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HOW SOCIAL EXPERIENCE SHAPES SONG REPRESENTATION IN THE BRAIN OF STARLINGS

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ABSTRACT

Birdsong, like speech, is a learned behaviour whose critical function is to communicate with others and whose development critically depends on social influences. Song learning is a complex phenomenon that involves not only the development of species-specific vocalisations, but also the development of the ability to organise these vocalisations and to use them in an appropriate context. Although the fact that interactions with adult experienced models are essential for song production to develop properly has been well established, far less is known about song perception and processing. The fact that songbirds learn to vocalise and to use their vocalisations selectively through interactions with adults questions whether such interactions are also required for songbirds to perceive and process their vocalisations selectively and whether social interactions may shape song perception and processing as they shape song production. In order to address these questions, our team uses an original neuroethological approach to study the neural bases of song behaviour in a highly social songbird species: the European starlings. We provide here a synthesis of the results we have obtained using this approach over the last decade. Our results show that direct social experience with adult experienced models not only shapes song behaviour but also shapes these songbirds' brains and their ability to perceive and to process acoustic signals whose communicative value, as well as their acoustic structure, have to be learned.

Keywords: vocal learning; communication; social interactions; sensory processing; brain development; experience; plasticity.

1. INTRODUCTION

Birdsong, like speech, is a learned behaviour whose critical function is to communicate with others and whose development critically depends on social influences (e.g. Baptista and Petrinovich, 1984; Doupe and Kuhl, 1999; Goldstein et al., 2003; Beecher and Burt, 2004). Song behaviour can easily be recorded and measured, quantitatively as well as qualitatively, and it is controlled by a highly-evolved and well-characterized network of interconnected brain regions (e.g. Nottebohm et al., 1976; Wild, 1997). Songbirds thus provide researchers with a unique opportunity to study the neural bases of vocal learning directly in relation to its communicative and social aspects.

Song learning is often described as a two-step sensory-motor process through which a young bird (i) memorizes the song of an adult model during a more or less restricted period of time early in life and (ii) develops its own species-specific song by comparing, through auditory feedback, its vocal production to the internal representation of the song to which it was exposed (thus using it as a template; e.g. Brainard and Doupe, 2002; Konishi, 1985, 1965). This somewhat simplified description highlights the importance of auditory experience and especially of the sensory input provided by species-specific signals produced by a to-be-copied model as well as by its own vocalisations. However, song learning is not under the unique influence of acoustic cues. Zebra finches, which are the most widely studied songbirds, for example need to see or to physically interact with their tutor in order to copy it (Adret, 2004; Eales, 1989; Slater et al., 1988). Social interactions thus appear to be at least as important as mere sensory exposure to species-specific acoustic signals for song learning and copying to

occur. This is strikingly similar to what happens with human infants who show phonetic learning from live but not pre-recorded exposure to foreign language (Kuhl et al., 2003).

Moreover, song learning is a complex phenomenon that involves not only the development of species-specific vocalisations but also the development of the ability to organise these vocalisations and to use them in an appropriate context. For this ability to develop, interactions with adult experienced models are once again essential. Indeed, adults not only provide acoustic models to copy but also provide feedback – that does not have to be auditory – that helps young to produce and to use vocal signals adequately. Thus, male cowbirds will for example crystallise those songs that elicit positive visual (non-vocal) displays from female cowbirds (who do not sing; West and King, 1988). Similarly in human infants, the phonological features of babbling are sensitive to non-imitative social stimulation (Goldstein and Schwade, 2008; Goldstein et al., 2003). Both songbirds and human infants therefore use social feedback to facilitate vocal learning.

The fact that songbirds learn to use their vocalisations selectively through interactions with adult experienced models questions whether such interactions are also required for them to perceive and process their vocalisations selectively and whether social interactions may shape song perception and processing as they shape song production (and as they shape infants' perception of speech in humans; e.g. Kuhl et al., 2001). In order to address these questions, our team developed an original neuroethological approach to study the neural bases of song behaviour in a highly social songbird species: the European starlings. We provide here a synthesis of the results we obtained using this approach over the last decade. All these results have already been

published. They show that direct social experience with adult experienced models (independently of auditory experience with adult song) not only shapes song behaviour but also shapes these songbirds' brains and their ability to perceive and process acoustic signals whose communicative value, as well as their acoustic structure, have to be learned. Of course, like song learning is not under the unique influence of acoustic cues, song perception and processing are not under the unique influence of social experience (e.g. see Woolley (2012) for a review including the influence of early auditory experience). The work of Gentner and his colleagues has for example shown, using starlings trained operantly to recognize songs, that song representation by starlings' forebrain neurons is plastic and can be modified by instrumental learning (e.g. Gentner and Margoliash, 2003; Jeanne et al., 2011; Thompson and Gentner, 2010). However, although the facts that social experience influences song learning and that song learning influences song representation have been well established, the influence of social experience on song perception and processing has been largely overlooked. This is why we decided to focus here on this question.

