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Neuronal Substrates of Sensory Processing for Song Perception and Learning in Songbirds: Lessons from the Mormyrid Electric Fish

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11.1 Introduction

The sensory processing and decoding of behaviorally relevant information is a basic problem that animals must resolve in order to succeed in an ever-changing environment. Sensory systems of various modalities have specialized in detecting key features conveying information for purposes as diverse as feeding, navigation, identification of conspecifics, defense from predators, and reproduction. A growing body of evidence indicates that sensory systems often compare incoming external patterns of sensory stimulation with predictions or expectations about these patterns. These predictions can be based on previous knowledge of self-generated sensory patterns, as occurs in some electric fish, or on sensory memories acquired through experience and learning, as is the case in songbirds.

Sensory systems of different modalities sometimes solve similar computational problems of information processing. By studying the mechanisms of sensory processing in one system, we can develop new hypotheses of mechanisms in another system.

The electrosensory system of mormyrid electric fish provides a good example of a well-characterized sensory system that has developed mechanisms to distinguish self-generated sensory stimuli from stimuli that arise from external sources. Songbirds, on the other hand, need to compare the sounds of the songs they and their neighbors produce with previously formed song auditory memories in order to effectively perform the perceptual discriminations and vocal learning required for reproductive success. This chapter explores aspects of the mormyrid electrosensory system that may help us to understand how the songbird brain is organized to extract behaviorally relevant information from auditory signals, either to identify other individual birds or to generate and maintain the bird's own song (BOS).

In mormyrid electric fish, a weak electric field is generated by a modified muscle in the fish's tail and the electric field is detected by electrosensory receptors in the fish's skin (Bullock and Heiligenberg, 1986). Objects in the vicinity of the fish cast an electrical shadow that contains information about the objects' shape and composition. Mormyrid fish use this active sensory system to identify objects, but fish must distinguish between self-generated electric fields and electric fields generated by other organisms that may indicate the proximity of predators or prey. Recent characterizations of the adaptive mechanisms in the mormyrid electrosensory system (Bell, 1990; Bell *et al.*, 1997) yield a model for temporal pattern learning (Bell and Szabo, 1986; Roberts and Bell, 2000) that depends on synaptic plasticity in the sensory-processing circuits.

In songbirds, vocal communication is very prominent, playing a significant role in basic behaviors such as territoriality, mate attraction and mate selection (see reviews in Catchpole and Slater, 1995; Kroodsma and Miller, 1996). To express these behaviors, songbirds need to perceive, discriminate, and remember the songs they encounter throughout life. A bird's exposure to song can impact a broad range of behaviors, both vocal and non-vocal ones, and auditory memories resulting from such exposure are required for at least two general purposes, namely: (1) the identification and discrimination of different conspecific individuals based on acoustic features of song and (2) the learning and maintenance of the BOS. Behaviorally, these two contexts are quite distinct and involve different brain pathways and mechanisms. In principle, however, the auditory processing and memorization of song, whether it subserves perceptual discrimination or vocal learning and maintenance, is fundamentally a sensory/perceptual process. Thus, it seems parsimonious to postulate that the same basic neuronal pathways and mechanisms may be used for the sensory processing and memorization of song required in the two different contexts.

We first describe some general aspects of perceptual processing and vocal learning and maintenance of song in songbirds to establish the key characteristics we must consider for our comparison with adaptation and learning in the electrosensory system. We follow this with a section that provides details of the mormyrid electrosensory system and discusses the known mechanisms for learning and adaptation. We then discuss neural substrates of the songbird auditory system that might contribute to the generation of song templates for perceptual discrimination and vocal learning. Finally, we compare some critical features between the two systems and conclude with the proposition that the neural pathways and mechanisms that the bird uses for storing memories of other conspecifics could also contribute towards a template for generating and maintaining the BOS.

11.2 Song perceptual processing and song learning

Male songbirds from each of several species are able to identify conspecifics based on their songs and use this ability to help establish long-lasting relationships with birds in neighboring breeding territories. Females frequently select males based on acoustic features of their songs, often showing preferences for specific song characteristics. These preferences can relate to general variables such as rates of singing, song length and repertoire size, or to the presence of syllables or phrases with specific spectro-temporal features. Such preferences can potentially shape the properties of song over generations, and thus exert a strong effect on population differences in vocal production patterns (for reviews, see Catchpole and Slater, 1995; Muller and Kroodsma, 1996). Thus, both male and female songbirds must have an elaborate song recognition system. As a consequence of their use of vocal communication, songbirds of both sexes must rely heavily on their auditory systems to process and discriminate the songs they encounter, as well as to form and retrieve long-lasting auditory memories of these songs.

The need for long-lasting auditory memories is also supported by the fact that song is a learned behavior in songbirds (Thorpe, 1958; Marler and Peters, 1977), as well as in two other avian orders, parrots and hummingbirds (Nottebohm, 1972). In many species that have been investigated, the development of species-specific song appears to be fundamentally dependent on vocal imitation (see discussions in Catchpole and Slater, 1995; Marler, 1997). This imitative vocal learning process consists of two phases, both of which require intact hearing. The first, or sensory acquisition phase of song learning consists of the young bird hearing and memorizing the adult song (Konishi, 1965). In some species, this occurs simply by the juvenile bird's exposure to the sound of song (e.g. tape-recorded song, as in Marler and Peters, 1977). Even though other variables may affect this sensory acquisition process, such as social interactions through visual/tactile stimulation, an absolute requirement is that the bird be exposed to the appropriate song auditory model. This sensory phase occurs, or in some cases starts, at an age when the vocal control circuitry has not yet matured and the juvenile bird is not yet able to actively produce its own song (Marler and Peters, 1977, 1981; Eales, 1985; Bohner, 1990). Since some species show innate recognition preferences for song elements of their own species over those of other species, the process of song memorization during this sensory phase appears to involve the modification of an intrinsic or innate template (Marler, 1970; Marler and Peters, 1987, 1988; Marler, 1997). The end product of the sensory phase of song learning (i.e. the acquired song template) is arguably an acquired auditory representation of song. In other words, it is a neural representation of what the song to be imitated sounds like.

Consistent with this notion is the observation that song in Bengalese finches deteriorates after deafening in adults, but normal song production can then be reinstated upon recovery of hearing function in the absence of further external auditory input (Woolley and Rubel, 2002). Thus, a representation of the acoustic properties of the song to be imitated is formed early in life, but this acquired song auditory memory is long lasting and has an extended influence on the bird's vocal behavior. It is likely that the song auditory memories for vocal imitation contain information on both the spectral structure of individual song syllables as well as on the temporal or syntactic aspects of song, since both aspects of song are disrupted by isolation or deafening.

