairing with separate components among the set of signals present during normal respiration was clearly less effective in these fish than pairing with normal respiration itself. The methods chosen to test the individual components may not have been adequate, but it is also possible that the strongest effects in these fish are obtained only when all the available predictive signals occur together.

Medial Octavolateral Nucleus of the Scorpion Fish

Results have been obtained in the mechanical lateral line system and MON of these marine teleosts that are very similar to the results in elasmobranchs. Water flow caused by the fish's own respiration has a strong effect on primary mechanical lateral line afferents, but the principal cells that receive this input appear to be much less modulated by the respiratory rhythm. An adaptive memory-like process appears once again to be an important part of the explanation. This was shown by giving an additional stimulus to the mechanical lateral line receptors at a fixed phase of the respiratory rhythm [Montgomery and Bodznick, 1994]. The response to the additional stimulus decreased over several minutes of associated repetition, and a pause in the firing of the principal cell was observed after turning off the extra stimulus. The pause occurred at the same delay as the previously paired stimulus. Thus, in this system also, a negative image develops that opposes the predictable aspects of the mechanical lateral line input.

The Gymnotid Electrosensory Lobe

Mormyrid and gymnotid fishes are well separated phylogenetically and are believed to have evolved their electrosensory systems independently [Bullock et al., 1983]. It

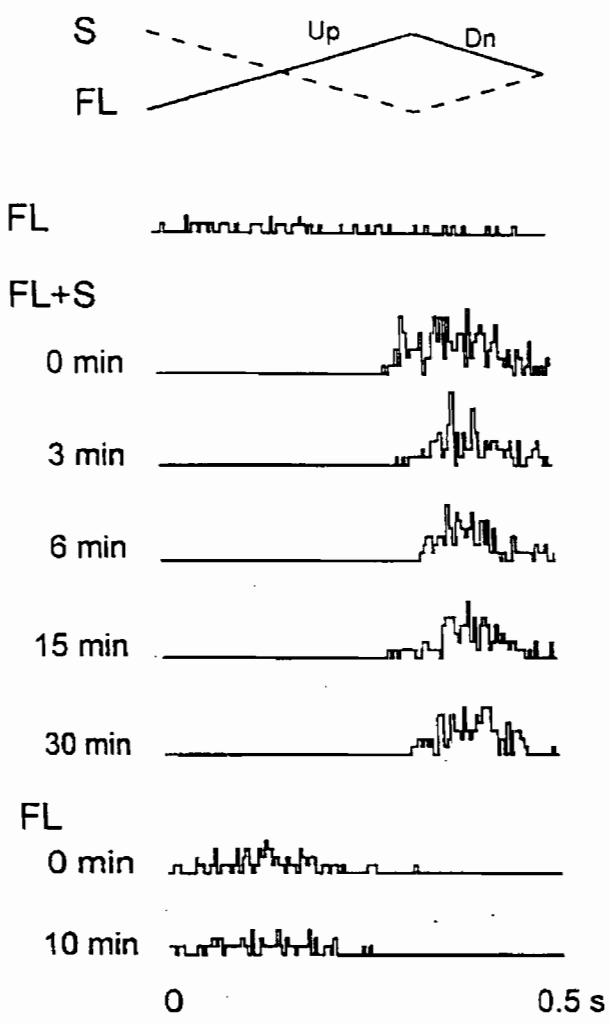

Fig. 6. Principal cell in a skate dorsal nucleus showing plasticity in the response to a proprioceptive stimulus due to pairing with an electrosensory stimulus. Histograms indicate the cell's activity during a cycle of passive lift to the ipsilateral pectoral fin (illustrated with a solid line labeled 'FL' at the top). Initially there is little response to the fin lift alone as indicated by the top histogram labeled 'FL'. A local electrosensory stimulus was then paired with the fin lift (histograms labeled 'FL+S'). The electrosensory stimulus was an amplitude modulated triangle wave which went from +1.5 μV to –1.5 μV with a time course that matched that used for the fin displacements. The records were taken in the order in which they are presented. Note that coupling of the local electrosensory stimulus with fin movements leads to a gradual decline in the response to the stimulus. This is due to the development of a response to the fin lift alone which is opposite to the effect of the stimulus, as seen in the two bottom histograms showing the responses to fin lift alone after the pairing [from D. Bodznick, J. Montgomery and A. Pachynski, unpubl. observ.].