2. THE EUROPEAN STARLING SONG: A PLASTIC BEHAVIOUR UNDER STRONG SOCIAL INFLUENCES

Starlings are highly social songbirds that breed in colonies of 3-15 nests, forage in flocks of 10-500 birds and sleep in night roosts that can contain up to 3 million birds (Feare, 1984; Hausberger, 1997). In all these contexts, starlings interact through a sophisticated and plastic song behaviour that has been well described (e.g. Eens et al., 1989; Hausberger, 1997). Observations in the field of hundreds of starlings have led to the description of three classes of songs that allow different levels of recognition

(Hausberger, 1997) (Figure 1). Classes I and II are discontinuous, loud, whistled songs that are used in long-distance communication. They are often involved in vocal interactions, that is bouts during which at least two starlings respond to each other using alternate vocalisations (like, for example, in song matching). Class-I whistles are common to all male starlings and thus allow population (through dialects) and species recognition. In the field, class-I whistles are used in long-distance vocal interactions between males – especially paired males during the breeding season (Henry et al., 1994) – or for recognition and tolerance between males of the same population (through dialects) within the exceptionally dense and noisy context of night roosts (Hausberger et al., 2008). By contrast, they are rarely produced in captivity (Henry, 1998). Class-II whistles are emitted by captive as well as free-living starlings (males and females) but, whereas each starling of a given colony appears to have (or to use) a unique repertoire of class-II songs in the wild (Adret-Hausberger et al., 1990), captive starlings can share some class-II whistles with same-sex close social partners. This song sharing reflects the social organisation of a captive group: starlings that spend more time close to each other share more whistles, and changes in group composition induce changes in class-II whistle repertoires, even by adult starlings (Hausberger et al., 1995). Finally, class-III song, also called warbling, is a continuous, soft song that is used in short-distance communication, especially between males and females, and that does not elicit vocal interactions. It is produced by both males and females, in long, highly organised sequences that contain highly individual motifs¹ at the beginning of a sequence and species-specific motifs (clicks and high-pitched trills) at the end of a sequence (Adret-

¹ A motif is a fixed, repeatable combination of notes.

Hausberger and Jenkins, 1988; Eens et al., 1989). Like class-II whistles, individual-specific class-III motifs (also called variable motifs by some authors; e.g. Eens et al., 1989) can be shared in captivity by a few starlings that are close social partners.

In addition to having different acoustic structures, starling song classes thus appear to have clear and distinct functions: individual recognition for class-II whistles and individual class-III motifs in the first part of warbling sequences; population and species-specific recognition for class-I whistles; species-specific recognition for species-specific motifs (clicks and high-pitched trills) in the last part of warbling sequences. Moreover, the production of these different song classes not only depends on the immediate context (breeding/non-breeding, captivity/wild, group size; Adret-Hausberger, 1982) but also depends strongly on the early experience of individuals (Figure 1). Vocal learning experiments have shown that hand-raised starlings kept in complete isolation do not develop such clear-cut song classes (e.g. Adret-Hausberger, 1989; Chaiken et al., 1993). Moreover, hand-raised starlings whose experience with adult models is restricted fail to develop all song classes fully, even when they can hear adult songs. Thus, pairs of naive starlings that can hear vocal interactions between young starlings and adult models through loudspeakers for example fail to produce class-II whistles and to crystallise their song (Poirier et al., 2004). As a rule, restricted experience with adult models almost always leads to the production of atypical warbling sequences that lack species-specific motifs (clicks and trills) at the end of a sequence, either because these motifs are missing or because they are found at an unusual place in the sequence. This also leads to a high degree of song sharing that drastically lowers song individuation (Bertin et al., 2007; Poirier et al., 2004). Thus the production of

starling song classes appears to depend on early acoustic as well as early social experience.

The fact that starlings that can hear adult songs (or even vocal interactions between adult and young starlings) fail to develop and produce all classes of starling song shows that mere vocal/acoustic interactions are not sufficient for starlings to develop fully all their functional classes of songs. This indicates that these song classes can be produced correctly only if they are learned/acquired in a context involving direct social contacts with adult experienced models, and questions whether socially-deprived starlings are still able to perceive and recognize these songs and the neural correlates of experience-induced vocal deficits. In order to address these questions, we need to know first where in starlings' brains song classes are processed.

3. SONG REPRESENTATION IN ADULT WILD-CAUGHT STARLINGS' BRAINS

Songbirds possess a highly-evolved network of interconnected brain regions that control vocal perception, production and learning (e.g. Nottebohm et al., 1976; Zeigler and Marler, 2004) (Figure 2). While nuclei involved in song production have been well characterized (e.g. McCasland, 1987), comparatively less is known about areas involved in song perception, discrimination and recognition (review in Theunissen and Shaevitz, 2006). Recently however, the caudal telencephalon has emerged as a plausible site for sensory representation of birdsong. The caudal telencephalon contains the thalamo-recipient Field L2, which is comparable to the thalamo-recipient layer IV in the mammalian auditory cortex, and two of its targets, the caudo-medial nidopallium (NCM) and the caudo-medial mesopallium (CMM), which can be compared to the supragranular cortical layers (Terleph et al., 2006). Our studies focused on the Field L

and on the NCM.