The second, or sensorimotor phase of song learning consists of the bird's active attempts to modify its vocal motor program(s) so that the sound of its own immature song can eventually match the acoustic properties of the internalized song model (Konishi, 1965; Marler and Peters, 1982; Marler, 1997; Tchernichovski *et al*., 2001; Tchernichovski and Mitra, 2002). In the previous sensory acquisition phase, the male songbird cannot have been instructed on how to execute specific song motor gestures and can only have acquired an auditory memory of the song to be imitated. In consequence, the sensory processing that occurs during the sensorimotor phase most likely consists of a comparison of the acoustic properties of the BOS with those of the song to be imitated. Intact hearing is needed during this phase of learning, as shown by the effect of cochlear lesions on song crystallization (Konishi, 1965). Through auditory feedback, the brain can be informed about the properties of the BOS, and use that information to guide vocal development. Importantly, once song has been learned, the brain's vocal motor program for producing the BOS is not sufficient, by itself, to maintain song structure. Rather, the brain requires continuous information that can be obtained through auditory feedback about the vocal output (Nordeen and Nordeen, 1992; Leonardo and Konishi, 1999; Woolley and Rubel, 2002).

Arguably, the comparison the brain needs to perform between the BOS and the song template is primarily sensory/perceptual in nature and consists of the comparison between the sound of the BOS and the internalized representation of auditory features contained in the song template (Fig. 11.1a). As the bird vocalizes, the resulting auditory feedback activates the cochlea and is then processed at various stations of the auditory pathways, as represented schematically in Fig. 11.1a left (BOS to auditory input). At some point, this incoming auditory feedback input must be compared with the internalized song auditory template, which contains information about how the BOS should sound like (Fig. 11.1a left, comparator element). The song template could be seen as a previously acquired auditory representation of song that sets an expectation for

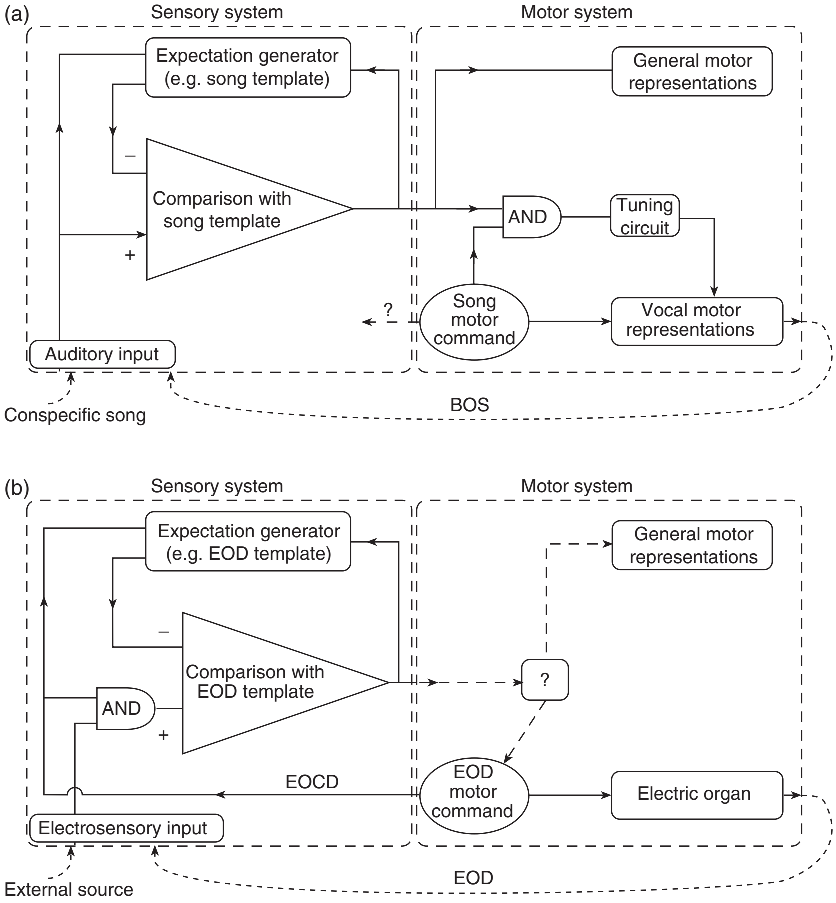

Figure 11.1. Comparison of two sensorimotor processing systems. (a) *Songbird model*: auditory input is compared with a song template by the subtraction of the expected spectral-temporal pattern of auditory stimuli from the direct input. The result of the comparison is used to update the song template by a mechanism that is not yet known. The output of the sensory system influences the song motor learning system by adjusting the motor program only if the bird is actively singing. This condition of active singing is enforced by the AND-gate. Deviations of the song from the expected song are used as an error signal to tune song production. (b) *Mormyrid electrosensory system*: electrosensory input is gated by a centrally generated electric organ corollary discharge (EOCD) signal to limit processing to only the fish's own self-generated electric field. The electrosensory pattern is compared with the expected electric organ discharge (EOD) template. The difference between the sensory pattern caused by the EOD and the expected pattern is passed for further processing and represents novel sensory information. This difference is also used to update the EOD template through a mechanism based on spike-timing dependent synaptic plasticity.

the incoming auditory input resulting from the act of singing (Fig. 11.1a left, expectation generator). In case a significant difference, or mismatch, is detected between this auditory feedback input and the template, an error signal is passed on to centers where vocal motor representations (i.e. the set of commands that lead to the generation of the song) are encoded, informing on the need to modify these representations (Fig. 11.1a right). Importantly, a message informing about an error or mismatch and the need to modify the current vocal motor representations should only be passed on to motor representation centers if such a mismatch occurs during singing. This could be accomplished by a filter mechanism (Fig. 11.1a right, AND-filter) that allows an error signal to be passed on to motor representation centers only if it is concurrent with a signal from motor command centers indicating that the bird is vocalizing. Changes in vocal motor representation would then be accomplished by the activation of tuning circuit(s) (Fig. 11.1a right), resulting in a modified vocal motor output.

