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A songbird forebrain area potentially involved in auditory discrimination and memory formation

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Songbirds rely on auditory processing of natural communication signals for a number of social behaviors, including mate selection, individual recognition and the rare behavior of vocal learning – the ability to learn vocalizations through imitation of an adult model, rather than by instinct. Like mammals, songbirds possess a set of interconnected ascending and descending auditory brain pathways that process acoustic information and that are presumably involved in the perceptual processing of vocal communication signals. Most auditory areas studied to date are located in the caudomedial forebrain of the songbird and include the thalamo-recipient field L (subfields L1, L2 and L3), the caudomedial and caudolateral mesopallium (CMM and CLM, respectively) and the caudomedial nidopallium (NCM). This review focuses on NCM, an auditory area previously proposed to be analogous to parts of the primary auditory cortex in mammals. Stimulation of songbirds with auditory stimuli drives vigorous electrophysiological responses and the expression of several activity-regulated genes in NCM. Interestingly, NCM neurons are tuned to species-specific songs and undergo some forms of experience-dependent plasticity *in-vivo*. These activity-dependent changes may underlie long-term modifications in the functional performance of NCM and constitute a potential neural substrate for auditory discrimination. We end this review by discussing evidence that suggests that NCM may be a site of auditory memory formation and/or storage.

[Pinaud R and Terleph T A 2008 A songbird forebrain area potentially involved in auditory discrimination and memory formation; *J. Biosci.* 33 145–155]

1. Introduction

Vocal learning, a behavior thought to constitute one of the components for human speech acquisition, is the ability to learn and produce vocalizations through imitation, rather than by instinct. Vocal learning is relatively rare: to date this behavior has only been found in humans, cetaceans (whales and dolphins), some species of bats, and in three avian groups: Passeriformes (songbirds), Psittaciformes (parrots), and in the family Trochilidae (hummingbirds) (reviewed in Kroodsma and Miller 1982; Hauser and Konishi 1999; Jarvis 2004; Zeigler and Marler 2004). Animal models commonly used in neuroscience research,

such as non-human primates and rodents, do not appear to have vocal learning; they instead are thought to produce only innately acquired vocalizations (Jarvis 2004).

The animal models most often used to study the neural basis of vocal learning are songbirds. This is due to a combination of factors that include, but are not limited to, the relatively well understood anatomical and functional organization of the brain circuits that underlie vocal learning, their superb vocal learning abilities, a well defined window for the development of this behavior, ease of use, and availability.

The acquisition of learned vocal communication signals in songbirds appears to involve two critical stages:

Keywords. Auditory learning; auditory processing; HVC; NCM; nidopallium; vocal learning

Abbreviations used: AFP, Anterior forebrain pathway; BOS, bird's own song; CMM, caudomedial mesopallium; DLM, dorsolateral thalamic nucleus; IEG, immediate early gene; LMAN, lateral magnocellular nucleus of the anterior nidopallium; NCM, caudomedial nidopallium; PFP, posterior forebrain pathway; RA, robust nucleus of the intercollicular complex; ZENK, zif268, egr-1, NGFI-A, Krox24

(i) a sensory phase, when birds must listen to and memorize the vocalizations of an adult tutor – the memorized tutor model vocalizations are known as the "template memory"; (ii) a sensorimotor phase, when young birds hear their own vocalizations and use the template memory to "calibrate" their vocal output through sensorimotor feedback (for reviews, *see* Zeigler and Marler 2004). Much is known about the neural basis underlying the sensorimotor phase. However, the processes and loci where template memories, and other auditory memories, are formed and/or stored remain largely unknown. This article reviews evidence that suggests that an auditory forebrain area residing outside of the traditional song-control circuit, namely the caudomedial nidopallium (NCM), may play a central role in auditory processing related to the formation of auditory memories required for auditory discrimination and vocal learning.

Understanding the neural basis of vocal learning in songbirds may shed light on the mechanisms responsible for the acquisition of spoken language in humans, as a number of similarities exist in how humans acquire and develop speech, and how songbirds learn their songs (Doupe and Kuhl 1999). For instance, both humans and songbirds must hear a tutor during a sensitive period early in life to form auditory memories (i.e. template memories) of how vocalizations are "expected" to sound. These auditory memory traces are thought to be used as templates against which the learning individual matches its own developing vocalizations through sensorimotor integration, using auditory feedback as an error-correcting mechanism (for reviews, *see* Doupe and Kuhl 1999; Zeigler and Marler 2004). Thus, after tutor exposure, vocal learners engage in vocal practice that requires auditory feedback to appropriately develop their learned vocalizations (Konishi 1985; Marler 1991; Okanoya and Yamaguchi 1997; Funabiki and Konishi 2003). Intact auditory processing, and seemingly the formation of auditory memories are, therefore, required for the normal development of vocal learning behavior. For example, deafening and other forms of interference with auditory feedback prevents both song learning in songbirds and normal speech acquisition in humans (Konishi 1965; Marler and Waser 1977; Woolley and Rubel 1997; Doupe and Kuhl 1999; Woolley 2004; Zeigler and Marler 2004). Intact hearing is also needed for the maintenance of learned adult songs. Impairment of auditory feedback in adult songbirds leads to a gradual deterioration of learned song structure (Nordeen and Nordeen 1992; Woolley and Rubel 1997; Leonardo and Konishi 1999). Interestingly, this is also the case in humans: adults that become deaf after learning to speak also experience a steady decline in the structural features of speech (Cowie *et al* 1982; Cowie and Douglas-Cowie 1983, 1992; Waldstein 1990). Given that auditory processing is not only required for vocal learning, but also