Field L is a putative unisensory, auditory area that is involved in the processing of complex sounds and that is analogous (or even homologous; Jarvis et al., 2005) to mammals' primary auditory cortex (Capsius and Leppelsack, 1999; Cousillas et al., 2005; Fortune and Margoliash, 1992; Leppelsack and Vogt, 1976; Leppelsack, 1978; Muller and Leppelsack, 1985; Sen et al., 2001). Whereas it is considered as an area that is mainly involved in processing the basic, physical properties of acoustic signals, one of its targets, the NCM, is thought to be involved in processing the biological relevance and value of these signals.

NCM auditory responses have been shown to be the strongest to conspecific songs, followed by heterospecific songs and non-song acoustic signals, and they are known to show rapid and long-lasting habituation effects that are song-specific (Chew et al., 1996, 1995; Mello and Clayton, 1994; Mello et al., 1995, 1992; Stripling et al., 2001, 1997). In addition to being selective for conspecific songs, NCM neurons exhibit experience-dependent plasticity tied to associative learning (Thompson and Gentner, 2010), and they are required for the formation of auditory memories (Bolhuis and Gahr, 2006; London and Clayton, 2008; Mello et al., 2004; Phan et al., 2006; Pinaud and Terleph, 2008; Terpstra et al., 2004). Moreover, the immediate early gene ZENK² response to a social stimulus has been observed to be proportional to the subject's preference for this stimulus: for example NCM of female European starlings that prefer long-bout male songs to short-bout male songs appears to show higher expression of ZENK in response to long-bout than to short-bout songs, independently of the total amount of song that the

² ZENK is the acronym (zif268, egr-1, NGFIA, and krox-24) of an immediate early gene whose expression is used as a marker of neuronal activity.

females heard (Gentner et al., 2001).

In order to investigate if and how Field L and NCM process song classes that have different functions and social values, we used systematic multi- and single-unit extracellular recordings of neuronal activity in response to starling song classes (see George et al., 2003) (Figure 2). The stimuli used to test neuronal responses were unfamiliar, familiar and the subject's own songs from the 3 classes of starling song (see above) and artificial non-specific sounds. These stimuli were randomly ordered so that one class of stimuli did not always come before or after the same other class. By systematically recording responses to these stimuli throughout the Field L or NCM of wild-caught adult male starlings that were awake and restrained, we could quantify and qualify neuronal responses by calculating the proportion of responsive sites that responded to each stimulus or to each class of stimuli and the magnitude of their response. Using a backward correlation method (Richard et al., 1995), we could also determine the acoustic features of the stimuli the most likely to induce a response.

Within Field L, mapping of the neuronal activity elicited by all the stimuli allowed us to confirm the existence of a tonotopic organization where ventral regions responded to lower frequencies than dorsal regions (Cousillas et al., 2005, 2004; Leppelsack and Vogt, 1976). Moreover, Field L neurons appear to respond to precise acoustic features – such as frequency modulation or inflection point – that are characteristic of starling species-specific songs (Hausberger et al., 2000) (Figure 3), and different sub-areas with distinct neuronal preferences can be observed (Cousillas et al., 2005). Field L neurons thus appear as feature detectors that respond to key acoustic features of starlings' species-specific songs and that are functionally and spatially

organised throughout this area (Hausberger and Cousillas, 1996). By processing key acoustic features of some song classes, these neurons may contribute to filter song categories according to these features before sending the information to NCM.

Within NCM, the proportion of responsive sites that responded to each stimulus was the highest for individual-specific songs (class-II whistles and individual class-III motifs). Although all stimuli within each stimulus class were not equally effective at driving neuronal responses, proportions of responsive sites appeared to increase from non-specific to species-specific stimuli and again from species-specific to individual-specific stimuli. This trend was confirmed by the responses to each stimulus class: both the proportions of responsive sites and the magnitude of the responses (as measured by Z scores; see Theunissen and Doupe, 1998) significantly increased from non-specific to class-I stimuli, from class-I to class-II stimuli and again from class-II to individual class-III stimuli. The fact that starlings' NCM reveals differential responses to behaviourally-defined song classes that have different functions and social values suggests that NCM may play a role in sorting out natural communication signals into functional categories of sounds (that is categories grouping sounds according to their function rather than their acoustic structure) (George et al., 2008) (Figure 4).

Our electrophysiological recordings in the Field L and NCM of wild-caught adult male starlings show that, whereas Field L appears to process key acoustic features of natural songs, NCM appears to process functional categories of songs (that is categories of songs having the same function – e.g. individual recognition). Acoustic features may thus be more important for Field L whereas songs' functional/social value may prevail in NCM. Although both types of processing may be equally important for song

perception and recognition, we could hypothesise that early acoustic experience may be more important for the development of Field L and early social experience for the development of NCM. Since both types of experience are crucial for starlings to develop fully all their classes of songs, we investigated song-evoked activity in both Field L and NCM when young starlings' access to experienced adult models was restricted.