The comparison process diagrammed in Fig. 11.1a left, is a particular case of comparing an external auditory input to an internal expectation. Such a process is analogous to the comparison the brain performs in the context of perceptual discrimination, for example between the song a bird hears at any given moment (Fig. 11.1a left, conspecific song) and the previously internalized auditory representations, or memories, of familiar songs that play the same role as the song template. In this situation, the brain is comparing the acoustic properties of a song heard with an internal representation of how a familiar song sounds like. Similarly to the song template for vocal learning, a previous auditory representation of a familiar song would set an expectation for the auditory system to analyze incoming input patterns from other songs (Fig. 11.1a left, expectation generator). A "mismatch" in this case signals an unfamiliar song (e.g. a potential intruder or rival) and informs motor control centers that mediate the appropriate behavioral responses (Fig. 11.1a right, general motor representations). As a song motor command is absent due to the lack of active singing behavior in this situation, the AND-filter prevents the song tuning circuits from being activated, so that vocal motor representations are not modified.

Based on the above discussion, the nature of the comparison process is fundamentally similar in the contexts of both perceptual discrimination and auditory feedback evaluation for vocal learning. In both cases, the task of comparing demands an analysis of the degree of similarity between the auditory stimulus and an internal auditory representation. The result of this analysis can then be used to inform brain centers that control behavioral programs or actions. Importantly, these comparisons differ markedly in terms of their behavioral consequences. The behavioral responses to the recognition of a familiar song or to the identification of an intruder's song (Catchpole and Slater, 1995) require the coordinated recruitment and action of the motor programs involved in the control of these responses: for example, aggressive behavior while confronting an intruder, or copulatory behavior triggered upon recognition of a familiar mate. In contrast, in the case of vocal learning, it is vocal motor centers that need to be informed on whether vocal motor representations require modification. Thus, the motor targets of the processed sensory information differ markedly in the two situations above, depending on the behavioral context in which the song percept is generated. Nonetheless, the same sensory-processing machinery, that is the auditory system, could, in principle, subserve the basic auditory task in the both situations.

It can be argued that the sensory information provided by auditory feedback during singing can only be effectively compared with the internal song auditory representation if the neuronal circuits involved in this comparison are informed that a motor command for singing has just been given by the song motor centers. In other words, the auditory system would need to be aware that the bird has just sung in order to process the resulting sound in a timely manner and to be able to compare it with the internalized song template. It is possible that the motor act of singing itself sets the auditory system into a mode whereby the auditory input that reaches the brain after a given time delay is interpreted as resulting from that motor act. This possibility requires a central pathway and mechanisms through which the song motor centers can influence the auditory system (Fig. 11.1a, question mark), but their existence has not been demonstrated.

11.3 Electrosensory processing in the mormyrid electric fish

Mormyrid electric fish are a fresh-water family of fish native to African rivers and lakes (Bullock and Heiligenberg, 1986). Mormyrids generate weak electric pulses using a modified muscle in their tail called an electric organ. The resultant weak electric field caused by the electric organ discharge (EOD) surrounds the fish and is detected by an array of electroreceptors on the body surface. Distortions of this self-generated electric field are then used by the fish to identify objects in its surrounding environment, allowing the fish to effectively navigate in the dark. This form of navigation that uses a self-generated electric field is called active electrolocation.

The signal to initiate an EOD originates in a motor command nucleus (Bell and Emde, 1995). In addition to initiating an electrical discharge, the command nucleus of mormyrids generates a so-called corollary discharge that informs the electrosensory circuits of *when* the electric pulse occurred (Zipser and Bennet, 1976; Bell, 1989). The timing information provided by the corollary discharge signal from the motor control center allows the electrosensory system to generate an internal representation, or expectation, of the reafferent electrosensory image that is generated as a result of an EOD (Bell, 1981). By comparing this internal expectation with the actual electrosensory image the fish can determine whether any distortions are present in its electric field caused by objects in the environment.

Figure 11.1b shows a schematic diagram of the active electrosensory processing system (Bell and Szabo, 1986). The EOD motor command (Fig. 11.1b right) causes the electric organ to discharge. Primary afferents from electrosensory receptors converge with the electric organ corollary discharge (EOCD) signal in a functional AND-gate (Fig. 11.1b left). The AND-gate eliminates signals that originate from external sources such as the EODs of other mormyrids. A branch of the EOCD pathway provides a timing signal to the "expectation generator" (Bell *et al.*, 1997) that contains a template of the reafferent EOD sensory image. This predicted image is compared with the reafferent electrosensory image and is effectively subtracted so that the output of the initial electrosensory processing circuit passes only novel stimuli. The output of the comparison proceeds to further processing, but also informs the expectation generator of any deviations of the sensory image from the predicted image to update the EOD template.

The motor system of mormyrid electric fish (Fig. 11.1b right) is less well characterized than the sensory system, particularly with regards to any direct influence that the sensory image cancellation system has on the motor output. Of course, the general motor representation of an EOD is quite simple when compared to vocalization in songbirds. The motor command initiates a single pulse from the electric organ during each cycle. However, the "novelty response" (Hall *et al.*, 1995) behavior of mormyrid electric fish suggests that some direct link (Fig. 11.1b, question mark) between the sensory system and the motor system exists. These fish respond to novel stimuli with a brief increase in the rate of their EOD. One potential trigger for the novelty response would be a deviation of the sensory image from the EOD template, but the exact neural pathways have yet to be determined. Our lack of knowledge of the motor pathways in the mormyrid EOD system is in contrast to songbirds where much of the research has concentrated on the song generation system. However, much of the neuronal circuitry involved in the electrosensory processing, corollary discharge, and expectation generation in mormyrids is quite well