for the maintenance of learned communication signals, a significant effort in the field has been directed at uncovering the anatomical and functional organization of circuits that underlie auditory processing and thus enable the formation of auditory memories.

2. The song-control system

The learning and production of birdsong is under the control of a system of brain structures known as the song-control system (Nottebohm and Arnold 1976; Nottebohm *et al.* 1982; Bottjer *et al* 1989, 2000; Vicario 1991; Vates and Nottebohm 1995; Wild 2004; Zeigler and Marler 2004). This system is generally divided into two pathways: A motor pathway (also known as the posterior forebrain pathway; PFP) that controls production of song through projections that originate from telencephalic brain areas and target brainstem centers associated with vocal and respiratory function (Nottebohm and Arnold 1976; Vicario 1991; Wild 1997), and an anterior forebrain pathway (AFP) that is associated with the learning and maintenance of the bird's own song (Bottjer *et al* 1984; Sohrabji *et al* 1990; Scharff and Nottebohm 1991; Brainard and Doupe 2000; Brainard, 2004 Wild, 2004) (figure 1). The PFP encompasses successive projections from the nidopallial nucleus HVC (a letter-based name), to the robust nucleus of the arcopallium (RA), and the descending projections of the latter onto the dorsomedial nucleus of the intercollicular complex (DM), the tracheosyringeal component of the hypoglossal nerve nucleus (nXIIIts), which innervates muscles of the vocal organ (syrinx), and medullary respiratory centers. The AFP encompasses a set of topographically organized projections from area X of the medial striatum to the medial part of the dorsolateral thalamic nucleus (DLM), from DLM to the lateral magnocellular nucleus of the anterior nidopallium (LMAN), and from the latter back to area X (Bottjer *et al* 1989; Johnson *et al* 1995; Vates *et al* 1996; Luo and Perkel 1999a; Luo *et al* 2001). This projection system is thought to be analogous to basal ganglia-thalamo-cortical loops found in the mammalian brain that appear to be involved in the acquisition and/or performance of movements requiring fine sequential sensorimotor integration (reviewed in Parent and Hazrati 1995; Bottjer and Johnson 1997; Bottjer 2004; Farries 2004; Perkel 2004).

Given that the song-control system plays a critical role in vocal learning in songbirds, it has been generally believed that auditory processing, discrimination and the formation of auditory memories required for vocal learning are performed by this set of brain structures. Indeed, song-driven electrophysiological responses have been reported in all of the nuclei of the song-control system (Williams and Nottebohm 1985; Doupe 1993; Margoliash 1997). These responses show selectivity to the bird's own song (BOS) (Margoliash 1983;

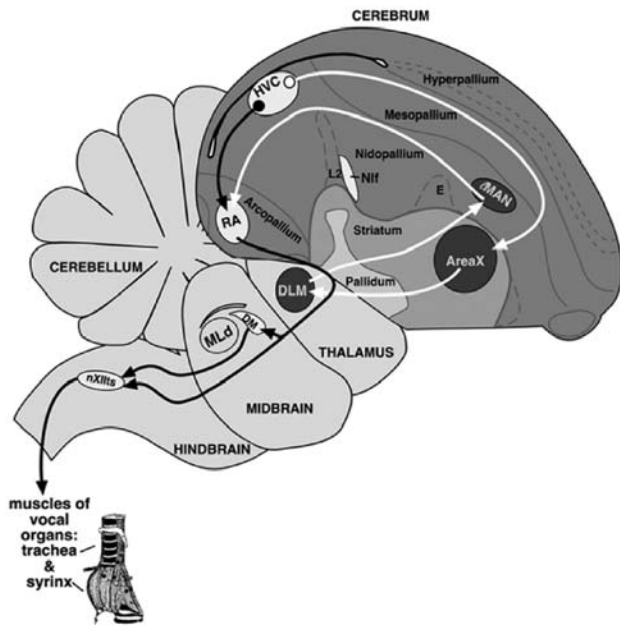


Figure 1. Schematic representation of a parasagittal section through a zebra finch brain detailing the connectivity of the main stations of song-control system. For clarity, only the main nuclei and projections are shown in this diagram. Projection systems participating in the PFP are indicated by black arrows, while projections that compose the AFP are detailed by white arrows. The illustration of the syrinx in this figure was adapted from Goller and Suthers (1996), while the remainder of the figure was partly assembled by Erich Jarvis. Anatomical abbreviations not mentioned above or in text: DM, dorsal medial mesencephalic nucleus; E, entopallium; H, hyperpallium; Hp, hippocampus; M, mesopallium; MLd, dorsal lateral mesencephalic nucleus; N, nidopallium; NIF, interface nucleus; Ov, ovoidalis; St, striatum; v, ventricle.