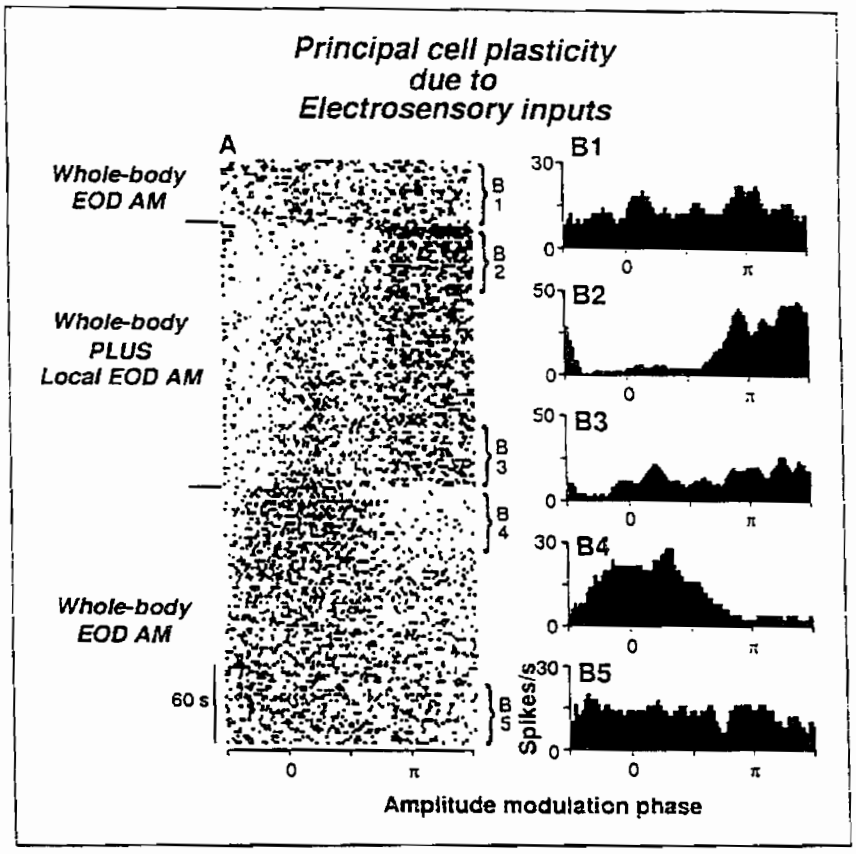

Fig. 7. Principal cell in a gymnotid ELL showing plasticity in response to a whole body transverse electrosensory stimulus due to pairing with a local electrosensory stimulus. Both the whole body and local electrosensory stimuli were amplitude modulations (AM) of the fish's own EOD [see Bastian, 1995, for methods]. **A** Raster display of responses to a 0.4 Hz AM signal applied to the whole body ('Whole-body EOD AM') before and after the pairing of this whole body stimulus with a synchronous local stimulus ('Whole-body plus local EOD AM'). Note the decline in the response to whole body plus local stimulus during the pairing and the development of a response to the whole body stimulus as a result of the pairing. The vertical bar at the lower left of the rasters shows the vertical time scale. **B1–B5.** Period histograms taken from the same data as the raster display at the epochs indicated by the labeled brackets in **A** [from Bastian, 1995].

is therefore of special interest that adaptive memory-like processes are also found in the ELL of gymnotid electric fishes [Bastian, 1995].

Active or passive bending of the body or tail in an electric fish alters the spatial relation between the electric organ and electroreceptors in the skin. Both theoretical [Heiligenberg, 1975] and experimental [Bastian, 1995] work shows that such bending will alter the electric organ-induced input to electroreceptors. Bastian has examined the responses of primary afferents from electroreceptors and principal cells of ELL to passive tail bending in a discharging fish of the species *Apteronotus leptorhynchus*. The primary afferents respond the same to tail bending and to an electrosensory stimulus that mimics the effect of the tail bending on EOD induced current at the receptor. In contrast, the principal cells of ELL respond poorly to tail bending but respond quite well to the pure electrosensory stimulus.

The difference between primary afferent and principal cell responses to tail bending is again due to an adaptive memory-like process in the ELL. Pairing excitatory electrosensory stimuli to the receptive field of the princial cell at a fixed phase of tail movement results in a decline of the response to the stimulus during several minutes of pairing. Turning off the stimulus reveals an inhibition at the time of the previously paired excitation. Pairing with inhibitory stimuli has the opposite effects. The effects are temporally specific to the phase of bending at which the stimulus is given. Repeated tail bending alone or repeated presentation of the electrosensory stimulus alone are ineffective. Thus, in gymnotid fishes, as in the other systems, a highly specific negative image of expected input can be generated and added to the actual sensory input.

At least two types of predictive signals are available for generating the expectation about sensory input during passive tail bending: proprioceptive and electrosensory signals. Proprioceptive inputs from muscles and tendons are activated by bending, and fibers conveying proprioceptive information terminate on granule cells of Egp. Electrosensory signals are also available because bending the tail will alter the pattern of electrosensory input over the whole

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Sensory and motor maps in the mammalian superior colliculus

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The sudden onset of a novel or behaviorally significant stimulus usually triggers responses that orient the eyes, external ears, head and/or body toward the source of the stimulus. As a consequence, the reception of additional signals originating from the source, and the sensory guidance of appropriate limb and body movements are facilitated. Converging lines of evidence, derived from anatomical, electrophysiological and lesion experiments, indicate that the superior colliculus (SC) is an important part of the neural substrate for the generation of orienting responses, involved in both the localization of sensory stimuli and the initiation of orienting responses[1].