4. HOW SOCIAL EXPERIENCE SHAPES SONG REPRESENTATION IN STARLINGS' BRAINS

In order to assess how early social experience influences song processing in starlings' brains, we disturbed song development by restricting interactions with adult experienced starlings from a few days after hatching until full adulthood. As we mentioned earlier, the fact that starlings whose access to adults during development is restricted fail to develop fully all typical song classes raises the question of whether these birds are still able to perceive and process these songs.

In a first experiment, young starlings were taken from their nests (when 4-8 days old), hand-reared until they reached independence (6-8 weeks old) and then divided into three groups. One group was kept in three indoor aviaries, all placed in the same room. Each aviary contained 3-4 young starlings and one wild-caught adult male starling. The two other groups were placed in individual cages containing either a single young starling or a pair of young starlings. Each cage was placed in a soundproof chamber that was acoustically connected to the aviaries through loudspeakers so that all birds could hear the vocal interactions coming from these aviaries. After the birds had been kept under these conditions for 2 years (that is until full adulthood), we recorded first their

vocalisations and then their Field L's song-evoked activity.

As expected, social experience with adults appeared to induce differences in the song structure of starlings, independently of their auditory experience with adult songs (Poirier et al., 2004). Analysis of the experimental birds' song behaviour showed that, whereas birds kept in aviaries with an adult model developed a fairly typical song presenting the typical organization of starling song in captivity, our subjects raised in pairs or alone in a soundproof chamber acoustically connected to the aviaries all developed songs with strong deficits. Subjects raised alone in a soundproof chamber produced class-II whistles and warbling, but their repertoires were relatively small and their warbling sequences were abnormally short. However, these birds copied a fair amount of the adult songs that they could hear through the loudspeakers that were connected to the aviaries. By contrast, starlings raised in pairs of naive subjects did not copy any element of the adult songs but copied each other largely. Their songs contained no class-II whistles and appeared to remain plastic since no stabilization of their repertoires was observed.

These song production deficits were reflected by a deficit in Field L's selectivity towards key acoustic features of starling songs (Cousillas et al., 2006). Measuring the proportion of non-specialized neuronal sites (defined as sites that responded to all stimuli) showed that starlings raised alone or in pairs in a soundproof chamber all had a higher proportion of non-specialized neuronal sites than did starlings raised in aviaries with an adult model. Moreover, these subjects did not differ from starlings that had never experienced adult starlings' songs (Figure 5). Although Field L is a putatively unisensory auditory area involved in the processing of acoustic physical features of

species-specific songs, these results show that depriving starlings of direct social contacts with adults may have as much impact on the development of this primary sensory area as depriving them of sensory (auditory) experience of adult songs (Cousillas et al., 2006, 2004).

As Field L is the main input to NCM and given that, in a hierarchical scheme of sensory processing, plasticity at the primary sensory areas level should influence higher-order regions, we expected NCM response properties to the different functional classes of starling song to be determined, or at least influenced, by starlings' early experience.

In a follow-up experiment (George et al., 2010), we once again interfered with song development by keeping nest-caught starlings away from direct contacts with adults. After being taken from their nests (when 5-16 days old) and hand-reared until they reached independence (6 weeks old), young starlings were placed all together in an outdoor aviary where they could hear and see wild birds, including starlings. After 4 months in this outdoor aviary, that is before full song began to emerge, they were moved into an indoor aviary where they had no contacts with other birds until full adulthood (2 years old). This protocol ensured that, although these birds had a chance to hear and see adult starlings during their first months of life, they never had a chance to interact with them and thus to use their song in a species-typical communication network. After these starlings had been kept under these conditions for 2 years (that is until full adulthood), we recorded first their vocalisations and then their NCM's song-evoked activity.

As expected, analysis of these experimental starlings' vocal behaviour revealed

that these birds presented deficits typical of socially-deprived starlings (George et al., 2010). All these experimental starlings produced class-II whistles and class-III songs whose elementary acoustic structure was similar to that of adult wild-caught starlings (as assessed by visual inspection of the sonograms by two experienced and one naive observers; see George et al. (2010) for details), but they produced short desultory warbling sequences interspersed with class-II whistles. However, these songs clearly differed from those of starlings that had never experienced adult songs. This shows that hearing adult songs during their first months of life in an outdoor aviary did impact these experimental starlings' vocal behaviour. However, although it was sufficient for them to acquire the elementary acoustic structure of starlings' song classes, it was insufficient for them to organise these song classes and to thus produce species-typical song sequences.

At the neuronal level, although NCM responses significantly increased from non-specific to class-I stimuli and again from class-I to class-II and individual class-III stimuli – like in wild-caught adult male starlings – no differences could be observed between responses to class-II and individual class-III stimuli. These stimuli correspond to the song classes that precisely were not differentiated in the experimental subjects' vocalisations. This contrasts with our observations of the significant increase of wild-caught adult male starlings' responses between class-II and individual class-III songs (George et al., 2008) (Figure 4).