Williams and Nottebohm 1985; Doupe and Konishi 1991; Vicario and Yohay 1993), and such selectivity emerges during a sensitive period for vocal learning, usually early in life (Solis and Doupe 1997, 1999, 2000; Theunissen *et al* 2004). Importantly, however, these vigorous song-evoked responses are generally only observed when birds are under anesthesia or asleep, and are significantly less robust or absent in the awake animal (Dave *et al* 1998; Schmidt and Konishi 1998; Dave and Margoliash 2000; Nick and Konishi 2001, 2005). At least in song nucleus HVC, song-evoked activity appears to be directly modulated, or gated, by specific behavioral states, such as arousal and attentional processing (Cardin and Schmidt 2003; Rauske *et al* 2003).

Although the likely contributions of the song-control system to the auditory processing of songs and the formation of auditory memories remains unclear, mounting evidence suggests that the central auditory pathways in songbirds are crucial for song auditory processing and perception,

and may also play a role in the memorization of song that is required for perceptual discrimination and possibly vocal learning (for reviews, see Gentner 2004; Mello *et al* 2004; Bolhuis and Gahr 2006). In fact, discriminating and memorizing the spectro-temporal properties of songs, which is necessary for a number of key behaviors in songbirds such as individual recognition and territorial defense, does not appear to require an intact song-control system. For most songbird species, auditory discrimination occurs in both sexes, even though females do not typically produce song and have either a largely atrophied, or an entirely absent song-control system (Kroodsma and Miller 1996; Ratcliffe and Otter 1996). In fact, females choose potential breeding partners based on auditory discrimination of songs' acoustic features, suggesting that the contributions of the song-control system to auditory discrimination and the formation of auditory memories may be limited (Ratcliffe and Otter 1996; Gentner and Hulse 2000; Nowicki and Searcy 2004). The zebra finch (*Taeniopygia guttata*) is a good example to illustrate this point. It is perhaps the most commonly used species for song learning studies, yet female zebra finches never sing and a large neuroanatomical sex difference exists in the song-control system (Brenowitz and Kroodsma 1996; MacDougall-Shackleton and Ball 1999). Both male and female zebra finches that are exposed to song early in life have been reported to show an equally strong influence of the tutor's song on adult song preferences (Riebel *et al* 2002). This finding suggests that the neural basis for song recognition learning is at least partially, if not completely, independent of that for song production learning. However, the presence of a song-control system may still have some influence on learning to recognize songs and other vocalizations, as behavioral assays have shown that some sex differences in discrimination occur in zebra finches. For instance, females need more trials than males in learning certain acoustic discrimination tasks (Cynx *et al* 1990; Cynx and Nottebohm 1992). Furthermore, female responses to conspecific (same species) calls appear to be influenced by stimulus duration and not spectral content (Vicario *et al* 2002). Conversely, only males show a categorical preference for female calls, with responses that are based upon both temporal and spectral characteristics of a call stimulus (Vicario *et al* 2002). It is not clear, however, to what degree these reported sex differences in responses to vocalizations reflect differences in perceptual processing of auditory signals, behavioural motivation, or other unknown variables. Sex differences in sensory processing might be related to differences in the song-control circuitry, but may also reflect a neural dimorphism elsewhere. Whatever the case may be, it is clear that females, the consumers of song in the context of mate selection, are able to process, discriminate and memorize biologically important learned social communication signals, suggesting that an intact

song-control system is not required for these behaviours.

3. Auditory telencephalic circuitry

These facts have encouraged researchers to look at brain regions outside of the traditional song-control system that may serve as neural substrates for song perceptual processing, recognition and memorization. Songbirds have a set of ascending and descending projections that are analogous to the mammalian auditory system. Much fruitful work has been done in studies of the ascending auditory pathway, especially at the level of the telencephalon. As with mammals, the songbird ascending pathway conveys auditory information from the cochlea to telencephalic centers via a chain of pontine, mesencephalic and thalamic nuclei (Karten 1967, 1968; Kelley and Nottebohm 1979; Brauth *et al* 1987; Vates *et al* 1996; Mello *et al* 1998) (figure 2). In the telencephalon, several auditory areas are located within the caudomedial region, and the pallial areas make up an interconnected circuit that is analogous, and possibly homologous, to the mammalian auditory cortex. The caudomedial telencephalon contains the thalamo-recipient field L2, which is comparable to the thalamo-recipient layer IV of the mammalian primary auditory cortex, and two of its targets, the NCM (former