The seven alternating cellular and fibrous layers of the mammalian SC form two major functional divisions: a superficial division and a deep division[2]. Inputs to the superficial division are almost exclusively visual and originate from two major sources: the retina and the visual cortex. Most efferent projections of the superficial layers ascend in fiber tracts that terminate in the pulvinar or other thalamic nuclei that, in turn, project to cortical areas implicated in visual function[3].

This review focuses upon the deep division of the SC, a site of convergence of sensory signals from several modalities and a source of efferent commands for the initiation of orienting movements. Many neurons residing in the deep division are responsive to auditory, somatosensory and/or visual stimuli[4–10]. Other cells in the deep division have motor properties, discharging before saccadic eye movements[11–13]; still other neurons may discharge before movements of the pinnae and/or head. Although the outputs of the deep division are both ascending and descending, collicular neurons can exert their most direct control over orienting movements through the descending pathways[14]. Brainstem nuclei receiving tectal inputs project, both directly and indirectly, to motor neurons innervating extraocular muscles, neck muscles and muscles controlling movements of the external ears[15].

The intrinsic organization of the SC is poorly understood. The question of whether or not there is extensive communication between neurons in the superficial and deep divisions has not yet been resolved.

The deeper layers of the SC: a source of motor commands

Microstimulation studies

In alert monkeys with their heads fixed, collicular stimulation produces conjugate, contralateral saccades with latencies of approximately 20–30 ms (Ref. 16). The amplitude and direction of the saccades are a function of the site of stimulation in the SC and, within broad limits, are independent of the intensity or frequency of stimulation. Robinson[16] developed a map of the amplitude and direction of saccades evoked by stimulation of different points of the SC (Fig. 1), and noted the alignment of this motor map with the retinotopic map in the overlying superficial layers (see below).

In monkeys free to move their heads, collicular stimulation rarely produces head movements[17]. The stimulation-induced head movements that do occur are variable in size and latency and do not have definite electrical thresholds. However, in animals with restricted ocular motility (such as cats), stimulation of the SC produces short latency movements of the eyes and head[18] as well as movements of the external ears (pinnae) and vibrissae[19]. In general, the direction and amplitude of all stimulation-induced movements (eyes, head, pinnae, vibrassae) depend upon the site of stimulation. Medial stimulation produces movements with upward components and lateral stimulation produces movements with downward components. In the anterior SC, relatively small move-

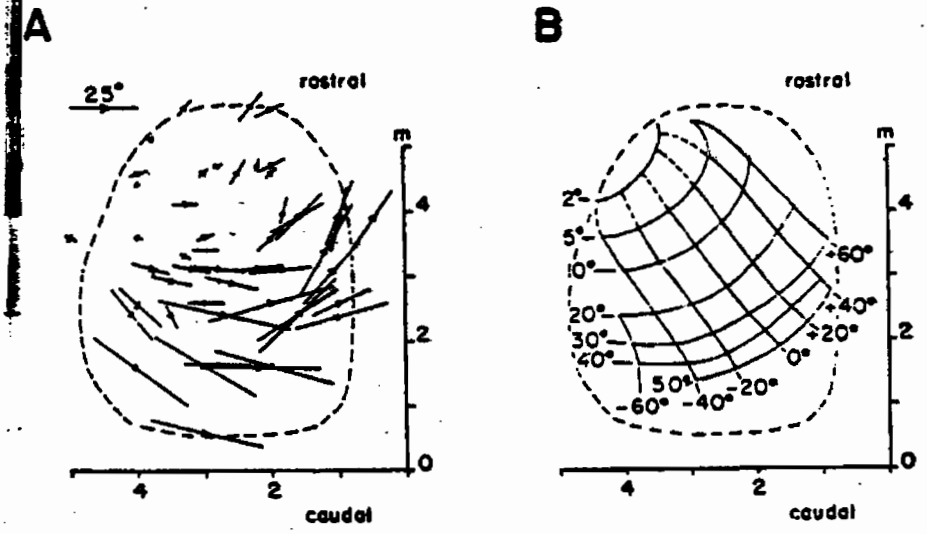

Fig. 1. *Maps of the direction and amplitude of stimulation-induced saccades.* **(A)** *Dorsal view of the left superior colliculus of a rhesus monkey. Arrows indicate the direction and amplitude of saccades produced by stimulation.* **(B)** *Smoothed contours of the motor map of the superior colliculus. Isoamplitude lines (2° to 50°) run from medial to lateral and isodirection lines (−60° to +60°) run from anterior to posterior.* (Taken from Ref. 16.)

