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Processing of Communication Sounds: Contributions of Learning, Memory, and Experience

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Abstract

Abundant evidence from both field and lab studies has established that conspecific vocalizations (CVs) are of critical ecological significance for a wide variety of species, including humans, nonhuman primates, rodents, and other mammals and birds. Correspondingly, a number of experiments have demonstrated behavioral processing advantages for CVs, such as in discrimination and memory tasks. Further, a wide range of experiments have described brain regions in many species that appear to be specialized for processing CVs. For example, several neural regions have been described in both mammals and birds wherein greater neural responses are elicited by CVs than by comparison stimuli such as heterospecific vocalizations, nonvocal complex sounds, and artificial stimuli. These observations raise the question of whether these regions reflect domain-specific neural mechanisms dedicated to processing CVs, or alternatively, if these regions reflect domain-general neural mechanisms for representing complex sounds of learned significance. Inasmuch as CVs can be viewed as complex combinations of basic spectrotemporal features, the plausibility of the latter position is supported by a large body of literature describing modulated cortical and subcortical representation of a variety of acoustic features that have been experimentally associated with stimuli of natural behavioral significance (such as food rewards). Herein, we review a relatively small body of existing literature describing the roles of experience, learning, and memory in the emergence of species-typical neural representations of CVs and auditory system plasticity. In both songbirds and mammals, manipulations of auditory experience as well as specific learning paradigms are shown to modulate neural responses evoked by CVs, either in terms of overall firing rate or temporal firing patterns. In some cases, CV-sensitive neural regions gradually acquire representation of non-CV stimuli with which subjects have training and experience. These results parallel literature in humans describing modulation of responses in face-sensitive neural regions through learning and experience. Thus, although many questions remain, the available evidence is consistent with the

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notion that CVs may acquire distinct neural representation through domain-general mechanisms for representing complex auditory objects that are of learned importance to the animal.

1. Introduction: Ecological and behavioral significance of conspecific vocalizations

Intra-species communication occupies an important niche when considering our most basic need: survival. In many species, there are a wide variety of instances in which communication sounds play a role in warning about predators, signaling reproductive circumstances, relaying information about food sources, and locating genetically-similar neighbors. These communication sounds may also signal the emotional state of the caller as interpreted by the listeners, as well as convey other pieces of information to the listener such as the sex or size of the caller based on frequency and vocal tract length (Fitch, 1997). Thus, for most mammals and birds, conspecific vocalizations (CVs) arguably constitute the most ecologically-significant class of sounds (Simmons et al., 2003; Snowdon et al., 1982).

Given the ecological relevance of CVs, it is perhaps not surprising that a number of experiments with humans and other animals have reported advantages for behavioral processing of CVs over heterospecific vocalizations (HVs) and other sounds. For example, non-human primates (Petersen et al., 1984), as well as several bird species (Dooling et al., 1992; Okanoya and Dooling, 1991) are more readily able to discriminate CVs compared to HVs. Moreover, in a set of studies by Petersen and colleagues (Beecher et al., 1979; Petersen et al., 1978, 1984; Zoloth et al., 1979), Japanese macaques more easily learned to discriminate sets of CVs that were divided by a communicatively-relevant dimension (the position of a frequency-inflection peak), rather than by an arbitrary one (initial pitch). Similarly, European starlings are capable of learning to recognize pitch-shifted conspecific songs, but not pitch-shifted piano melodies (Bregman et al., 2012). A mnemonic advantage for CVs has also been reported in two recent studies of auditory short-term memory in humans (Weiss et al., 2012) and non-human primates (Ng et al., 2009).