This study shows that starlings that never had a chance to interact with adult models (although they could hear and see some early in life) failed to differentiate starlings' typical functional song classes not only in terms of song production but also in

terms of song perception and processing. Moreover, as these experimental starlings did not show any acoustic (or phonological) deficits in their vocalisations (as assessed by visual inspection of the sonograms by two experienced and one naive observers; see George et al. (2010) for details), the observed deficits in both song organisation (or syntax) and neural responses were likely to be linked to a failure to acquire songs' functions. Thus the functional/social value of acoustic signals acquired through direct contacts with experienced adult models could be as important as their acoustic structure.

5. CONCLUSION

Our studies of song processing in starlings' brains show that Field L and NCM are two brain areas that play a key role in processing starlings' functional song classes. Whereas Field L appears mainly to process key acoustic features characteristic of species-specific songs, NCM appears to process the three classes of starlings' songs differentially and thus to play a major role in categorising and recognising these functional classes of songs (i.e. classes of songs having the same function). Moreover, in Field L as in NCM, these processing abilities appear to be highly plastic and to depend strongly on early experience. Depriving starlings of direct social contacts with adults as well as depriving them of sensory experience of adult songs thus leads to an abnormal functional organisation in Field L, with non-specialized neurons that appear to be unable to process the characteristic acoustic features of species-specific songs. At the NCM level, the fact that early deprivation of direct social contacts with adults leads to undifferentiated responses to individual-specific songs suggests a disability to recognise conspecific songs. Early deprivation of direct social contacts with adult models therefore not only impacts vocal production – as already shown by a number of studies

of several songbird species (e.g. Beecher and Burt, 2004) – but also impairs song perception and processing: sensory-deprived birds seem to be unable to “hear” songs properly, and adult-deprived birds seem to be similarly unable to “hear” and to recognise these songs. This means that the functional/social value of songs, as well as their acoustic structure, has to be learned.

This questions how this information is learned or, in other words, how an individual acquires the “signification” (or informational content) of its species-specific vocalisations. In order to acquire this “signification”, individuals have to associate acoustic information with social information and the acoustic communication channel appears insufficient for this to happen. Multimodal, attention and reinforcing factors are likely to be also at play in this learning process (Snowdon and Hausberger, 1997). Recently, we have shown that auditory responses of starlings' Field L neurons are modulated by visual cues and that this modulation depends on familiarity with the acoustic and visual cues (George et al., 2011). This is reminiscent of what happens with speech perception that has been shown to be influenced by visual information to the extent that it can produce auditory illusions (e.g. (McGurk and MacDonald, 1976; Sumbly and Pollack, 1954)). Moreover, we have shown that this property of Field L auditory-responsive neurons is shaped by experience with adults: adult-deprived starlings show as much modulation by visual cues as do wild-caught starlings, but familiarity does not influence this modulation (George et al., 2012). These studies of multisensory interactions in the starlings' brains again show fascinating parallels with human studies. In humans, the integration of auditory and visual cues for example provide powerful cues for the development of early social skills (e.g. Coulon et al.,

2011; Guellai and Streri, 2011). Visual information thus can influence the perception of acoustic signals involved in social interactions and could play a key role in the perception of these interactions and in the development of this perception. Through the visual modality, attention processes and social reinforcement could for example contribute to the consolidation of the neural networks that underlie the ability to process learned vocal signals used to communicate with others. Now, much remains to be done to characterize fully the exact nature of social interactions and to understand fully how they shape communication skills and the neural substrates of these skills. One promising line of research, in our opinion, is the crucial role of social attention defined as selective attention to social information (i.e. information that is exchanged as part of social interactions), which may reveal to be ubiquitously important for all species that have evolved the ability to learn their vocalisations, including humans. In humans, social attention is conveyed primarily by gaze, which has been the focus of a large body of studies in recent years (reviewed in Birmingham and Kingstone, 2009a, 2009b; Nummenmaa and Calder, 2009). In songbirds, future studies will have to determine how precisely social attention may be conveyed. Such studies will play a critical role in determining the mechanisms by which social interactions and vocal learning interact, in both human and non-human animals.

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FIGURE CAPTIONS

Figure 1: Structure, function and context of emission of starlings' song classes. See explanation in the text (2. The European starling song: a plastic behaviour under strong social influences).

Figure 2: (A) Schematic representation of a sagittal view of a songbird's brain showing some of the nuclei that are involved in song perception (in grey) and production (in black). Structure names are based on decisions of the Avian Brain Nomenclature Forum as reported in (Reiner et al., 2004). An: nucleus angularis; DM: dorsal medial nucleus of the intercollicular complex; HVC: used as a proper name; Mld: dorsal part of the lateral mesencephalic nucleus; NCM: caudal medial nidopallium; NXIIIts: tracheosyringeal part of the hypoglossal nucleus; Ov: nucleus ovoidalis; RA: robust nucleus of the arcopallium. (B) Dorsal view of the brain. Black dot: penetration site of an electrode. (C) Sagittal view of the brain. Black dot: recording site.