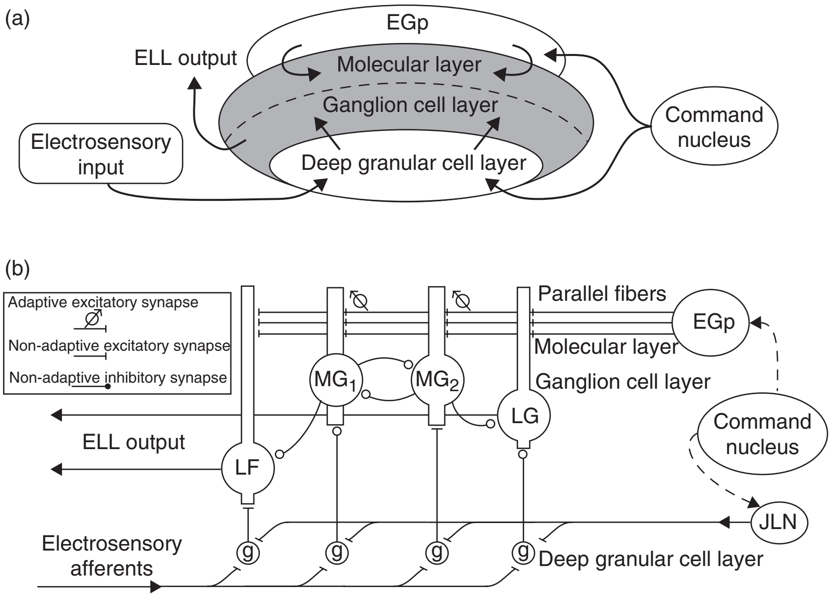

Figure 11.2. Adaptive sensory processing in the electrosensory lateral line (ELL) lobe. (a) Primary electrosensory input enters the deep granular cell layer and combines with information from the command nucleus about *when* there was an electric pulse. This combination is passed to the neurons of the ganglion cell layer. Neurons with cell bodies in the ganglion cell layer have dendrites in the molecular layer that receive command information. The summation of the sensory and motor pathways is transmitted out of the ELL for further processing. (b) The cell types and connectivity of the ELL (Han *et al*., 1999; Meek *et al*., 1999) shows how electrosensory signals are combined with command timing-information. Electrosensory afferents converge onto granular cells (g) with inputs from the juxtalobar nucleus (JLN) that carry a spike following each EOD command. The granular cells are the AND-gates of Fig. 11.1b, and transfer the self-generated electrosensory signal to the medium ganglion cells (MG_1 and MG_2) and the efferent cells, large ganglion (LG) and large fusiform (LF) cells. The MG cells exhibit the strongest synaptic plasticity at their apical dendrites that are contacted by parallel fibers from the eminentia granularis posterior (EGp) that receives EOD command timing-information.

characterized (Han *et al*., 1999; Meek *et al*., 1999) as shown in Fig. 11.2. Adaptive electrosensory processing initially takes place in the electrosensory lateral line (ELL) lobe, a region of the mormyrid brain that receives primary electrosensory afferents. The ELL is a member of a class of neural structures called "cerebellum-like" structures because of their laminar similarity to the cerebellum. This class includes the gymnotid ELL (Bastian, 1995), the octavolateral nucleus of sharks and rays (Montgomery and Bodznick, 1994), and the dorsal cochlear nucleus of mammals (Oertel and Young, 2004).

In the active electrosensory regions of the ELL, electrosensory information enters the ELL via electrosensory primary afferents in the deep granule cell layer (Fig. 11.2a). The afferents encode electric field strength in a latency code where the time delay between the EOD and the first spike of the afferent response to the EOD provides a precise representation of the reafferent field strength in the center of the receptive field. The AND-gate appears to be located in the deep granule cell layer and the information about self-generated electric fields is delivered to the ganglion cell layer, where a comparison is made with the EOD template. The output of the ELL (Fig. 11.2b) represents the electrosensory image that is filtered by a neural expectation of that image.

The EOCD from the command nucleus arrives via two separate pathways. One pathway is through the EGp, a granule cell layer that projects to the ELL by way of parallel fibers into the molecular layer. The EGp also receives sensory inputs such as proprioceptive afferents (Bell and Grant, 1992) that aid in generating an EOD template (Fig. 11.2a). The second pathway by which the command signals arrive in the ELL is to the deep granule cell layer. The final nucleus on this pathway before the ELL is the juxtalobar nucleus (JLN) where the neurons generate a single spike during each EOD (Fig. 11.2b). Between the command nucleus and the JLN there are five synaptic junctions, yet the variability of the JLN spikes is less than a millisecond with respect to the motor command (Bell and Emde, 1995). This remarkable precision of the spike arrival time suggests that the timing of the EOD is critical for the efficient operation of active electrosensory processing.

The AND-gate in Fig. 11.1b is critical for the fish to filter externally generated electrical fields so that the active electrosensory system is focused on the fish's own field during electrolocation tasks. In addition to the mechanism of the AND-gate, the convergence of the EOCD signal from the JLN with the primary afferents onto granular cells provides a decoding mechanism for the afferent spikes. The present hypothesis for the decoding of the afferent latency is that the primary sensory afferents converge with JLN afferents onto deep granular cells (Bell, 1990), and the overlap of excitatory postsynaptic potentials from these two synaptic inputs determines the response of the deep granular cells. Recordings of granular cells show a burst response that varies in number of spikes during their burst depending on the electrosensory stimulus delay with respect to the EOD command (Bell and Grant, 1992).

The number of spikes in each burst of the granular cells provides electrosensory information to the principal cells of the ELL (i.e. the medium ganglion cells, MG_1 and MG_2), and to the efferent cells of the ELL (i.e. the large fusiform (LF) and the large ganglion (LG) cells). The MG cells are GABAergic, Purkinje-like cells that inhibit each other and the efferent cells. All of the principal cells