In view of the salient ecological and behavioral status of CVs, as well as their distinct representation in the brain (Section 2), several investigators have asked whether CVs are “special” (Belin, 2006; Chartrand et al., 2008; Kuhl, 1986; Moore, 2000). Specifically, this question refers to the possibility of “special” or domain-specific neural mechanisms dedicated to processing CVs. These mechanisms might have been selected for, over evolutionary history, because of the advantage they would grant in interacting with the environment. Alternatively, the “special” or distinctive behavioral status and neural processing of CVs might result from extensive exposure to CVs within the lifespan of the individual organism, including learned associations between CVs and other behaviorally-relevant events. According to this view, domain-general mechanisms for representing meaningful acoustic stimuli would gradually augment representation of CVs based on their learned behavioral significance. Although these questions have only recently received experimental attention, in this review, we present evidence from several species that is consistent with the position that the brain flexibly represents CVs and other meaningful sounds according to experience and learned significance. We begin with a summary of

species-typical neural representation of CVs, followed by a brief overview of plasticity in the auditory system, which may enable expanded representation of CVs based on experience and learning.

2. Neural representation of conspecific vocalizations

Consistent with their ecological and behavioral significance, there is abundant evidence for distinctive neural representation of CVs in humans, non-human primates, other mammals, and songbirds. More specifically, brain regions have been identified in a number of species that are selective for CVs in some way, i.e., differential responses are observed for CVs compared to non-CV stimuli, such as HVs, environmental sounds, or artificial sounds. In the survey of literature contained herein, such selectivity is usually assessed in terms of overall neuronal firing rate: some neurons may respond exclusively to CVs, or they may respond to CVs more robustly than other classes of stimuli. Similarly, in neuroimaging studies, greater activation may be observed in response to CVs compared to other classes of sounds. Differential responses to CVs may also be observed in temporal spike patterns, or in the form of asymmetric responses between cerebral hemispheres (see below). Although our understanding of the neural substrates of CVs is far from complete (Romanski and Averbeck, 2009; Wang, 2000), two basic principles have received experimental support in humans and other animals. First, auditory information processing is organized in a hierarchical manner, such that distinctive representation of CVs is more frequently observed in hierarchically-advanced areas. Second, perception of CVs is often associated with asymmetric processing between the cerebral hemispheres.

Many studies in humans and other mammals have shown that auditory processing pathways are organized in a similar fashion to the visual system (Ungerleider and Mishkin, 1982), in that there are at least two major information-processing pathways outside of the primary sensory cortices: one pathway in the dorsal direction specialized for identifying where objects are in space and how to interact with them, and a second pathway in the ventral direction specialized for object identification (Adriani et al., 2003; Kaas and Hackett, 2000; Lomber and Malhotra, 2008; Poremba et al., 2003; Rämä et al., 2004; Rauschecker and Tian, 2000; Romanski et al., 1999b; Wang et al., 1995). A hierarchical organization has been observed along the ventral object-processing pathway in the temporal lobe in humans and non-human primates, such that cells in relatively anterior regions preferentially respond to increasingly complex stimuli, such as CVs over simple, artificial stimuli. Thus, cells in primary sensory cortex tend to respond to specific acoustic features or combinations of acoustic features (Medvedev et al., 2002; Sadagopan and Wang, 2009; Wang, 2007; Wang et al., 2005), such as spectral content and temporal dynamics, whereas hierarchically-advanced areas are more selective for complex auditory objects and sound categories, including CVs (DeWitt and Rauschecker, 2012; Kikuchi et al., 2010; Leaver and Rauschecker, 2010; Miller and Cohen, 2010; Rauschecker et al., 1995; Rauschecker and Scott, 2009). Correspondingly, a number of studies in humans (Belin, 2006; Belin et al., 2000; Belin and Zatorre, 2003; Petkov et al., 2009; Talkington et al., 2012) and monkeys (Kikuchi et al., 2010; Perrodin et al., 2011; Petkov et al., 2008; Poremba et al., 2004) have described regions of the anterior temporal lobe that respond differentially to CVs over control sounds such as HVs, environmental sounds, and simple stimuli. The temporal lobe in

