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# Vocal learning beyond imitation: mechanisms of adaptive vocal development in songbirds and human infants

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Studies of vocal learning in songbirds typically focus on the acquisition of sensory templates for song imitation and on the consequent process of matching song production to templates. However, functional vocal development also requires the capacity to adaptively diverge from sensory templates, and to flexibly assemble vocal units. Examples of adaptive divergence include the corrective imitation of abnormal songs, and the decreased tendency to copy over-abundant syllables. Such frequency-dependent effects might mirror tradeoffs between the assimilation of group identity (culture) while establishing individual and flexibly expressive songs. Intriguingly, although the requirements for vocal plasticity vary across songbirds, and more so between birdsong and language, the capacity to flexibly assemble vocal sounds develops in a similar, stepwise manner across species. Therefore, universal features of vocal learning go well beyond the capacity to imitate.

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Vocal imitation is among the most mysterious forms of developmental learning. In humans vocal play (babbling) begins shortly after birth, and it develops gradually over the first year of life [1]. Early babbling vocalizations are composed of simple and unstructured sounds, but within several months one can identify vocal elements that are clearly derived from the native language, and those structured sounds then further evolve into words [2]. However, little is known about the developmental trajectories leading from primitive vocalizations into specific words, and about the brain mechanisms involved in developmental vocal learning in humans. Much more is known about vocal development in songbirds. Song development goes through similar stages to those of infant babbling [3]. Juvenile songbirds can copy song syllables of adult birds ('tutors') with striking accuracy [4,5]. It is now possible to track trajectories of vocal changes leading to imitation continuously over development [6••], and to identify the emergence of syllable types and the differentiation of prototype syllables [6••,7]. Song learning and production is controlled by a set of distinct brain nuclei collectively called 'the song-system' [8,9••]. The role of specific song nuclei in song production and learning is relatively well understood, including mechanisms of producing rhythm [10–12], spectral features [13,14], and gestures [15]. Patterns of gene expressions in song nuclei [16–18] were identified and associated with the song learning process. Even the role of transitory behavioral states, such as sleep, on song learning can be examined at behavioral and brain levels [19–21] over development. We understand fairly well the role of reinforcement learning [22••] in correcting vocal errors [23] and in matching the fine temporal structure of the sensory template [24,25]. Of particular interest is how vocal exploration (variability) is actively regulated by specific song nuclei during the natural time course of song learning [26••,27].

However, the success of birdsong neuroscience in discovering mechanisms of vocal imitation detracts attention from the fact that *exact* vocal imitation is not the typical developmental endpoint in songbirds [28] or in human infants [29]. For example, over-regularizations during early speech development are not direct imitations of the caregivers [30,31]. Further, language capacities of infants may surpass that of their parents [31] or otherwise diverge from the spoken language they perceive leading to a rapid language changes across generations [30]. Similar effects were observed in songbirds. When a single juvenile zebra finch is raised together with a single adult bird (tutor) a near-exact match to tutor song typically emerges [28]. However, if instead of one-to-one vocal tutoring, five juvenile males are raised together with a single tutor, some birds will diverge from the tutor song by copying only parts of it [28,32]. Juvenile birds often copy song elements from each other [33,34], or improvise and remix syllables across tutors to create new song types [35,36]. Further, in both songbirds and human infants social feedback can strongly affect vocal development [37]. Overall, imitation per se is only one component of a complex vocal development, and we suggest that song learning can be used for studying vocal learning beyond imitation, as a model for language development.

## Vocal learning capacities beyond imitation

Figure 1 illustrates that vocal learning is an iterative process with a strong inertia, such that vocal changes transform already-established vocal sounds. Quite often, the scope of those vocal changes is highly localized to a specific syllable type [26••]. Vocal changes are subject to strong developmental constraints. For example, HVC is the principal song nucleus that drives song production in adult birds. However, HVC has no apparent role in the production of subsong (babbling) in juvenile birds. Instead, the early subsong is driven by a set of forebrain song nuclei, collectively called the Anterior Forebrain Pathway (AFP) [38]. During song learning, there is a gradual transition of control from AFP, which produces noisy and exploratory song patterns, to HVC, which produces stereotyped song patterns. Song learning takes place within the framework of this brain development [39].