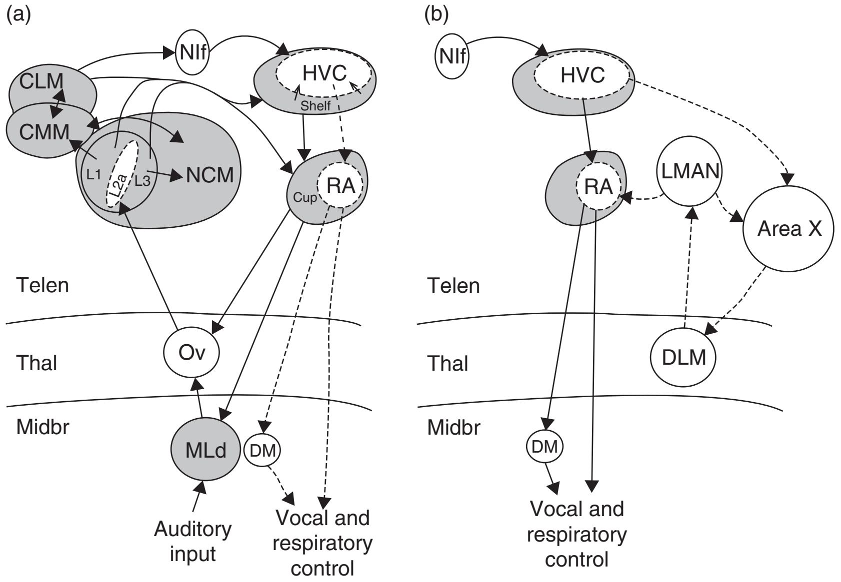

Figure 11.3. Organization of auditory and motor control pathways in songbirds (modified from Mello, 2002). (a) The auditory system consists of an ascending pathway that includes midbrain and thalamic nuclei, intratelencephalic projections among the thalamo-recipient area field L and its targets, and a descending projection from the cup to nuclei of the ascending auditory pathway. Note the close apposition of nuclei of the direct song motor pathway (HVC and RA) to auditory structures. (b) The song control system consists of the direct motor pathway (solid lines) and the anterior forebrain pathway (dashed lines). Areas at the interface between the auditory and motor control systems (e.g. NIf, shelf) are likely candidate mediators of sensorimotor integration. Abbreviations: CLM, caudolateral mesopallium; CMM, caudomedial mesopallium; DLM, medial nucleus of the dorsolateral thalamus; DM, dorsomedial intercollicular nucleus; L1/L2/L3, field L subdivisions; LMAN, lateral magnocellular nucleus of the anterior nidopallium; midbr, midbrain; MLd, dorsal part of the lateral mesencephalic nucleus; NCM, caudomedial nidopallium; NIf, interfacial nucleus of the nidopallium; Ov, nucleus ovoidalis; telen, telencephalon; thal, thalamus.

of ELL receive parallel fiber inputs, but the MG cells show the strongest adaptive properties.

A comparison of the electrosensory input with the EOD template appears to take place in the MG cells. The basilar dendrites of MG cells receive inputs from deep granular cells providing an EOD-command-gated sensory input, and the apical dendrites receive an EOD template. The mechanism for generating the EOD template is based on spike-timing dependent plasticity (STDP) at the synapse from parallel fibers onto the MG cells (Bell *et al.*, 1997). A special

STDP learning rule causes the MG cells to sculpt a negative image of the electrosensory image from parallel fiber input (Roberts and Bell, 2000). The parallel fibers carry all of the timing information necessary to generate a negative image of the sensory response to the EOD so that, when combined with the predicted sensory inputs, the output of MG cells is constant. This learning mechanism requires many EODs, so the slow adaptive process generates a prediction of the sensory image based on the recent history of sensory stimulation, and novel sensory information is emphasized.

Thus, the neurons that process the comparison between an internal expectation and the electrical field that is actually sensed by the fish belong to sensory-processing circuits and constitute an eminently sensory processing system. Importantly, even though the ELL receives a motor-related input and is modulated by a motor command, it is still primarily involved in the sensory processing of the electric field.

The electrosensory system described above is used for active electrolocation. However, a parallel electrosensory system is used for passive detection of electrical signals that originate in the environment. Electroreceptors specialized for passive electrolocation, the ampullary receptors, modulate their spike rate in response to changing electric field strength across the skin (Bell and Szabo, 1986). Electrosensory information from ampullary afferents are also initially processed in the ELL, but in a separate region (Bell, 1990) with similar structure to the regions that process the active electrolocation signals. An important difference between the two regions of ELL is the absence of an AND-gate in the passive electrolocation region so that all electrosensory information is passed into the ELL. The passive electrolocation region also receives strong EOCD that is used in an expectation generator to eliminate predictable electrosensory patterns. Most notably, the passive electrolocation system eliminates the response of the ampullary afferents to the fish's own EOD in the ELL (Bell, 1981; Bell *et al*., 1993). The mechanism is the same as described above, where synaptic plasticity generates an EOD template of the predictable electrosensory response that cancels the afferent input. A similar template of predictable sensory patterns is presumed to exist in the songbird sensory system, but the mechanisms for the generation of the song template, and for making comparisons with auditory stimuli, are still unknown.

11.4 The perceptual processing and memorization of song: in search of a neuronal substrate

Remarkable progress has been made in identifying the brain areas and circuits involved in the production and learning of birdsong. Some of these motor control areas have also been implicated in the perceptual aspects of vocal communication. We will start this section by a brief review of these areas. A set of discrete brain nuclei known as the song control system (Nottebohm *et al*., 1976) is involved in vocal motor control of song production and in song learning, based on the combined evidence from lesions, anatomic tract-tracing, electrophysiologic recordings, and the mapping of activity-dependent gene expression (see review articles in Brenowitz *et al*., 1997; Zeigler and Marler, 2004; see also Mello, 2002). The song control system consists of a series of interconnected forebrain nuclei: nucleus HVC of the nidopallium, the robust nucleus of the arcopallium (or RA), area X of the medial striatum, the medial nucleus of the dorsolateral thalamus, (or DLM), and the lateral magnocellular nucleus of the anterior nidopallium (or LMAN). We follow here the revised avian brain nomenclature (as detailed in Reiner *et al*., 2004) whose main output is to brainstem areas involved in vocal and respiratory control.

As shown in Fig. 11.3b, two main pathways have been described in the song control system. The direct motor pathway consists of the projections from HVC to RA onto the dorsomedial intercollicular nucleus (DM) and the tracheosyringeal portion of the hypoglossal nucleus (nXIIts), the latter containing motorneurons that innervate the syrinx, the avian vocal organ (Nottebohm *et al*., 1982; Vicario and Nottebohm, 1988; Vicario 1991; Wild, 1993, 1997). This direct motor pathway is required for the production of song, its maturation during development correlates with the emergence of song vocal behavior in juveniles (Nottebohm *et al*., 1976; Konishi and Akutagawa, 1985), and its component nuclei are activated coordinately with singing behavior (Yu and Margoliash, 1996; Hahnloser *et al*., 2002). The anterior forebrain pathway consists of the serial projections from LMAN to area X to DLM and back to LMAN; area X also receives pallial input from HVC (Okuhata and Saito, 1987; Bottjer *et al*., 1989; Luo *et al*., 2001). The main output of this anterior pathway is to song motor nucleus RA, through the LMAN to RA projection. In many respects, this anterior pathway is analogous to cortical-basal ganglia-thalamic-cortical loops found in motor control systems in mammals (Farries and Perkel, 2002). The pallial nucleus interface (NIf) and the thalamic nucleus uvaeformis (Uva) provide major inputs to HVC (Nottebohm *et al*., 1982). Telencephalic nuclei that resemble those in both the direct motor and anterior forebrain pathways have also been identified in the brains of parrots and hummingbirds (Paton *et al*., 1981; Striedter, 1994; Brauth *et al*., 1997; Durand *et al*., 1997; Jarvis and Mello, 2000; Jarvis *et al*., 2000), two other avian orders that exhibit vocal learning (Nottebohm, 1972); such nuclei are apparently absent in avian orders that lack vocal learning (Karten and Hodos, 1967; Kuenzel and Masson, 1988; Kroodsma and Konishi, 1991).