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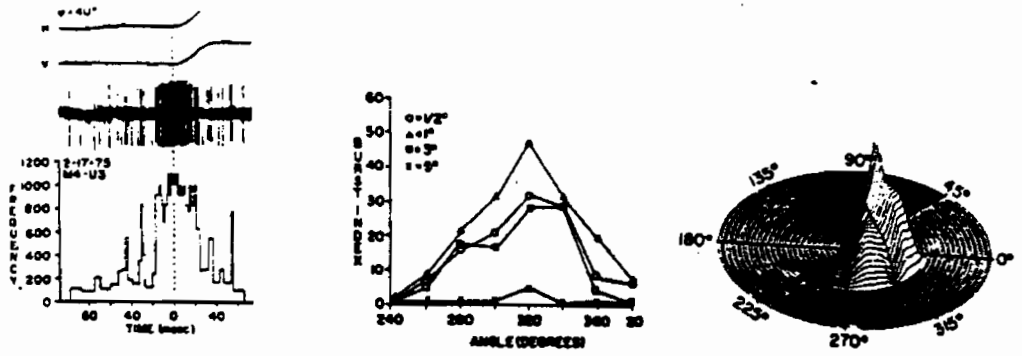

cell in the superior colliculus of monkey. H, horizontal eye position; V, vertical eye position. The middle trace is the spike discharge and the bottom graph shows instantaneous spike frequency as a function of time. The dotted line represents the onset of the eye movement. (B) Burst index (number of spikes) as a function of the direction and amplitude of saccadic eye movements for a single collicular cell. Each point represents the median value of three observations. (C) Three-dimensional representation of burst index as a function of saccade direction and amplitude. (Taken from Ref. 12.)

ments are produced, whereas caudal stimulation produces larger movements. Thus, based upon stimulation data, the SC may contain multiple motor maps as well as multiple sensory maps (see below). Since in most experiments, simultaneous measurements of the movements of the eyes, head, vibrassae and pinnae are not obtained, it is not clear whether the SC contains several completely independent motor maps or a single motor representation that coordinates the various subcomponents of an orienting response.

Chronic unit recording studies.

The neuronal basis of movements produced by microstimulation has been examined by recording the activity of collicular neurons in alert, unanesthetized animals. In rhesus monkeys, many neurons in the deep division generate a high frequency burst of activity beginning 18–20 ms before saccadic eye movements (Fig. 2). Each of these cells discharges maximally before saccades of particular directions and particular amplitudes (the movement field of the cell), regardless of the initial position of the eye in the orbit[13,20]. Movements to the center of the movement field are preceded by a vigorous discharge, but movements deviating from this optimal direction and amplitude are accompanied by less vigorous responses (Fig. 2). Neurons discharging prior to small saccades have small and sharply tuned movement fields; cells discharging before large amplitude saccades have large movement fields and tuning is relatively coarse[12]. Cells generating saccade-related bursts of activity are organized topographically[13], and correspond to the motor map revealed by microstimulation.

Although the vigor of discharge of a particular saccade-related burst cell varies for different movements within the movement field, information concerning saccade direction and amplitude is not contained within the discharge of a single cell. Except for the maximal discharge that precedes saccades to the center of the movement field, the discharge of SC neurons is ambiguous with respect to saccade direction or amplitude. Identical discharges may precede many saccades with different directions and amplitudes[20]. Thus, it is the location of active neurons within the topographical map of movement fields, not their frequency of firing, that specifies saccade direction and amplitude.

Stimulation data suggest that the SC of some animals may also contain neurons discharging before movements of the pinnae, vibrassae and head[21], but this possibility has not been explored extensively.

The deep layers of the SC: a site of sensory convergence

Responses to visual, somatosensory and auditory stimuli

The convergence of inputs from many brain areas representing a variety of sensory modalities is a striking feature of the organization of the deep division of the SC. Cortical inputs originate in the frontal and prefrontal cortex, parietal cortex, temporal lobe and occipital lobe[15]; more than 40 subcortical areas have been identified that project to the deep division of the SC[22]. Presumably, inputs from these areas provide the SC with both sensory and motor signals, but relatively little is known about the information conveyed to the SC from these sources (but see Ref. 1 for more details).

The receptive fields of visually responsive neurons in the SC of rhesus monkeys are larger and less precisely tuned for stimulus features than the receptive fields of cells in the lateral geniculate nucleus or striate cortex. For example, cells in the striate cortex have small receptive fields (only a few degrees in diameter) and display precise tuning for the spatial orientation of edges of light, for stimulus wavelength and for the direction and velocity of stimulus movement. In contrast, the activity of collicular neurons appears to be more concerned with the location of the stimulus than with stimulus features. Collicular cells have large receptive fields, respond to the presence of a stimulus regardless of shape, size or orientation, are responsive to stimuli of all visible wavelengths, and have only poor tuning for the direction and velocity of stimulus movement (see Ref. 1 for references).

Cells in the superficial layers of the SC of each colliculus are activated by stimuli appearing in the contralateral visual field and are topographically organized according to receptive field location. Neurons with receptive fields in the upper visual field are located medially; those with receptive fields in the lower visual field are found laterally. Units with receptive fields near the center of the visual field reside anteriorly; those responsive to peripheral stimuli are located posteriorly.