turn sends auditory projections to the prefrontal cortex (PFC; Galaburda and Pandya, 1983; Kaas and Hackett, 2000; Morán et al., 1987; Romanski et al., 1999a), where selectivity for CVs has also been observed (Averbeck and Romanski, 2006; Romanski and Averbeck, 2009; Romanski et al., 2005; Russ et al., 2008a; Wollberg and Sela, 1980). For example, Romanski and Goldman-Rakic (2002) reported that CVs were more effective in driving auditory-responsive neurons in the lateral PFC of monkeys than a wide variety of comparison stimuli including HVs, environmental sounds, and simple stimuli. A neuroimaging study in human subjects similarly found that human speech and nonlinguistic vocalizations elicit greater activation in the lateral PFC than HVs and nonvocal sounds (Fecteau et al., 2005).

Beyond the organization of the two major information processing pathways, hemispheric specialization for processing CVs has been widely reported in humans, and to a lesser degree in non-human primates and other mammals. In humans, left-hemispheric specialization for processing speech and language in humans is well documented (Gazzaniga, 2000; Price et al., 1996). Additional studies have indicated that certain aspects of vocal communication processing in humans are dominated by the left hemisphere, while other functions are dominant in the right hemisphere. Abundant evidence suggests that the left hemisphere is activated preferentially by communication sounds compared to control sounds such as artificial or environmental sounds and HVs (DeWitt and Rauschecker, 2012; Talkington et al., 2012). Additional studies have shown that the left hemisphere may be specialized for processing the fine temporal aspects of speech (Lazard et al., 2012; Zatorre and Belin, 2001). For example, in a study based on detection of brief temporal events, subjects committed fewer errors and responded more rapidly when the stimuli were presented to the left hemisphere (Nicholls et al., 1999). Moreover, electroencephalographic activity recorded during the task was greater at electrodes recorded over the left compared to the right temporal lobe. These results were supported by a subsequent study by Zatorre and Belin (2001), who used positron emission tomography (PET) to examine hemispheric differences in perception of tone sequences that were modulated in terms of temporal or spectral features. Consistent with the results of Nicholls et al. (1999), responses to the temporal features were more lateralized to the left hemisphere. On the other hand, responses to spectral features were more lateralized to the right hemisphere. Additional functions attributed to the right hemisphere include discriminating speaker identity (Belin and Zatorre, 2003; Kriegstein and Giraud, 2004; von Kriegstein et al., 2003), processing spectral information including prosody (Lattner et al., 2005; Lazard et al., 2012; Pell, 2006), and perhaps processing some aspects of the emotional content of vocal communication (Blonder et al., 1991; Kotz et al., 2006).

Studies in non-human primates have also suggested hemispheric specialization for perception of CVs. Heffner and Heffner (1984) first reported that lesions of the left superior temporal gyrus, but not the right, disrupted discrimination of CVs in monkeys. Using PET imaging, Poremba et al. (2004) found significantly greater activation of the left temporal pole when monkeys were exposed to CVs, but not other control stimuli including scrambled CVs, HVs, and environmental stimuli. A follow-up study by Ng (2011) revealed that individual neurons in this area are highly selective, with some responding only to CVs. This outcome is consistent with the findings of Kikuchi et al. (2010), who observed an increasing

degree of selectivity for CVs over HVs and other sounds in the most rostral portions of the left superior temporal gyrus. As in the human literature, Petkov et al. (2008) observed sensitivity to caller identity in the right hemisphere of monkeys using fMRI. Several additional studies have provided neural and/or behavioral evidence for lateralized processing of CVs in chimpanzees (Tagliabata et al., 2009), Japanese macaques (Beecher et al., 1979; Petersen et al., 1978, 1984), sea lions (Böye et al., 2005), and mice (Ehret, 1987; Geissler and Ehret, 2004), raising the possibility that hemispheric specialization may be common in mammals.