Some features relevant to the present discussion are immediately evident from the organization of the song control system:

1. There exists both a direct and an indirect projection from HVC to nucleus RA. The indirect projection is part of a pathway involved in the learning and active maintenance of song, and has been postulated to modulate synaptic and cellular plasticity in its target motor nucleus RA (Johnson *et al.*, 1997; Kittelberger and Mooney, 1999; Brainard and Doupe, 2000) (see also Kittelberger and Mooney, Chapter 10, present volume). Such a design may facilitate the implementation of mechanisms for error correction through the tuning of the motor control pathway.
2. Based on its anatomic organization, the song control system consists of a set of nuclei and projections dedicated to vocal motor control, as its output is specifically directed to vocal and respiratory control areas.
3. The song system presents marked sexual dimorphism, with several song nuclei and their projections being very prominent in males, but much smaller or absent in females (Nottebohm and Arnold, 1976).

Interestingly, auditory responses selective for conspecific song (particularly the BOS) can be recorded in the nuclei of the song control system (Margoliash, 1983; Williams and Nottebohm, 1985; Margoliash, 1986; Doupe and Konishi, 1991; Vicario and Yohay, 1993; Volman, 1996). These responses are modulated by exposure to song (Solis and Doupe, 1997, 1999) and may reflect a role of song nuclei in learning the BOS. Studies on mechanisms generating these responses have helped clarify how auditory input modulates activity in the song control system (Mooney, 2000; Rosen and Mooney, 2000). Since these song-evoked responses are mostly seen under anesthesia or during sleep, but are weaker or absent during wakefulness (Dave *et al.*, 1998; Schmidt and Konishi, 1998; Dave and Margoliash, 2000; Nick and Konishi, 2001; Cardin and Schmidt, 2003; Rauske *et al.*, 2003), their role in perceptual processing is unclear. Lesions targeted at song nuclei reportedly affect song-dependent auditory discrimination (Brenowitz, 1991; Del Negro *et al.*, 1998; Scharff *et al.*, 1998; Gentner *et al.*, 2000), but such lesions also affect nearby auditory processing areas or fibers of passage that are part of the auditory projection system (MacDougall-Shackleton *et al.*, 1998). Thus, the evidence for the participation of the song control system in the perceptual processing of birdsong is still inconclusive.

Another important argument against a prominent role of the song system in perceptual discrimination is that female songbirds are typically capable of performing fine song discrimination and recognition both in terms of discriminating conspecific and heterospecific songs, as well as discriminating individual conspecific songs (Ratcliffe and Otter, 1996; Searcy and Yasukawa, 1996; Gentner and Hulse, 2000; Riebel *et al.*, 2002). In that sense, there is no compelling reason to believe that females are intrinsically inferior to males in terms of their auditory processing and discriminatory capabilities. However, their song nuclei and projections are often small or absent (Nottebohm and Arnold, 1976; Arnold *et al.*, 1986), suggesting that areas other than the song control system are primarily involved in song perception in females (see also Williams, 1985).

Much of the search for a neuronal substrate for song perception and discrimination has been dominated by the notion that such processes occur at the level of the song control system. Strictly speaking, however, we still know very little about the exact areas involved in song perception and discrimination, and the formation and storage of song auditory memories. We therefore do not know how the processes outlined in Fig. 11.1a are implemented by neuronal circuits. It has become increasingly clear, however, that both male and female songbirds possess a set of brain areas that are constituent parts of the central auditory pathways and that are involved in various aspects of song auditory processing. The evidence derives from anatomic studies, the expression analysis of activity inducible genes, and electrophysiologic recordings.

Auditory information ascends along a brainstem pathway that is conserved in vertebrates (Butler and Hodos, 1996), reaching the telencephalon through field L (Karten, 1967, 1968; Kelley and Nottebohm, 1979; Brauth *et al.*, 1987). Field L projections to its targets, that is the adjacent caudomedial nidopallium (NCM) and caudomedial mesopallium (CMM), and the shelf and cup areas adjacent to song nuclei HVC and RA, respectively, represent ways for auditory information to reach higher-order telencephalic areas (Bonke *et al.*, 1979; Kelley and Nottebohm, 1979; Fortune and Margoliash, 1995; Vates *et al.*, 1996; Mello *et al.*, 1998). Altogether, these brain areas and projections constitute an avian central auditory system. Similar areas and projections have been described in different avian species (e.g. see Wild *et al.*, 1993; Metzger *et al.*, 1998) regardless of whether they evolved vocal learning and a telencephalic song control system. The nuclei and projections of this central auditory system are pallial and, thus, analogous and possibly homologous to the circuits that constitute the mammalian auditory cortex (Reiner *et al.*, 2004). It is possible that only in vocal learners, which possess telencephalic vocal control nuclei (Brenowitz, 1997; Jarvis *et al.*, 2000), do the vocal control areas have access to song auditory information processed at the pallial/cortical level.

Mapping of activity-dependent gene expression, in particular of the transcription factor *zenk*, has been instrumental in the identification and analysis of areas that respond to song auditory stimulation and thus likely participate in song processing and/or perceptual memorization. Several telencephalic areas distinct from the song control nuclei respond to song presentation with a rapid and robust increase in *zenk* expression (Mello *et al*., 1992; Mello and Clayton, 1994; Mello and Ribeiro, 1998), whereas the direct motor and anterior forebrain pathways within the song system do not show this response (Mello and Clayton, 1994; Jarvis and Nottebohm, 1997). The *zenk*-expressing areas include field L subfields L1 and L3, NCM, CMM, and the shelf and cup regions, all of which are part of the avian central auditory pathway, as described above. Although the lack of *zenk* induction in specific areas needs to be interpreted with caution, the detection of song-induced *zenk* expression in a given area provides strong and direct evidence for the participation of that area in the sensory processing of song (see further discussion in (see further discussion in Mello, 2002).

Most *zenk* studies have focused on NCM, the area with the most marked *zenk* response to song (Mello *et al*., 1992). NCM is a field L target (Vates *et al*., 1996) and is arguably comparable to supragranular layers of the mammalian auditory cortex (Karten and Shimizu, 1989; Mello *et al*., 1998). Song-induced *zenk* expression in NCM is rapid and transient (Mello and Clayton, 1994; Mello *et al*., 1995; Kruse *et al*., 2000), and it is highest for conspecific song, as compared to heterospecific song or tones (Mello *et al*., 1992). In addition, *zenk* induction decreases markedly upon repeated song presentations (song-specific “habituation”), but it is re-elicited upon presentation of a novel song (Mello *et al*., 1995). Variations in the spatial distribution of *zenk* expression in NCM correlate with acoustic features of the song stimulus (Ribeiro *et al*., 1998; Gentner *et al*., 2001). Altogether, *zenk* expression studies have provided consistent evidence for the participation of NCM in the perceptual processing of birdsong and in song auditory memorization (for reviews, see Ball and Balthazar, 2001; Mello, 2002; Bolhuis and Eda-Fujiwara, 2003).