caudomedial neostriatum) and the caudomedial mesopallium (CMM; former caudomedial hyperstriatum ventrale). NCM is thought to be comparable, based on anatomical connectivity studies, to the supragranular cortical layers of the mammalian primary auditory cortex (Karten 1967, 1968; Kelley and Nottebohm 1979; Brauth *et al* 1987; Vates *et al* 1996; Mello *et al* 1998) (figure 2). From field L2 and its targets, auditory input reaches other telencephalic areas, including those that contribute to descending auditory projections, such as the shelf region underneath song nucleus HVC and the cup area anterior to song nucleus RA (Mello *et al* 1998). One or more of these central auditory pathways are likely to be involved in the song memorization required for perceptual discrimination and song learning (for reviews, *see* Gentner 2004; Mello *et al* 2004; Bolhuis and Gahr 2006; *see also* Terpstra *et al* 2004; Terpstra *et al* 2006; Gobes and Bolhuis 2007). Possible candidates include NCM and CMM, given that these regions exhibit the highest neuronal activation, as revealed by immediate early gene (IEG) expression, as a result of hearing songs in the awake, behaving songbird (in both males and females), relative to other acoustic stimuli (detailed below). In this review we focus primarily on NCM, an auditory forebrain area that exhibits functional features analogous to the mammalian auditory association cortex, as a potential site involved in the perceptual processing and formation of auditory memories required for auditory discrimination and possibly vocal learning.

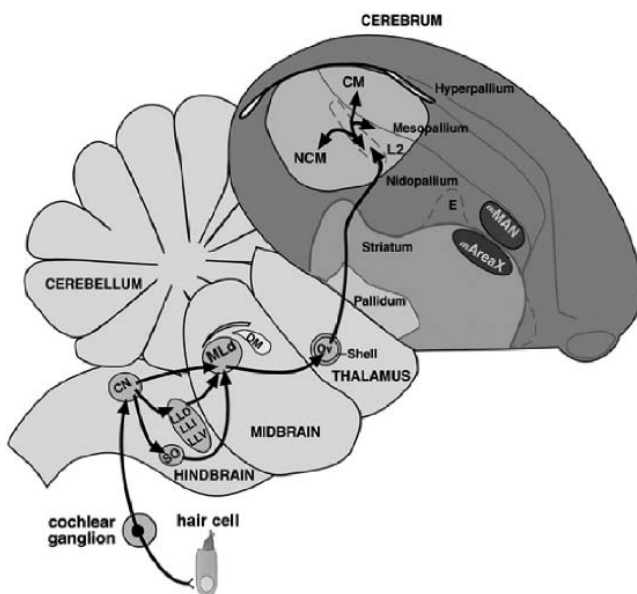


Figure 2. Schematic diagram of a parasagittal section through a zebra finch brain illustrating the main stations of the ascending auditory pathway. For clarity, only the main nuclei and projections are shown in this diagram. The focus of the present study, NCM, receives input from the thalamo-recipient layer Field L2, and has reciprocal connectivity with the caudal mesopallium (CM). This figure was partly assembled by Erich Jarvis. Anatomical abbreviations not mentioned above or in text: CN, cochlear nuclei; LL, lateral lemniscal nuclei; SO, superior olive.

4. The songbird NCM: Possible involvement in auditory discrimination and memory formation

The field's current understanding of the anatomical and functional organization of the auditory stations in the songbird brain has been significantly advanced by the use of activity-dependent markers, especially the expression of IEGs. Members of this class of genes are expressed rapidly and robustly as a result of many types of cellular stimulation, including neuronal activation (for reviews, *see* Herdegen and Leah 1998; Kaczmarek and Robertson 2002; Pinaud and Tremere 2006). The activity-dependent IEG *zenk* (an acronym for the names of this gene in other species: *zif268*, *egr-1*, *NGFI-A* and *krox-24*) is the most commonly used IEG in avian studies. It encodes a transcriptional regulator (*zif268*, *egr-1*, *NGFI-A*, *Krox24*, *ZENK*) that is extremely sensitive to neuronal depolarization and has been repeatedly implicated in paradigms of neuronal plasticity (Kaczmarek and Robertson 2002; Mello *et al* 2004; Pinaud 2004; Pinaud and Tremere 2006). The expression of *zenk* has proved very useful to map global patterns of neuronal activation that occur in response to a variety of experimental paradigms in the songbird field, including hearing, singing and song-learning (for reviews, *see* Mello 2002a; Zeigler and Marler 2004; Bolhuis and Gahr 2006;