Although cutaneous stimulation is most effective for activating somatosensory collicular cells, somatosensory inputs to the deeper layers of the colliculus arrive via both lemniscal and spinothalamic pathways. In acute experiments, vigorous neural activity is evoked by rapid movement of a tactile stimulus along a particular axis, light tapping of the skin and displacement of the hair and vibrissae[10]. Somatic receptive

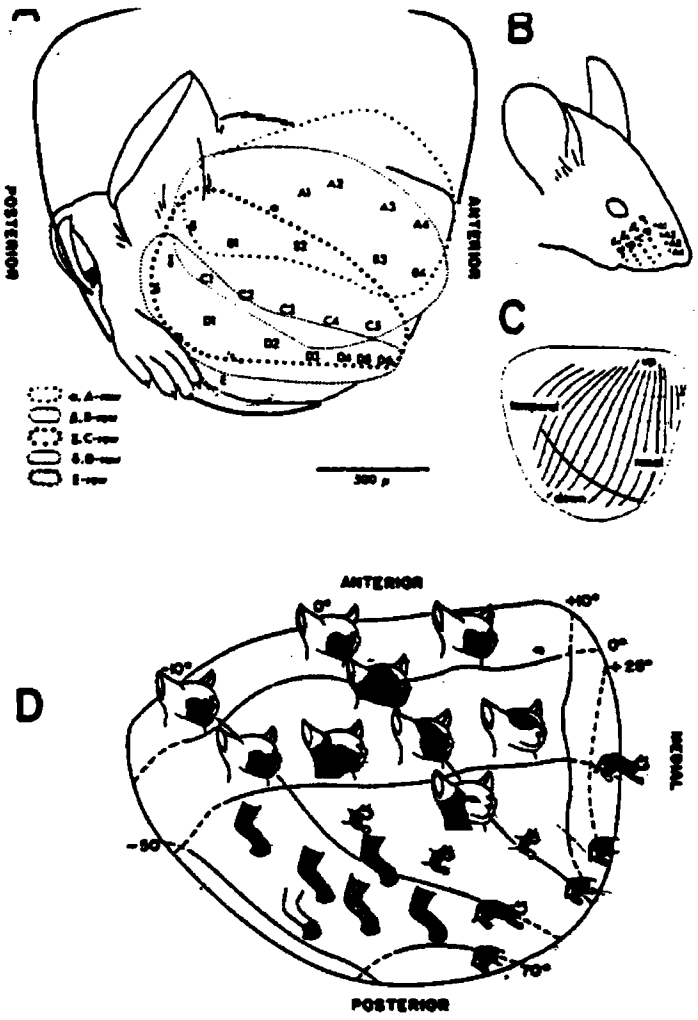

Fig. 3. *Maps of the tactile and visual projection onto the tectum of mouse (A–C) and cat (D).* **(A)** *Somatosensory projection onto the superior colliculus of the mouse. Letters refer to whiskers (see B) and indicate the site of neural activity evoked by stimulation of the whiskers. The overlapping ovals represent regions activated by the five rows of whiskers.* **(C)** *Retinotopic representation of the visual receptive fields for the mouse.* **(D)** *Schematic illustration of how different body sectors are represented in the cat superior colliculus. Coordinates are shown for the topographical map of visual receptive fields. Note that the disproportionately large representation of the head and forelimb corresponds to the large area devoted to the representations of central and inferior-temporal visual receptive fields.* (A–C taken from Ref. 5; D from Ref. 10.)

fields of collicular neurons range from 2 mm diameter to the entire dorsal surface of the body[10].

Tactile receptive fields are also organized topographically in the SC[5,10]. In each colliculus, representation of the contralateral forelimb and body regions innervated by the trigeminal nerve is extensive. Consequently, only a small part of the colliculus is allocated to representation of the large cutaneous surface area of the trunk and hindlimb[10].

Acoustically responsive cells in the SC have fairly non-specific frequency sensitivity. Complex sounds such as hisses, whistles, finger snaps, or jangling keys and even early studies using qualitative methods suggested a topographical representation of auditory space in the deep division of the SC[6]. Recent studies[8,23] indicate that although acoustically responsive cells have large receptive fields, the response of these neurons is selective for the location of the sound. Each cell has a 'best area', a range of stimulus locations that elicit responses greater than 75% of maximum. The best areas of cells vary systematically with cell location, forming a map of auditory space in the SC[23].

Alignment of sensory maps in the SC

In experiments using anesthetized or paralysed preparations, the auditory, somatosensory, and visual maps are found to be aligned. For example, in paralysed cats, collicular neurons responding to both auditory and visual stimuli have visual and auditory receptive fields that overlap spatially[6]. For cells responding to auditory but not to visual stimuli, the location of the auditory receptive field is correlated with the spatial location of the receptive fields of nearby visually responsive neurons. Thus, Gordon[6] inferred a topographical map of auditory space by referring the location of auditory receptive fields to the location of visual receptive fields known to be topographically arranged. Similarly, the visuotopic organization of superficial layer neurons can be used as a reference for plotting the receptive fields of underlying cells responsive to tactile stimuli[4,5,10] (Fig. 3).