The evidence from electrophysiologic studies is also consistent with a participation of the areas revealed with *zenk* expression in birdsong auditory processing and perceptual memory formation. For example, robust electrophysiologic responses to song can be recorded in caudal nidopallial areas including NCM, and these responses are of longer latencies and show a higher degree of selectivity towards complex stimuli including conspecific vocalizations than in field L (Bonke *et al*., 1979; Muller and Leppelsack, 1985; Müller and Scheich, 1985; Ang, 2001). More interestingly, song-evoked responses in NCM decrease, or habituate, in response to repeated song stimulation (Chew *et al*., 1995, 1996; Stripling *et al*., 1997, 2001). This habituation is song-specific, as a high response level can be reinstated upon presentation of a novel song stimulus, consistent with the *zenk* studies discussed in the preceding paragraph. The habituated state in NCM can persist for long periods (hours to days), depending on the amount of song stimulation, and its maintenance depends on local gene expression, as indicated by local injections of RNA and protein synthesis inhibitors at specific time windows during and after song stimulation (Chew *et al.*, 1995). Habituation to song in NCM thus consists of an experience-dependent plasticity phenomenon that bears remarkable similarities to hippocampal long-term potentiation, and it has been proposed as a cellular correlate of a song perceptual memory (but also see discussion in Bolhuis and Eda-Fujiwara, 2003).

Electrophysiologic recordings have revealed that song-responsive neurons in CMM also display an experience-dependent plasticity that could be considered a correlate of a perceptual memory trace (Gentner and Margoliash, 2003). More specifically, CMM neurons in starlings show significant selectivity towards songs with which the birds were previously trained in conditioning tasks involving song perceptual discrimination. Thus, the auditory response properties of CMM neurons depend on the previous perceptual history of the bird. Like NCM, CMM presumably represents a higher-order processing station compared with the primary auditory area field L from which it receives a major input, as responses to song in CMM show longer latencies and somewhat higher selectivity towards complex auditory stimuli than those in field L (Heil and Scheich, 1991; Sen *et al.*, 2001). NCM and CMM are highly interconnected (Vates *et al.*, 1996), and can potentially influence each other's response to song and other complex auditory stimuli.

In combination, the anatomic, molecular and physiologic studies indicate that the auditory areas in the caudomedial telencephalon of both sexes play a prominent role in the auditory processing and possibly the memorization of birdsong in the context of perceptual discrimination. These large areas, particularly NCM and CMM, constitute a considerable portion of the telencephalon, indicating that songbirds dedicate a large amount of brain space to the processes above. As argued earlier, because the sensory processing of birdsong is quite likely similar in the contexts of perceptual discrimination and of auditory feedback evaluation for vocal learning, the same or similar pathways/mechanisms may be used in these two contexts. If songbirds evolved an elaborate system to perform song discrimination based on the acoustic properties of song, it would make sense to also utilize that machinery for the process of auditory feedback evaluation of self-vocalizations. NCM and CMM occupy a privileged position within the auditory pathway, as they constitute higher-order areas than the thalamo-recipient field L, and they are in close relationship with vocal control centers. Thus, these auditory areas receive processed sensory input from the ascending auditory pathway, and could later convey the output of their perceptual processing to vocal command centers. For instance, CMM receives a projection from NCM and projects to the caudolateral mesopallium (CLM), which in turn projects to NIf (Vates *et al.*, 1996), providing a possible entry of auditory input from the caudomedial telencephalon into the song control system.

Some evidence that areas like NCM and CMM participate in song auditory feedback processing comes from *zenk* studies. Expression of *zenk* is markedly induced in both structures during singing, but it is abolished in singing birds that have been deafened (Jarvis and Nottebohm, 1997). Thus, *zenk* expression in NCM and CMM during singing is related to the processing of song auditory feedback. In contrast, *zenk* expression in song control nuclei is not abolished by deafening (Jarvis and Nottebohm, 1997), indicating that the activation of the latter areas based on *zenk* expression is more directly related to the motor control of singing than to auditory feedback evaluation (but see also Cardin and Schmidt, 2003; Rauske *et al*., 2003). The z*enk* expression studies have also provided some evidence that the neuronal circuitry in the caudomedial telencephalon may encode song auditory memories required for both familiar versus unfamiliar song discrimination and auditory feedback evaluation. Song-induced *zenk* expression in NCM is initiated developmentally in association with the onset of the sensitive period for song learning (Jin and Clayton, 1997; Stripling *et al*., 2001). In addition, the strength of *zenk* induction in adult NCM correlates with the degree to which the bird learned to imitate the stimulus song during vocal learning (Bolhuis *et al*., 2000, 2001). This effect is independent of the birds' familiarity to the song auditory stimulus (Terpstra *et al*., 2004). Furthermore, *zenk* expression in NCM of females is modulated depending on the birds' early exposure to song and according to the birds' familiarity to the song stimulus (Maney *et al*., 2003; Hernandez and MacDougall-Shackleton, 2004). Thus, the available evidence is consistent with a role for NCM in the perceptual processing and discrimination of song in both sexes.

11.5 Implementing feedback evaluation: what do we learn from comparing songbirds and the electric fish

In comparison with the electrosensory system, not enough is known yet about the organization of the circuitry in song processing areas to determine how the comparative processes in Fig. 11.1a are implemented in the brain of songbirds. Based on the discussion above, however, it is apparent that caudomedial telencephalic structures like NCM and CMM likely play a central role in the processing of both external song stimuli and of auditory feedback evaluation during singing. More specifically, these areas appear to be part of an elaborate sensory network involved in the processing of birdsong for both perceptual discrimination and vocal learning. These structures are in a privileged position to access the required auditory information and then send the results of their computations to vocal motor control centers. In addition, in contrast to song control nuclei, the output of caudomedial auditory areas is not exclusively dedicated to vocal motor control. Although further studies are needed, the output of these auditory areas is more likely to modulate sensory and/or motor representations and programs involved in broader, non-vocal aspects of songbird behavior (as in Fig. 11.1a, right panel, general motor representations). Thus, as occurs in the cerebellar-like networks of the electric fish, the processing of sensory feedback evaluation in relation to sensory expectations or predictions in songbirds may involve structures that have an eminently sensory/perceptual function.