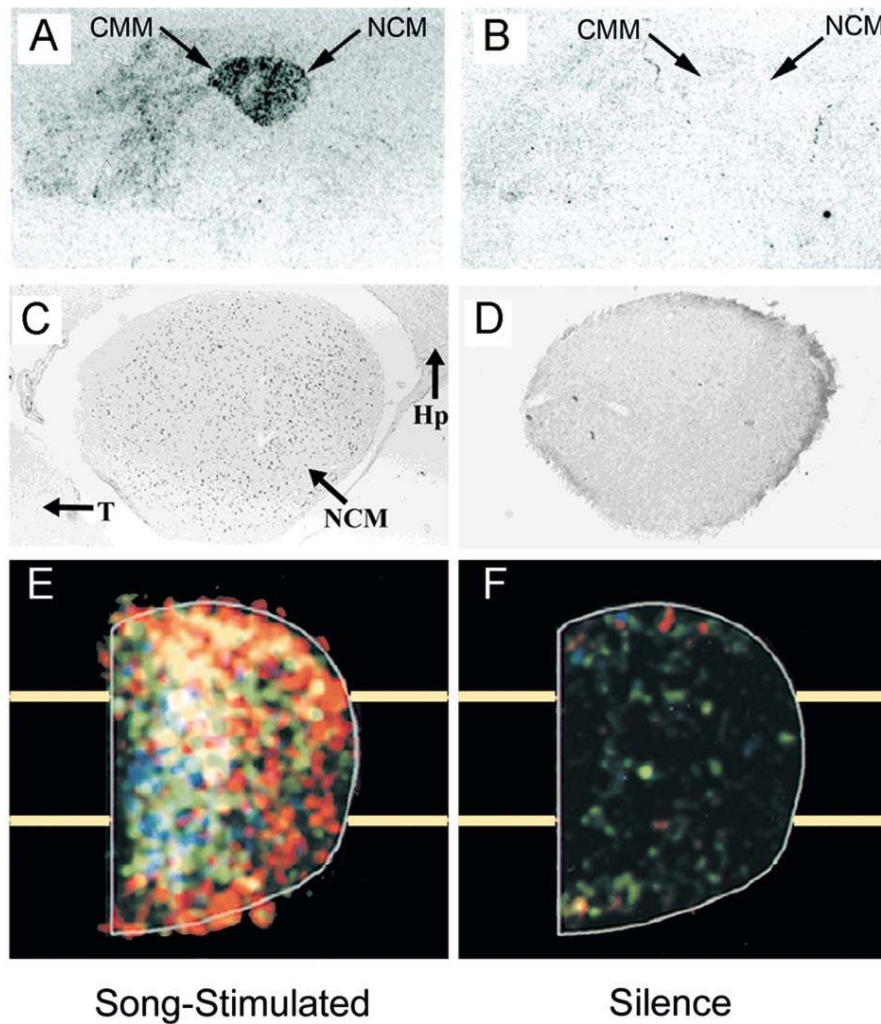


Figure 3. Induction of *zenk* mRNA and protein levels in the songbird forebrain following exposure to song. (A) In-situ hybridization autoradiogram of a section of an adult male zebra finch exposed to 45 minutes of playbacks of conspecific songs. (B) Unstimulated control. These sections correspond to parasagittal plane 250 μm lateral to the medial surface of the brain. (C) ZENK expression, revealed by immunocytochemistry, in the caudomedial telencephalon. Notice the presence of numerous ZENK-labeled cell nuclei after song stimulation in the zebra finch caudomedial nidopallium (NCM). (D) Unstimulated control. (E) Map of ZENK expression in the NCM of a canary resulting from presentation of a playback of conspecific songs. (F) Unstimulated control. Colors and brightness correspond to relative density and intensity of labeling of ZENK positive cells. Anatomical abbreviations not mentioned above or in text: Hp, hippocampus; T, telencephalon. Adapted from Mello *et al* (1992), Mello and Ribeiro (1998), Ribeiro *et al* (1998) and Mello and Pinaud (2006).

Mello and Pinaud 2006). Song playback triggers a rapid and robust induction of *zenk* in multiple structures of the songbird auditory telencephalon, including CMM, NCM, the thalamo-recipient field L (subfields L1 and L3, but not L2) and the cup and shelf regions that are adjacent to song-control nuclei RA and HVC, respectively (Mello *et al* 1992, 1998; Mello and Clayton 1994; Mello 2002b). Importantly, the highest expression of *zenk* in response to auditory input anywhere in the songbird brain is in NCM (Mello *et al* 1992, 2004), while hearing songs does not drive *zenk* expression in the song-control nuclei (reviewed in Mello 2002b; Mello *et al* 2004) (figure 3). These findings

show that auditory input in freely-behaving animals drives significant activity-dependent gene expression in multiple stations of the auditory telencephalon, especially in NCM, but significantly less, if any, in all stations of the song-control system.