The organization of the auditory system in songbirds has many characteristics in common with the mammalian system (Bolhuis and Gahr, 2006; Jarvis, 2004). The mesencephalicus lateralis dorsalis (MLd), which is homologous to the mammalian superior colliculus, integrates inputs from several auditory brainstem nuclei, and in turn provides the main input to the thalamo-cortical pathway. The nucleus ovoidalis (Ov), analogous to the ventral portion of the mammalian medial geniculate body, projects to the forebrain structure field L, which is comparable to mammalian primary auditory cortex. Field L is surrounded by two additional auditory regions, the caudal mesopallium (CM) and the caudal medial nidopallium (NCM), which are thought to be similar to mammalian auditory association cortex. Neurons in the MLd as well as each of the auditory forebrain regions have been shown to respond selectively to CVs, particularly the “auditory association” areas CM and NCM. Moreover, hemispheric specialization has also been observed in the NCM, where CVs evoke larger overall responses in the right hemisphere (e.g., Phan and Vicario, 2010). The songbird brain has additional highly specialized circuitry enabling song production, including the sensory/motor nucleus HVC, which exhibits selectivity for the bird’s own song over other conspecific songs (e.g., Lehongre and Del Negro, 2011; Margoliash, 1986). However, because these structures have fewer characteristics in common with the mammalian brain (Miller and Cohen, 2010), we focus herein on the songbird circuitry involved in auditory perception.

In summary, a number of brain regions in humans, non-human primates, and songbirds have been shown to respond selectively to CVs. Regions with the greatest degree of selectivity for CVs in each of these species are found in auditory association areas. In humans, the left hemisphere is preferentially activated by CVs including speech, whereas the right hemisphere may be specialized for processing spectral details in communication sounds, including prosody as well as vocal identity. Hemispheric asymmetries in CV-sensitive areas have similarly been observed in monkeys, songbirds, and several other species.

3. Plasticity of neural representation of acoustic features in the auditory system

Within the last three decades, a large body of research has accumulated showing that plasticity is an inherent property of the auditory system, both in adulthood and early postnatal development (Dahmen and King, 2007; Parks et al., 2004; Suga and Ma, 2003; Syka and Merzenich, 2003; Weinberger, 2004, 2007). Many studies have demonstrated that manipulating the behavioral significance of a particular acoustic feature, through classical or operant conditioning, often leads to a corresponding change in the neural representation of

that feature. For example, in rats trained to press a bar for water during the presentation of a 6-kHz tone conditioned stimulus (CS), an increase was observed in the relative proportion of the primary auditory cortex preferentially responsive to 6-kHz tones (Rutkowski and Weinberger, 2005). Further, the degree of expanded representation of the CS tone frequency was related to the level of water deprivation in the rats, underscoring the role of behavioral relevance in reshaping the response properties of the auditory cortex. Responses to a number of additional acoustic features are susceptible to learning-dependent plasticity, including sound intensity (Polley et al., 2006), temporal information (Bao et al., 2004; Fritz et al., 2005a; Kilgard and Merzenich, 1998b), and context-dependent facilitation (Kilgard and Merzenich, 2002). While it should be acknowledged that not all training paradigms have resulted in expanded representation of behaviorally-relevant sound features in the auditory cortex (e.g., Brown et al., 2004, but see also Recanzone et al., 1993), the majority of studies in which a specific acoustic feature was associated with an unconditioned stimulus have reported such changes (see reviews by Suga and Ma, 2003; Weinberger, 2004, 2007). Moreover, these changes in representation have been shown to occur rapidly (e.g., within minutes; Edeline et al., 1993; Fritz et al., 2003, 2005a, 2005b), and can persist for months (Weinberger et al., 1993).