Figure 3: Neuronal preferences in Field L of adult male wild-caught starlings evidenced by backward correlations (A-F). The results of the backward correlations are expressed as sonograms (frequency as a function of time) in relation to frequencies (from 0 to 6 kHz, vertical axis) and time (from –128 to 0 ms before excitation, horizontal axis). (A) Inflection point: a short response occurs whenever the signal contains a modulation around a given frequency. (B) Inflection: the response follows an inflection well defined in both time and frequency. (C) Frequency modulation: the neurons respond to a constant frequency modulation. (D) Double voice: the neurons respond to two signals occurring either simultaneously or separately. (E) Pure tone: the neurons are activated only when the stimulus is a pure tone and are inhibited by any modulated signal in the

same bandwidth. (F) On/off: on or off responses for any frequency. Right panel: Examples of species-specific songs containing the acoustic features for which Field L neurons are selective. IT: Inflection theme; ST Simple theme; HT: Harmonic theme; RT: Rhythmic theme (Hausberger, 1997).

Figure 4: Mean (+SEM) percentage of responsive sites (top graphs) and Z scores (bottom graphs) obtained for each class of stimuli in the secondary auditory area (NCM) of wild-caught (n=6) and experimental (n=10) starlings. Insets above the right graphs indicate the subjects' experience (see text). Small black dots: experimental starlings, large black dots: wild adult starlings. *: post-hoc tests, $p < 0.05$.

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Figure 5: Mean (+SE) proportions of non-specialized neuronal sites (i.e. that responded to all stimuli) in the primary auditory area (Field L) of experimental and wild-caught starlings (see text). Insets above the graph indicate the subjects' experience. Small black dots: starlings whose experience has been manipulated, large black dots: wild adult starlings. *: Mann-Whitney U test, $p < 0.05$. Examples of non-specialized (on the left) and specialized (on the right) responses are shown on each side of the graph. (A) Raster plots of the neuronal activity recorded during ten repetitions of the stimuli. (B) Peri-stimulus time histograms (PSTHs) of the action potentials (that is, number of action potentials per 2-msec time bin) corresponding to the raster plots presented above. (C) Spectrograms and oscillograms of the acoustic stimuli. Traces (B) and (C) are time aligned.