Subsequent electrophysiological findings supported and expanded upon the *zenk* expression data. Stimulation of awake songbirds with a variety of auditory stimuli (detailed below) drives vigorous multi-unit responses in NCM (Chew *et al* 1995, 1996; Stripling *et al* 1997, 2001; Terleph *et al* 2006 2007). NCM responses to stimuli usually consist of bursts of action potentials associated with onset,

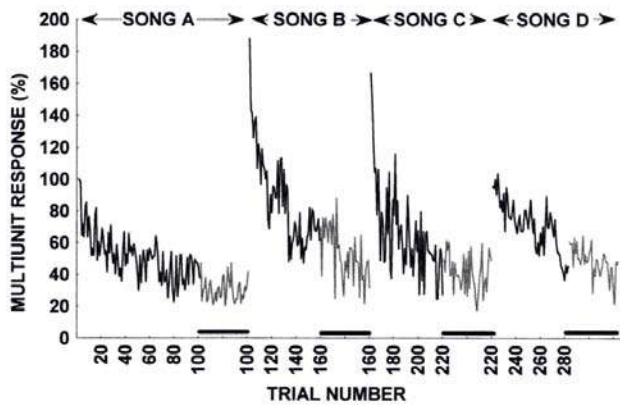


Figure 4. Electrophysiological recordings (multi-unit activity) obtained from NCM in response to the sequential presentation of four different conspecific songs. Note that repeated presentations of the same song lead to a rapid and significant decrease in the responsiveness of NCM units for each of the songs (inter-song interval 11-12 s). Once responses are habituated to a given song and re-tested later (grey dotted lines, dark bars on x axis), electrophysiological activity remains decreased in a song-specific manner even after training with the other songs. Adapted, with author's permission, from Chew *et al* (1995); PNAS 92: 3406-3410. Copyright © 1995 by The National Academy of Sciences of the United States of America, all rights reserved.

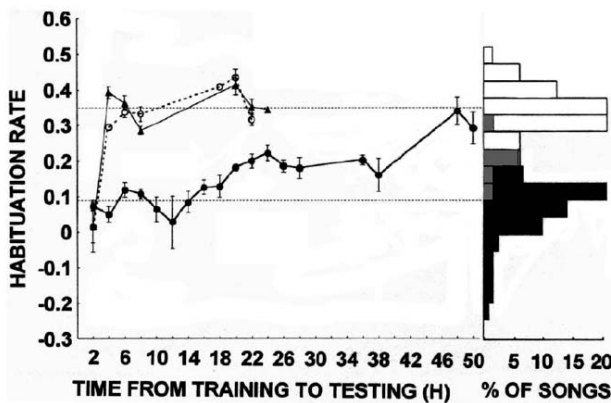


Figure 5. Habituation of NCM responses are long-lasting, especially for conspecific songs. Plotted are habituation rates (\pm SE) for conspecific (\bullet), heterospecific songs (\circ) and human speech (\blacktriangle) at various delays from training to testing. The histograms show the percentage frequency distributions of habituation rates for novel songs (open bars) and familiar songs tested after ≤ 10 h (solid bars). The small area of overlap of these distributions is represented by shaded bars. The dashed horizontal lines indicate the mean habituation rates for novel (upper line) and familiar (lower line) songs. Adapted, with author's permission, from Chew *et al* (1995); PNAS 92: 3406-3410. Copyright © 1995 by The National Academy of Sciences of the United States of America, all rights reserved.

and sometimes offset, of each song syllable, followed by sustained firing that may bridge the intervals between syllables (Terleph *et al* 2006, 2007).

Interestingly, these auditory-evoked responses in NCM are more selective towards complex stimuli (Müller and Leppelsack 1985) and have longer latency than hierarchically earlier auditory stations, such as field L (Sen *et al* 2001). Recent findings indicate that, not surprisingly for a structure in the ascending auditory pathway, NCM has a tonotopic organization. Electrophysiological responses to low and high frequencies are observed dorsally and ventrally, respectively, in both canaries and zebra finches (Terleph *et al* 2006, 2007). ZENK expression experiments have also revealed a tonotopic organization in the canary NCM: neuronal ensemble activity follows a frequency-dependent organization with low frequency whistles (canary song syllables) activating clusters of cells dorsally in NCM, while stimulation of animals with whistles of higher frequencies activates neurons that are located more ventrally (Ribeiro *et al.*, 1998). Thus, findings obtained with ZENK expression are consistent with those obtained with electrophysiological approaches (Terleph *et al* 2006, 2007).

5. Song-specific habituation may serve as a neural basis for auditory discrimination

Perhaps one of the most interesting features of NCM neurons is that their electrophysiological responses undergo a marked decrease (or "habituation") as a result of repeated presentations of the same stimulus in both zebra finches (Chew *et al* 1995) and canaries (Terleph *et al* 2006) (figures 4 and 5). Habituation to repeated song presentation is rapid, occurring in a time-scale of seconds, and is song-specific, as presentation of novel auditory stimuli re-instate vigorous electrophysiological responses (Chew *et al* 1995) (figure 4). Song-specific habituated responses in NCM are long-lasting and exhibit conspecific song selectivity; habituated responses last far longer (>40 h) for conspecific song stimuli than for heterospecific songs (~ 5 h) (Chew *et al* 1995, 1996) (figure 5). Moreover, the long-lasting maintenance of habituated responses depends on protein synthesis, as the phenomenon is blocked by either RNA or protein synthesis inhibitors (Chew *et al* 1995).