Learning-dependent representational plasticity has been observed in a variety of species in primary and association auditory cortices, as well as subcortical structures (See Figure 1, Table 1 for summaries). The expanded representation of behaviorally-relevant features of the auditory environment may occur in conjunction with, and/or be modulated by other areas such as the amygdala and limbic system (Poremba and Gabriel, 2001; Suga and Ma, 2003; Weinberger, 2004), which may encode the behavioral relevance of the sounds. Indeed, a number of studies have reported that these areas are responsive to CVs, perhaps because of their learned associative value and emotional content (Morris et al., 1999; Parsana et al., 2012; Sander et al., 2007; Wiethoff et al., 2009). Because CVs consist of combinations of acoustic features (Miller and Cohen, 2010) and have a high degree of behavioral significance (Simmons et al., 2003; Snowden et al., 1982), representational plasticity in the auditory system comprises a plausible means whereby distinctive representation of CVs can emerge.

4. The effects of experience in shaping neural responses to conspecific vocalizations

4.1. Songbirds

Although there are differences in neural circuitry involved in human speech processing and song learning in songbirds, perception and production of conspecific song has been widely used as a model for understanding the development of human speech perception and vocal learning (Bolhuis and Gahr, 2006; Bolhuis et al., 2010; Doupe and Kuhl, 1999; Jarvis, 2004). Accumulating evidence, particularly within the last decade, strongly suggests that selectivity for conspecific songs over other sounds in the avian brain is heavily influenced by experience (reviewed at length by Woolley, 2012). Cousillas et al. (2004) first reported that, in starlings raised without normal adult song exposure, neurons in field L exhibited abnormally low song selectivity. Specifically, field L neurons in the isolated birds they were

broadly responsive to all tested stimuli, whereas precise responses to specific song characteristics were observed in wild-caught birds. Similarly, George et al. (2004) found that the duration of isolation from adult song predicted the degree to which field L neurons in starlings responded broadly to all tested stimuli, instead of selectively to specific song features. Consistent with these deprivation studies, Amin et al. (2007) have observed that overall responsivity and selectivity for songs over artificial stimuli in field L neurons are greater in adult zebra finches than in juveniles. A study by Maul et al. (2010) found that depriving male zebra finches of song from posthatch days 7-29 was sufficient to reduce song selectivity of the auditory forebrain (neural responses did not differ among different songs, syllables, and a pure tone), and that this could be partially, but not completely restored by exposing the birds to 30 s of recorded song playback from posthatch days 30-100. As in field L, neuronal firing rates in NCM are less selective for conspecific song features in starlings that have been deprived of adult song experience than in wild-caught starlings (George et al., 2010). Collectively, these studies show that early auditory experience is crucial for species-typical neural representation of CVs.

A particularly interesting study by Woolley et al. (2010) investigated neural responses to both zebra finch and Bengalese finch songs in zebra finches that had been cross-fostered by Bengalese finches. The neural responses in the cross-fostered birds were compared to normally-reared zebra finches and normally-reared Bengalese finches. In both the midbrain (MLd) and forebrain (field L), neural responses of the normally-reared zebra finches had a greater capacity to encode information about both the zebra finch and Bengalese finch songs than the neural responses of the Bengalese finches (based on firing rate, change in firing rate, rate of change in firing rate, and response reliability), perhaps resulting from differences in the songs produced by each species. In the cross-fostered zebra finches, the information-coding capacity of neural responses to both zebra finch and Bengalese finch songs did not differ significantly from the neural responses of the Bengalese finches, whereas both groups differed significantly from the normally-reared zebra finches. In other words, the information coding capacity of neurons in MLd and field L of zebra finches cross-fostered by Bengalese finches was more similar to the that of the Bengalese finches than that of the zebra finches. Curiously, in both zebra finch groups, field L neurons did not exhibit significant selectivity for either zebra finch or Bengalese finch songs in terms of overall firing rate, whereas field L neurons in the Bengalese finches were selective for conspecific songs. Thus, while the cross-rearing manipulation in this study did not significantly affect selectivity among the tested song types, the species-typical information coding capacity of neurons in this study was strongly influenced by early auditory experience.