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Figure 1

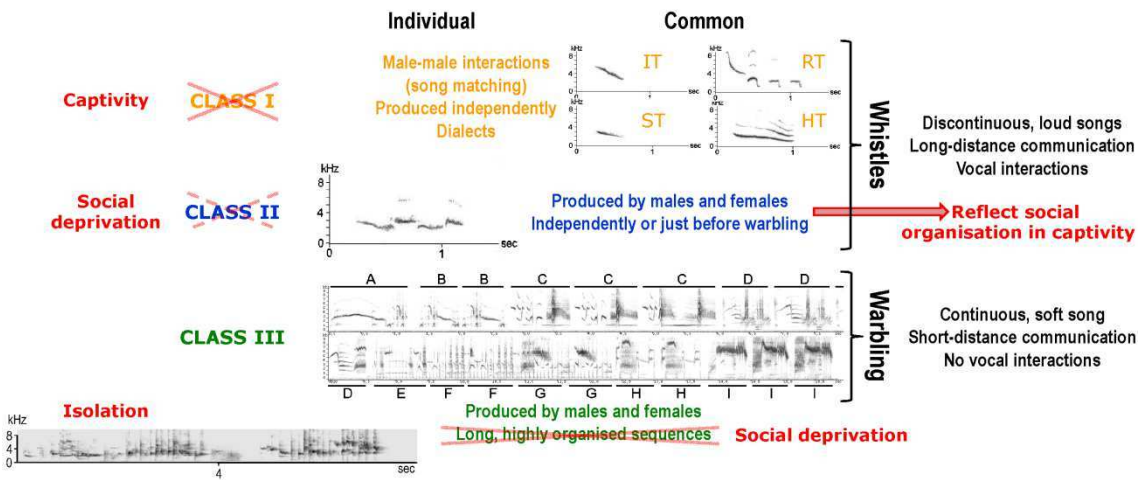


Figure 2

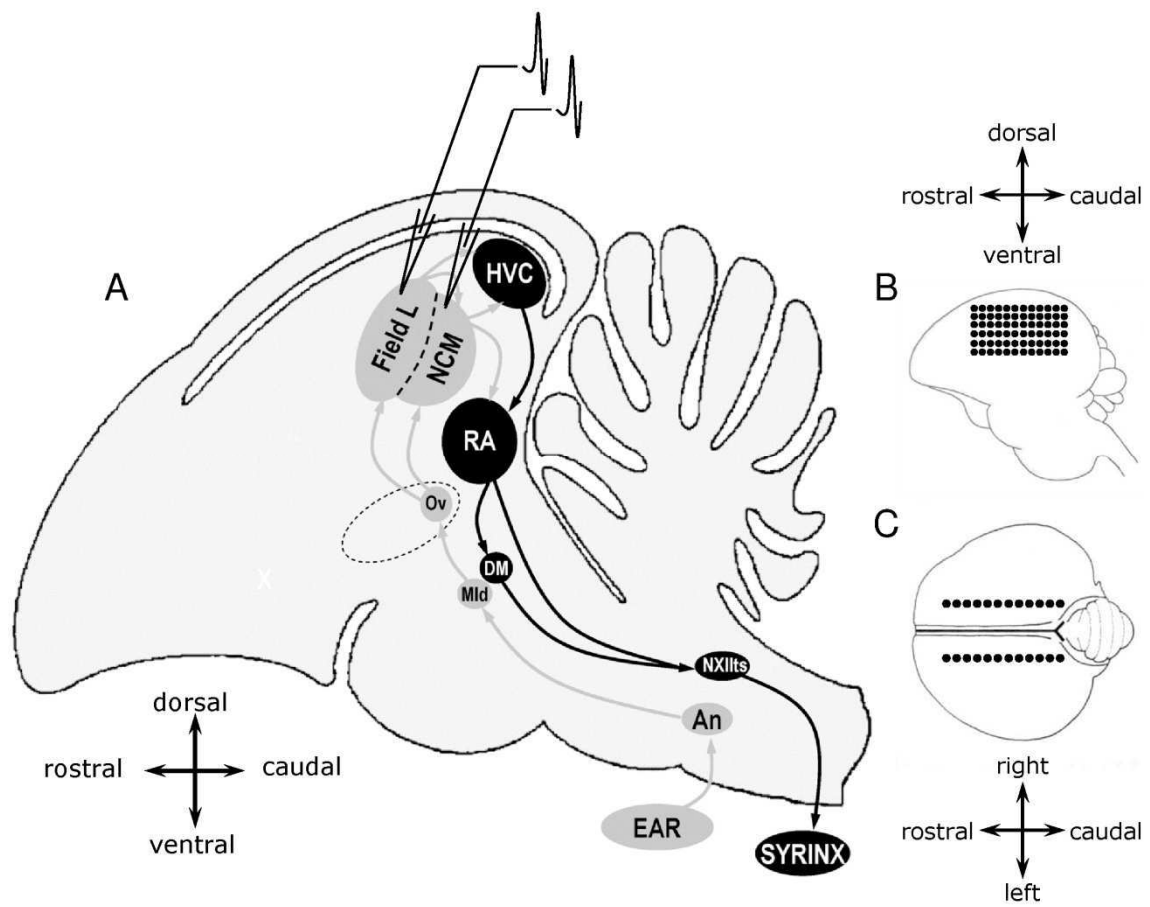