Multimodal neurons and sensory–sensory interactions

Neurons responding to sensory stimuli from more than one modality have been identified in the optic tectum of fish, reptiles, birds and the SC (the mammalian homologue of the optic tectum) of mammals. For example, in pit vipers, many tectal cells respond to both visual and infrared stimuli; in the weakly electric fish, tectal cells respond to both visual and electrosensory stimuli. In mammals, many cells are responsive to visual, auditory and/or somatosensory stimuli.

When combinations of visual, somatic and auditory stimuli are presented to cats[9] and guinea-pigs[8], dramatic enhancement effects and inhibitory effects can be observed in the response of collicular neurons. These interaction effects depend upon the spatial and temporal overlap of the multimodal stimuli. Enhancement usually occurs if each stimulus is in the center of its receptive field and if the two stimuli are temporally contiguous. Response depression occurs most commonly when one of the two stimuli is outside or on the fringe of the cell's receptive field or if there is a large temporal disparity in the onset of the two stimuli[8,24].

Functional significance of multimodal interactions and map alignment

Multimodal interactions

That the responsiveness of collicular neurons to one sensory stimulus can be dramatically altered by simultaneous presentation of stimuli from other modalities is a recent observation. Therefore, neither the actual site of convergence nor the functional consequences of multimodal interactions are well understood. Although the site of convergence may be in the SC, there is no direct evidence for this hypothesis. The multimodal responses observed in collicular neurons could origin-

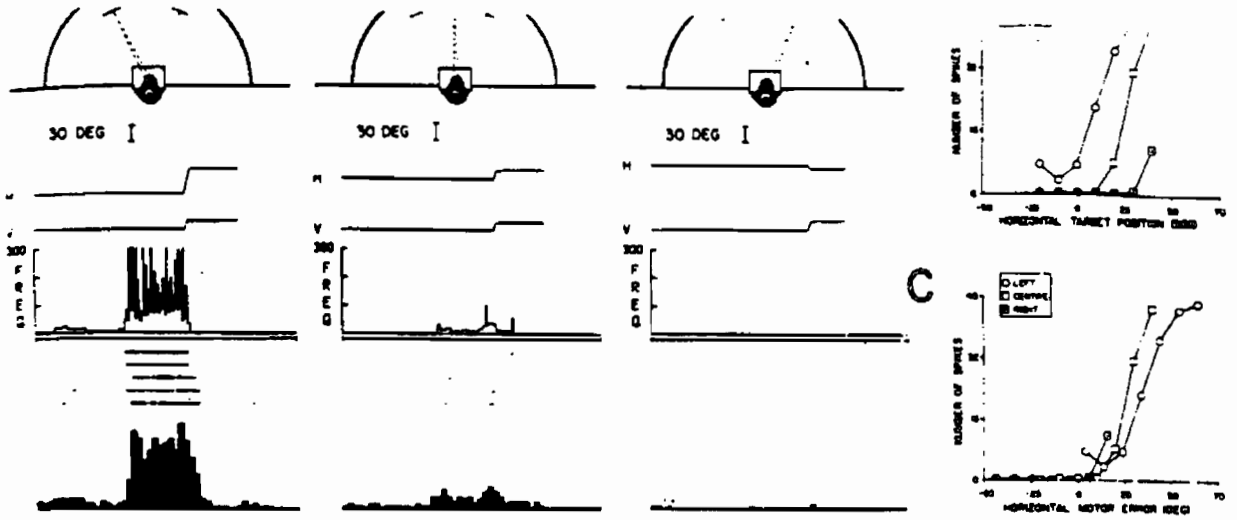

Fig. 4. *The effects of eye position upon the response of a single cell in the superior colliculus of rhesus monkeys to an auditory stimulus.* (A) *Speaker was placed 20° right, 6° up from center while the fixation position was varied between 24° left (left), center (center) and 24° right (right). The time base represents 3 s; target presentation occurred at 1 s. Horizontal (up = right) and vertical eye position traces are shown in the top row; instantaneous firing rate for single trials are shown in the second row followed by rasters illustrating unit activity for five trials. The bottom row is a cumulative histogram for these trials.* (B) *A summary plot of the auditory receptive fields for this one cell as a function of horizontal target position (top) showing the shift in the position of the receptive fields as eye position was varied. The data are replotted in motor error (the difference between current eye position and saccade target location) coordinates in* (C). *The plots are better aligned in motor error coordinates.* (Taken from Ref. 30.)

ate in cortical or subcortical areas sending signals to the colliculus.

The question of the functional consequences of sensory–sensory interactions also needs further study. It has been hypothesized[24,25] that multimodal convergence onto neurons triggering orienting responses would allow cues from any of several sensory modalities to initiate orienting responses. Another conjecture is that the potency of different stimuli might depend upon environmental conditions. For example, auditory stimuli could be more effective in dim illumination while visual cues would be prepotent in higher light levels. Also, summation of signals from several modalities could function to enhance signal-to-noise ratios. Weak stimuli that cannot, alone, be used to identify or locate targets might increase the responsiveness of collicular cells to other types of sensory stimuli (see Refs 24 and 25 for further discussion of the functional role of multimodal interactions). Several of these hypotheses could be tested, explicitly, in experiments using alert, behaviorally trained animals. In such experiments it should be possible to vary the relative intensity, timing and location of paired auditory, visual and/or somatosensory stimuli while obtaining, simultaneously, behavioral reports of stimulus detectability, measures of the probability, magnitude and vigor of orienting responses, as well as concomitant records of neuronal activity.