Interestingly, a marked decrease in the expression levels of the activity-dependent gene *zenk* have also been reported after repeated presentations of a given song (Mello *et al* 1995), a response that is similar to the electrophysiological habituation described above. Likewise, *zenk* expression levels remain strong in response to novel songs (Mello *et al* 1995). Although a causal relationship between *zenk* expression and the long-term maintenance of habituated electrophysiological responses has not been established, these findings suggest that NCM neurons are able to keep

cellular memory traces of songs that they have been exposed to (as habituated responses persist for long periods of time), and are able to discriminate across songs (as habituated responses can be immediately reinstated upon presentation of a novel song).

6. NCM activity is selective to conspecific auditory stimuli and likely modulated by behavioral salience

Previous electrophysiological studies have also demonstrated that NCM neurons respond preferentially (more vigorously) to conspecific songs, as compared to heterospecific songs or artificial stimuli, such as pure tones (Chew *et al* 1996; Stripling *et al* 2001), although at least one study did not find such a preference (Stripling *et al* 1997). Importantly, unlike in areas of the song-control system, these preferential song-evoked responses occur in awake animals. The selectivity of NCM neurons to conspecific songs has also been documented on the basis of *zenk* expression. Stimulation of songbirds (either zebra finches or canaries) with playback of conspecific songs triggers significantly higher *zenk* expression levels in NCM as compared to stimulation with heterospecific songs or pure tones (Mello *et al* 1992). This evidence that NCM neurons are tuned to conspecific acoustic stimuli suggests that this auditory area may play a role in auditory discrimination. Direct data to support this hypothesis, however, remains to be found.

In addition to a species-specific preference, ZENK activity in NCM may depend upon the social relevance of songs. For example, NCM activity in white-crowned sparrows (*Zonotrichia leucophrys oriantha*), as revealed by ZENK expression, is proportional to a bird's behavioral preference for a stimulus. Greater numbers of ZENK-positive cells are detected in response to the song of one's hatch-dialect, relative to a foreign dialect song (Maney *et al* 2003). Similarly, the expression of a behavior that is a part of copulation solicitation display (wing quivering) correlates positively with this increased ZENK response to song in NCM (Maney *et al* 2003). Furthermore, ZENK induction is greater in the NCM of female European starlings (*Sturnus vulgaris*) in response to long conspecific song bouts, which are thought to be more attractive than short song bouts (Gentner *et al* 2001).

These ZENK expression findings suggest that NCM does not likely respond in a simple way to broad categories of acoustic stimuli, but may also be influenced by sounds that vary subtly in their behavioural relevance (beyond a mere species preference), a central factor in the gating and facilitation of memory formation. However, the relevance of a song for a receiver is not necessarily restricted to the signal's social context. For instance, it has been reported that re-introduction of a "familiar" (habituated) song in a new context (from the opposite side of the cage, at a reduced sound

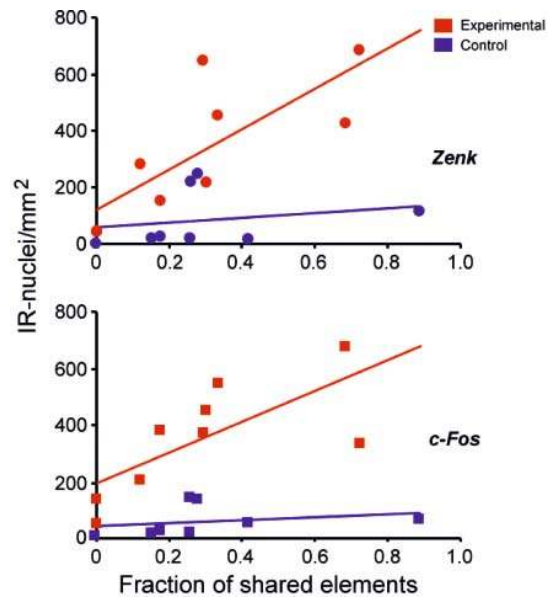


Figure 6. Graph sets illustrating the correlation between the number of neurons immunoreactive for the IEGs *zenk* (top) and *c-fos* (bottom) in NCM and the strength of song learning in individual zebra finches that were tutored and re-exposed to the tutor song (red). In control animals, that were tutored but not re-exposed to the tutor song, the correlation is not significant. Adapted, with author's permission, from Bolhuis *et al* (2000); PNAS 97: 2282-2285. Copyright © 2000 by The National Academy of Sciences of the United States of America, all rights reserved.

level, or paired with colored lights) leads to a re-induction of ZENK expression to that song (Kruse *et al* 2004). Moreover, it has been shown that previous pairing of a song with shock results in an increase in the ZENK response to that song when presented alone (Jarvis *et al* 1995). Together, these studies suggest that activity in NCM is not only tuned to behaviorally meaningful vocal communication signals, but may also be influenced by many factors other than the auditory input alone. NCM may, therefore, be involved in the integration of behaviorally-relevant sensory information to enhance the salience of acoustic stimuli.