Figure 3

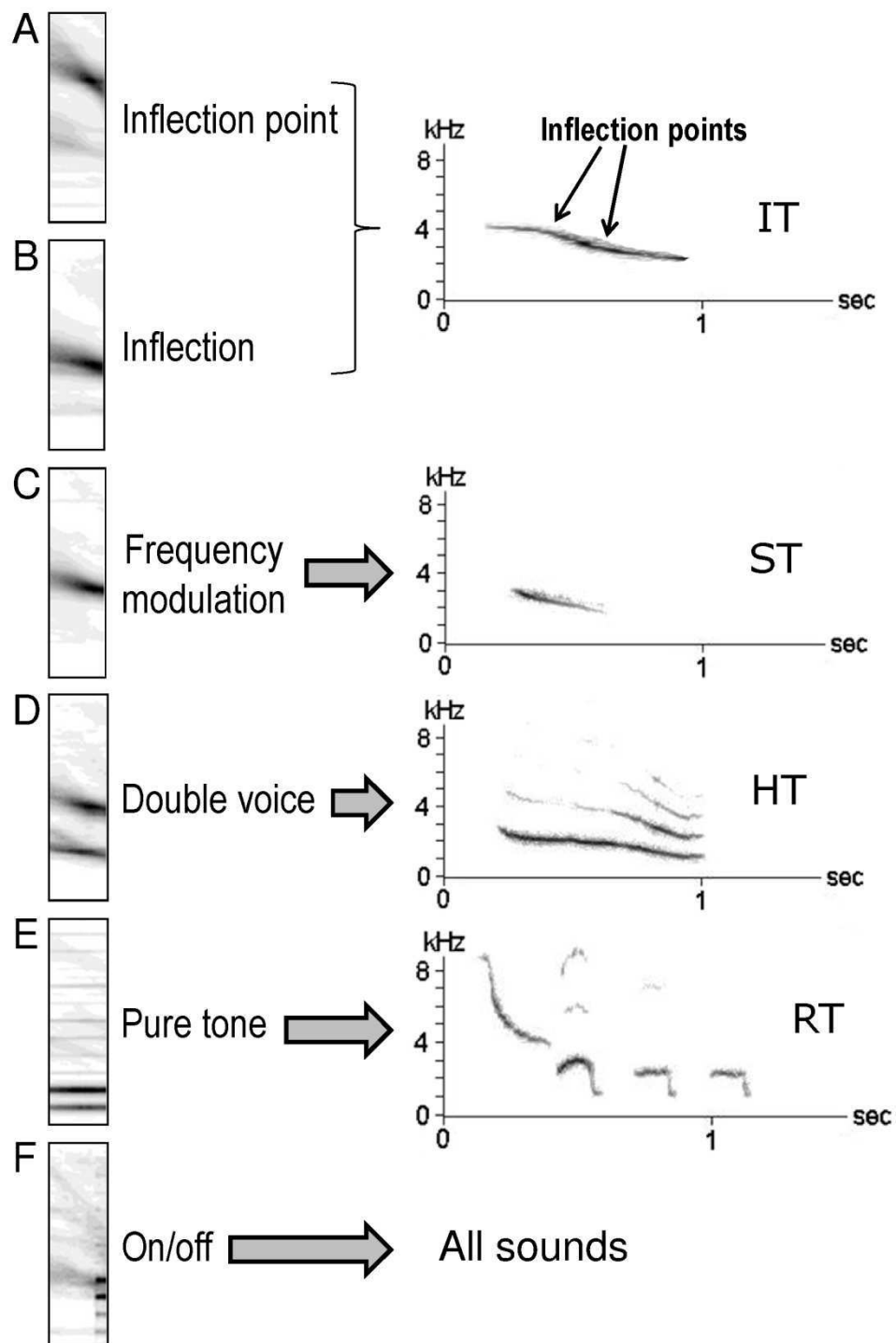


Figure 4

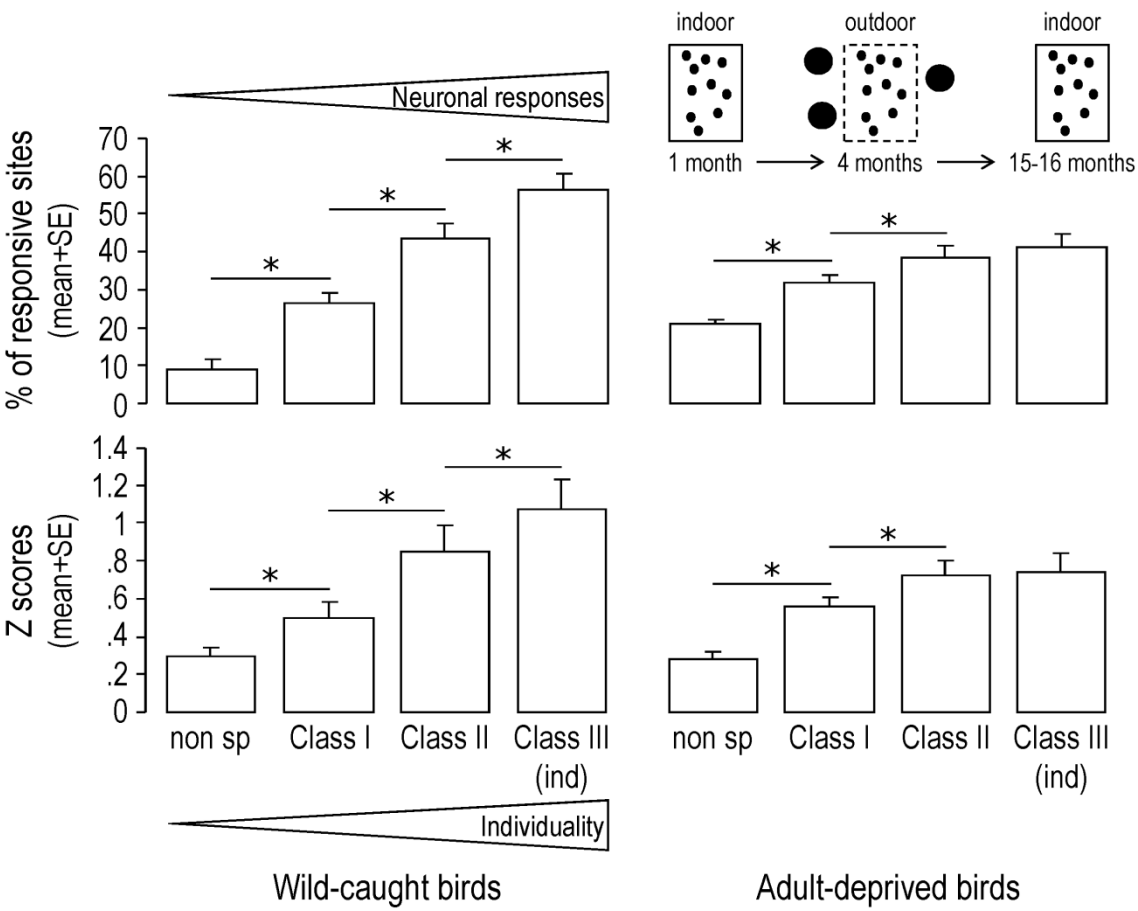


Figure 5