Alignment of visual and motor maps

The foveation hypothesis of collicular organization proposes a specific functional role for the alignment of the retinotopic map of visual space found in the superficial division and the subjacent motor (saccadic) map[11,16]. According to this hypothesis, the SC codes the location of a visual target relative to the fovea and initiates a saccade that produces foveal acquisition of the target. Retinal error (the distance and direction of the target image from the fovea) is represented by the site of visually triggered activity in the retinotopically organized superficial layers of the SC. Visually triggered discharges in the superficial layers are assumed to activate, relatively directly, underlying regions of the colliculus containing neurons that discharge before saccadic eye movements. Since the map of the movement fields of the deeper neurons corresponds to the retinotopic map of the overlying superficial neurons, a saccade will be produced that brings the foveal projection onto the region of the visual field containing the target.

The foveation hypothesis encounters several difficulties. Two problems are cited (see Ref. 1 for additional discussion). First, the timing of neuronal activity in the superficial and deep division is not consistent with the proposed hypothesis. The onset of visual activity in the superficial layers begins 100–120 ms before the onset of the saccade-related burst of neurons in the deep division. Since 100 ms is not required for direct superficial-to-deep connections, the transmission of signals between these divisions must be neither simple nor direct. Second, the presumed coupling between the activity of neurons in the superficial and deep divisions has not received experimental support. Under some experimental conditions, superficial neurons display vigorous visual responses that do not result in the activation of underlying saccade-related neurons[26]. Conversely, saccade-related neurons may produce vigorous bursts of activity in the absence of changes in the activity of overlying cells in the superficial layers. Thus, for most saccade-

related neurons, the discharge of overlying neurons ... is neither necessary nor sufficient to activate most cells generating saccade-related bursts[28]. The reason for the alignment of the visual map in the superficial layers and motor maps in the deep layers is unknown.

Alignment of sensory maps

Considerable effort has been devoted to demonstrating an alignment of auditory, somatosensory, and visual maps in the SC, but the functional significance of the observed correspondence remains obscure. One possibility is that the alignment of the sensory maps observed in the colliculus has little functional relevance. The separate representations of visual, somatosensory and acoustic space could be completely independent, with each sensory system using its allocated space to map the environment with a particular magnification factor. The observed correspondence between the visual and auditory maps, for example, might be an epiphenomenon resulting from the fortuitous alignment of retinal and head coordinates occurring, in acute experiments, when the head and eyes are in the primary position. Indeed, the observed correspondence between sensory maps in the SC of anesthetized and/or paralysed subjects is curious because the spatial location of a stimulus is encoded differently for each of these sensory systems. The neural code for the location of a visual stimulus must be based upon information about the locus of retinal stimulation and the position of the eyes in the orbits. In contrast, the location of sound sources is encoded using head-centered cues such as interaural differences in the timing and intensity of incoming sound waves. Tactile stimuli are localized in a third, body-centered, reference system. The apparent alignment of auditory, visual and somatosensory maps in the SC implies that these sensory signals have been translated into a common coordinate system, but this hypothesis cannot be tested in the anesthetized animal[27] because, under these conditions, the axes of the head-centered auditory system, the retinotopic visual system and body-centered somatosensory system are aligned.

Nonetheless, most researchers assume that the alignment of the sensory maps observed in the deep division of the SC is functionally significant. It is commonly assumed that the deep division of the SC contains a topographical map of sensory space such that a point in the space surrounding the animal is represented by neurons residing at a particular location in the SC. Furthermore, it is assumed that sensory signals from different modalities originating from the same point in space activate a common pool of collicular neurons located within this representation. Similar to the foveation hypothesis, the activation of these sensory neurons, in turn, is hypothesized to initiate motor responses resulting in orienting movements toward the source of the stimuli.

These hypotheses have not yet been formalized into a model of collicular function and many of the assumptions remain implicit and untested. For example, if the alignment of the maps is functionally significant, what is the basis of the alignment? Is the topography of the visual map imposed upon the other modalities, or have visual, auditory and somatosensory signals all been translated into common (other than visual) coordinates? What happens to the correspondence of sensory ... or body?

If the sensory maps are static, what is the basis of the correspondence between sensory maps? One view is that the topography of the visual map is imposed upon the other modalities. Drager and Hubel[5] are the strongest proponents of this view. They noted that a major part of the visual field of the mouse is crossed by whiskers, and described a topographical relationship between somatosensory receptive fields, especially those involving the whiskers, and the visual receptive fields of overlying cells. They suggested that '. . .the somatosensory projection in the tectum is thus determined by the way in which particular tactile body parts are seen from the eye . . .' and 'At deeper levels other systems are represented, all arranged so as to be in registration with the visual world coded above . . .' However, there is no experimental evidence to support the assumption that in mammals, the alignment of the maps is imposed by the visual system. Would, for example, the somatosensory and auditory maps be modified in dark-reared animals in which tactile and acoustic stimuli were never associated with visual stimuli? Also, it is known that in cats, visually guided behavior appears around 14 days after birth, a few days after acoustically guided and tactually guided behaviors have developed[29]. Thus, auditory, somatosensory and motor maps are present and functioning prior to the development of visually guided behavior and prior to the development of normal receptive-field properties by visual neurons in the SC[29].