According to this postulate, the acquired song representations (the song template and the memories of familiar songs) either reside in caudomedial telencephalic structures like NCM and CMM, or these structures have access to such representations. Additionally, neuronal mechanisms for performing perceptual discrimination and auditory feedback evaluation (the comparator in Fig. 11.1a, left panel) would need to be present in these areas. An intriguing possibility is that the phenomenon of habituation observed in NCM plays that role, or at least a contributing one. By decreasing the neuronal responsiveness to a familiar song, habituation sets the auditory system in a state that is mostly sensitive to novelty (i.e. to acoustic features that are present in the incoming auditory input but absent from the internalized memory of the familiar song, and vice versa). This would be somewhat analogous to the negative image mechanism of mormyrids. If such a mechanism were also operative for vocal learning, the strongest responses would be obtained for auditory feedback from vocalizations that differ mostly from the acquired auditory template, whereas vocalizations that match well the template would produce only weak responses. In this regard, the output of an auditory station that habituates would be signaling the extent of a mismatch, as diagrammed in Fig. 11.1a. It is hard to conceive, though, that a mechanism for auditory template formation only makes use of a decrease in responsiveness to song, and further research may reveal correlates of a potentiation-like phenomenon as well. At any rate, habituation could help generate the highly selective responses to song and to specific song features known to occur in areas such as the song control nuclei. In that sense, an acquired song auditory template could be seen as a distributed network with elements recruited from various auditory stations, each with varying degrees of responsiveness to different acoustic features of song.

A very prominent feature of the electrosensory system, at least in mormyrids, is the corollary discharge signal that allows a motor center to create an expectation within the sensory processing system. In songbirds, a modulation of the auditory system by vocal control centers would provide a means for the latter to set the song processing circuits for the comparison between song auditory feedback and the acquired song template. Although no such a mechanism has been directly demonstrated, some limited anatomic evidence suggests the existence of a projection from a song motor nucleus to an auditory structure, namely from the medial extension of HVC, the so-called "paraHVC", to NCM (Foster and Bottjer, 1998). In addition, the finding that *zenk* expression in NCM of singing birds is inversely proportional to the number of song bouts produced (Jarvis and Nottebohm, 1997) suggests that the auditory system can be modulated during vocalizations.

The strong corollary discharge signals in the initial electrosensory processing structure are used for two aspects of electrosensory processing in mormyrids. Firstly, the EOCD gates the electrosensory input to pass only the fish's own EOD and, presumably, to provide a time-reference for decoding the electrosensory afferent spikes. Secondly, the EOCD provides a time-reference in the molecular layer of the ELL for the expectation generator. In songbirds, there is no evidence for a parallel auditory pathway for active sensory processing during singing, so the same pathway is most likely used for active and passive listening. The absence of an AND-gate in the primary auditory pathway allows all auditory information to pass into the system, regardless of the origin. Since the songbird must make the distinction between its own song and external sources late in auditory processing, we have proposed that an AND-gate is present as the sensory information is entering the song motor system as shown in Fig. 11.1a, right panel. The AND-gate then has information about recent motor activity and can be prepared to pass auditory information that shortly follows the generation of song. This mechanism also simplifies the character of the information that is passed to the motor system. Since the auditory information has already been compared with the song template in the auditory pathway, all that needs to be passed to the motor system is the deviation from the expected auditory pattern of the previously learned song.

The corollary discharge signal in the mormyrid fish is also used by the ELL as a time-reference to cancel predictable electrosensory information that immediately follows the EOD. In the songbird auditory system, the absence of a corollary discharge signal implies that the temporal structure of the auditory stimulus itself must be used to form the song template. In addition, neurons in the auditory processing system exhibit habituation in the absence of active singing. Thus, the source of timing information for the generation and recall of the song template might differ from the motor-command driven mechanism in the electrosensory system. One possibility would be that the timing information arises from the song itself, where earlier temporal patterns of the song predict later patterns. Such a hypothesis might lead to experimental tests that could identify which spectro-temporal patterns in the song are the cues upon which the song template is built.

Since bird song is often a very stereotyped sequence of syllables, patterns of syllables early in a song would predict the patterns of later syllables. A mechanism could be proposed where each syllable acts as a surrogate EOCD to provide a series of delayed inputs to generate a template of predictable auditory stimuli. Such a learning system could be based on synaptic plasticity, as in the electric fish, and would be suitable for providing an error signal to the motor system. In addition, this mechanism of template generation would also be precisely what female birds would need to discriminate how consistently male birds are able to repeat their song. Tests for such a hypothesis of auditory learning will involve knowing the details of the song auditory system to characterize responses in candidate substrates for this adaptive template mechanism of auditory learning.

In contrast to the electrosensory processing system in the electric fish, very little is known about the cellular and circuit organization of sensory-processing areas like NCM and CMM. Recent evidence in zebra finches indicates that GABAergic neurons are prevalent and show a marked *zenk* induction response to song in both structures, and that active GABAergic synapses are prevalent in NCM slices (Pinaud *et al.*, 2004). These observations are consistent with previous findings in chickens (Muller and Scheich, 1988), and indicate that inhibitory neurons are likely to play a prominent role in song auditory processing and in the phenomenon of song habituation. It will now be necessary to determine how these neurons are organized into circuits, and to test for their potential role in modulating the response properties and plasticity of song-responsive neurons in NCM and CMM. In testing our postulates, it will also be important to determine the exact outputs of the caudomedial auditory structures, and whether they modulate the physiologic properties of neurons that constitute the song control circuits or other motor representations.

11.6 Conclusion

The comparison between sensory processing systems presented here suggests that similar processing algorithms may be used in systems of widely different sensory modalities and habitats. Data from molecular, anatomic, physiologic and behavioral studies have indicated that brain areas that constitute the central auditory pathways are involved in the perceptual processing and memorization of birdsong. A considerable portion of the songbird telencephalon, distinct from the song control system, may participate in basic perceptual aspects of vocal communication and vocal learning. However, a clearer definition of the sites and mechanisms involved in song auditory memories will require a more refined understanding of how song-responding areas are functionally organized and how they interact with the pathways involved in the motor representation of birdsong. We have attempted to use the well-studied electrosensory processing system to suggest likely mechanisms that account for the observed habituation and learning in the songbird auditory system. It is our expectation that such a comparison will lead to novel hypotheses about songbird auditory learning and suggest new avenues of research.

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