7. NCM as a key site for the formation of auditory memories?

As described above, the sensory phase of vocal learning behavior involves the memorization of a tutor song (the "template memory") that may be used as a reference in the calibration of the developing bird's own song. A significant effort in the field has been to uncover where the auditory memory associated with the tutor song is formed and/or stored in the songbird brain. Given that the song system is

clearly involved in the vocal learning process, it is generally thought that the neural substrate of these auditory memories is embedded in the song-control system and that auditory information (from feedback of hearing one's-self) must reach the song-control system for correction of the vocal output. However, as indicated above, auditory-evoked responses are primarily seen under anesthesia and are weak or mostly absent in awake songbirds (Dave *et al* 1998; Schmidt and Konishi 1998; Dave and Margoliash 2000; but see Cardin and Schmidt 2003; Rauske *et al* 2003).

Recent electrophysiological findings suggest that NCM neurons of adult male zebra finches are selectively tuned to the song of a tutor heard early in life, and that the strength of this selectivity correlates with the fidelity of vocal imitation (Phan *et al*, 2006). Similarly, Bolhuis and colleagues found a strong and positive correlation between the strength of song learning (the number of elements that males copy from a tutor's song) and the number of neurons that were immunoreactive to the proteins encoded by the activity-dependent IEGs *zenk* and *c-fos* in NCM, also suggesting that NCM's activity is higher when song memories are presumably stronger or more established (Bolhuis *et al* 2000, 2001) (figure 6). These findings also suggest that NCM may be part of the neural substrate for representing the tutor song memory trace. The thalamo-recipient field L2, which projects to NCM, also exhibits vigorous electrophysiological responses to sounds and shows a tonotopic gradient, but lacks the selectivity to complex sounds and habituation to repeated song stimulation found in NCM (Muller and Leppelsack 1985; Terleph *et al* 2006). This suggests that the response properties described above likely arise from within NCM circuitry and not from earlier stations in the ascending auditory pathway.

A recent study provided further evidence that tutor-song memories may be represented within NCM. It was found that restricted bilateral neurotoxic lesions of NCM in adult male zebra finches impaired tutor-song recognition, but did not affect song production (Gobes and Bolhuis 2007). Furthermore, this lesion-induced decrease in tutor-song preference did not appear to be related to an impact in behavioural motivation or a reduced ability to discriminate auditory information, as lesioned animals retained the capacity to discriminate calls (Gobes and Bolhuis 2007). These findings suggest that NCM circuitry, or processing at the level of this auditory area, may be necessary for the representation of tutor-song memories.

Based on the data discussed above, NCM is a likely candidate site for song-memory formation. Little evidence exists for a significant sexual dimorphism in the anatomical and functional organization in the NCM of developing and adult songbirds, and the dimorphisms described to date are far less pronounced than those observed in the highly

sexually-dimorphic song-control system (Bailey and Wade 2003, 2005; Pinaud *et al* 2006; but see Terpstra *et al* 2004, 2006). If this hypothesis proves to be correct, the similarities between the male and female NCM may explain why song discrimination, which requires the formation of auditory memories, is possible for either sex. Both males and females also show robust electrophysiological and IEG responses to conspecific songs in NCM and, under normal housing conditions, the frequency tuning width of responses to tone stimuli does not show a sex difference in NCM for either zebra finches or canaries (Terleph *et al* 2007).

8. Concluding remarks

The body of data described above shows that song stimulation triggers vigorous activity in NCM; this activity is selective to conspecific auditory stimuli and results in long-lasting, experience-dependent plasticity that may promote memory formation required for key behaviours in songbirds including vocal learning for males, preference learning for females, and auditory discrimination. These long-lasting modifications presumably involve the engagement of molecular cascades that are associated with electrophysiological activity, and underlie experience-dependent anatomical and functional changes in NCM circuitry (Clayton 2000; Mello *et al* 2004; Mello and Pinaud 2006). A few molecules that participate in this cascade are currently known and involve four transcription factors (Mello *et al* 1992; Nastiuk *et al* 1994; Velho *et al* 2005) and two signalling molecules (Cheng and Clayton 2004; Huesmann and Clayton 2006). Recent experiments involving large-scale quantitative proteomics screening strategies have uncovered multiple signaling pathways that are activated in NCM as a result of auditory experience (Pinaud *et al* 2008). Future studies will be directed at fully characterizing the molecular cascades that mediate experience-dependent plasticity events in NCM and investigating how they are dynamically regulated. Finally, efforts will also be focused at establishing the precise roles that plasticity-related molecules play in modifying the physiology of single cells and neuronal ensembles in NCM in the process of generating adaptive neural responses that guide behavior.

In summary, NCM does not appear to play a minor role in relaying auditory information in the ascending auditory pathway, but rather may play a significant role in higher order network properties that guide the behaviors that rely on auditory information.

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