A possibility less frequently considered is that the maps of sensory space observed in the deep division of the SC are dynamic and that they are encoded in motor, rather than sensory, coordinates. Recently, Jay and Sparks[30,31] conducted experiments to test this hypothesis. The experiments were based upon the observation that collicular neurons with saccade-related activity are organized topographically and that it is the location of active neurons within the topographical map of movement fields, not their frequency of firing, that specifies the change in eye position required to direct gaze to the target location. Thus, they reasoned that the task of sensory systems is to specify, by activating a particular subset of collicular neurons, the *change* in eye position required to look to a target, not merely the location of the target in head, body or retinal coordinates. Consider, for example, a monkey with the head positioned 'straight ahead' but with gaze directed 24° to the left of center. When an auditory stimulus is presented 10° to the right of center, interaural cues will be used to localize the target in head coordinates ('target is 10° right'). However, since the eyes are directed 24° left of center, looking to the target requires a 34° rightward saccade, and neurons in caudal regions of the left SC must be activated to produce this movement. If an auditory target is presented in the same location on another trial with gaze directed 24° to the right of center, cells in the right SC must be activated to produce the 14° leftward saccade required to look to stimulus.

Jay and Sparks[30,31] plotted the receptive fields of neurons responsive to auditory and visual stimuli while the eye position of trained, alert monkeys was systematically varied. If auditory signals are organized in head coordinates, then in these experiments in which

sive neurons should be independent of initial fixation position and depend entirely upon the azimuth and elevation of the sound source. However, if auditory signals have been translated into motor error coordinates, then the response of collicular neurons to acoustic stimuli should depend upon the trajectory of the movement required to look to the stimulus and, therefore, be sensitive to both the position of the speaker in space and the position of the eyes in the orbits. They found that the auditory receptive fields shifted with changes in eye position and that, in rhesus monkeys, the map auditory space in the deep layers of the SC is not static. With each change in eye position, the site of neural activity induced by a fixed auditory stimulus shifts to a new location – a location that specifies the metrics of the movement that would direct gaze to the target location. Harris *et al.*[7] conducted a similar experiment in cats and concluded that the sensory maps were not dynamic. Noting that eye movements in cats are usually accompanied by head movements, they suggested that sensory maps will only be out of alignment for brief periods of time. Although the functional properties of neurons in the SC of cats and monkeys may differ, there are several problems with the Harris *et al.* study (see Ref. 31 for a critique), and the conclusion that sensory maps in the SC of cats are not dynamic is premature.

Concluding remarks

The deep layers of the SC contain separate representations of auditory, somatosensory, and visual space as well as maps of motor space. In acute experiments, the sensory and motor maps appear to be aligned and it is commonly assumed that the retinotopic map of visual space is the basis for the alignment. However, recent data suggest that, in rhesus monkeys, the sensory maps in the deep division of the SC are organized in motor coordinates. According to this view, the sensory maps are dynamic and the receptive fields of collicular neurons shift with relative movements of the eyes, head and body. A dynamic mapping of sensory space is required because of constraints imposed by the organization of the motor map.

Future or ongoing experiments should provide needed information about the intrinsic organization of the SC as well as information concerning the functional significance of multimodal interactions. Other studies are needed to determine whether or not the sensory maps in the SC of animals with restricted ocular mobility are static or dynamic. Collectively, these studies will contribute much to our understanding of the complex transformations of signals required for the sensory guidance of coordinated movements.

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Errata

In the article 'Patterns of cell loss in Huntington's disease' by Neil W. Kowall, Robert J. Ferrante and Joseph B. Martin (Jan. 1987, Vol. 10, pp. 24–29) there were two minor errors. In Table I the neurochemical profile for substance P was deleted. Substance P is depleted in HD and is also depleted by KA/IBO and QUIN injections. Also, Ref. 18 was partially deleted in the reference list. It should read:

18 Graybiel, A. M. and Ragsdale, C. W. (1983) in *Chemical Neuroanatomy* (Emson, P. C., ed.) pp. 427–504, Raven Press

In the article 'Axonal bifurcation on the visual system' by Jean Bullier and Henry Kennedy (May 1987, Vol. 10, pp. 205–210) the proportions of doubly labelled cells were omitted in Fig. 3. The bifurcated bars linking the circles and boxes representing visual structures correspond to the following proportions: the thin dark bars correspond to proportions of doubly labelled cells below 5%, the medium-size stippled ones represent proportions between 5 and 30% and the large hatched bars correspond to percentages above 30%.

We apologize for these errors.