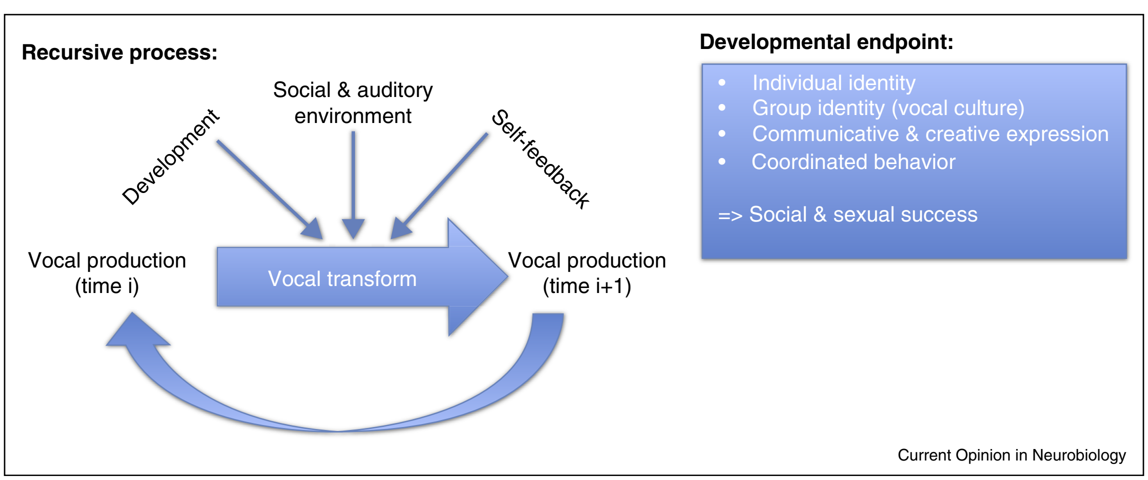
How do those internal constraints and external social and auditory inputs shape vocal changes that eventually add up to an adaptive developmental outcome? Accurate imitation is an important capacity that allows birds to generate songs that attract mates, deter intruders, and carry information about group identity (song dialects) via cultural transmission [40]. But songs also carry information about the individual identity of the bird, and — perhaps most importantly — they should provide information about the qualities of the singing bird. From this functional perspective, the cases where the outcome of song learning is *not* exact imitation are most interesting.

## Range limited and frequency dependent vocal imitation

Spoken language can change remarkably across generations [30], and so does birdsong [41••]. As noted earlier, in one-to-one tutoring setups zebra finches usually imitate their tutor very accurately. But there is an important exception to this rule, which is the biased imitation of 'abnormal' songs [42]. For example, canaries' songs include several back-to-back renditions (trills, rolls & tours) of the same note type (e.g., AAAA, BBB). Training canaries with species-atypical playbacks such as ABCDE... that lack repetition, initially results in imitation of that atypical song. But when the bird approaches sexual maturity (or after an injection of testosterone), the bird abruptly transforms its song into the typical reduplicative AAA, BBB... pattern — which it never heard [43••].

Another example is the imitation of isolates' songs in zebra finches [41••]. Zebra finches raised in complete social and acoustic isolation develop abnormal song, called isolate song. Abnormalities include long and monotonous syllable types, and deviation from the species-typical song syntax, wherein each syllable type normally appears only once (non-reduplicatively) within each song motif. Intriguingly, when juvenile zebra finches imitate isolates' songs they copy them in a biased manner, transforming acoustic features, rhythms and song-syntax to approximate the wild-type song — which they never heard. Similarly, human children can 'regularize' inconsistent input in sign languages [31]. In songbirds, such

**Figure 1**




A scheme of developmental vocal learning. Vocal learning is a slow, iterative developmental process of progressively shaping vocal change that eventually leads to an integration in a complex communication system that endows an animal with individual identity (e.g., a unique song), a group identity (integrated in a vocal culture) and a means for coordinating behavior with other individuals (including affiliation, aggression and courtship behaviors). The capacity to imitate is only one factor that shapes the outcome of vocal learning over development.