Phan and Vicario (2010) recently investigated the role of auditory experience in shaping hemispheric specialization for CV processing in zebra finches. The auditory environment of the developing finches was manipulated in two ways: a first set of birds was divided into two groups that either received song exposure (“tutored”) or were deprived of normal song during development (“untutored”); a second set of birds was surgically devocalized, rendering them incapable of producing audible vocalizations, and then similarly divided into tutored and untutored groups. In the intact adults, the response magnitude of NCM neurons to both conspecific songs and calls was greater in the right hemisphere than the left,

regardless of whether they had been exposed to song. Similarly, devocalized birds that had experienced conspecific song exhibited a right-hemispheric preference for songs and vocalizations, although the extent of specialization was less than in the intact birds. Critically, however, the devocalized birds that did not receive exposure to conspecific song did not exhibit a hemispheric preference for songs or vocalization as was observed in the other groups. These results strongly suggest experience with CVs as a key factor in the emergence of species-typical neural representations of CVs. They further demonstrate the ability of the animals' own vocalizations to shape these representations.

In summary, sensitivity of neuronal responses to CVs in the songbird auditory forebrain (field L and NCM), as well as the midbrain (MLd), are heavily reliant on exposure to song and vocalizations. There are several differences between the neural substrates of birdsong and the representation of CVs in humans and other mammals that call for caution when drawing inferences about representation of CVs in the mammalian brain from the birdsong literature, such as sex differences (Hauber et al., 2007; Maul et al., 2010; Phan and Vicario, 2010), hormonal influences (Del Negro et al., 2005; Fusani and Gahr, 2006; Tremere and Pinaud, 2011), and differences between songs and other communication vocalizations. However, it is clear in these bird species that significant brain resources are devoted to perception of these sounds, and that experience with the CVs including self-vocalizations plays a significant role in elevating these sounds above others.

4.2. Humans and other mammals

Relatively few studies have directly investigated the role of experience in shaping responses to CVs in humans and other mammals. However, the existing studies suggest that, like in songbirds, experience is a key factor in the emergence of species-typical neural representations of CVs. One such study by Cheung et al. (2005) investigated the neural representation of CVs in marmosets that had undergone a vocal tract modification surgery that permanently lowered the frequency content of the twitter call (e.g., the minimum frequency of the altered call was approximately one octave lower than the natural call). After 5–15 months of experience with the altered self-vocalizations, the response properties of neurons in the auditory cortex were assessed for both altered and natural CVs. Compared to controls, neurons in the vocally-modified subjects exhibited reduced temporal precision and overall response magnitude in response to both the altered and natural calls. The authors suggested that the responses to the altered calls might have been diminished rather than augmented because of their reduced communicative efficacy. The receptive-field properties of neurons defined by simple tone bursts as well as the tonotopic organization of the auditory cortex did not differ between controls and vocally-modified subjects, indicating that the observed plasticity was specific to the change in experience with CVs.

Another notable study by Liu and Schreiner (2007) provided evidence for the role of experience in shaping neural representation of CVs in the auditory cortex in the context of the ultrasonic communication system between mouse pups and mothers. A variety of pup calls were presented to both mothers who exhibited behavioral preference for pup calls over neutral sounds, and to pup-naïve females who did not exhibit behavioral preference for the calls. While the mean firing rate evoked by the pup calls did not differ between the mothers

and naïve females, the peak evoked firing rate was greater, and of shorter latency in the mothers. Further analyses revealed that the information contained in the evoked responses for detection and discrimination of pup calls, but not for unnatural control sounds, was significantly improved in mothers compared to naïve females. Thus, although traditional measures of selectivity for CVs were not assessed in this study, the communicative significance of the pup calls was evident in the detection and discrimination abilities of auditory cortical neurons in the experienced mothers.

Nourski et al. (2012, 2013) have recently presented data from human neurosurgical patients highlighting the plasticity of regions of the brain that typically respond to speech. In normal-hearing patients undergoing invasive monitoring for refractory epilepsy, neurophysiological responses were recorded in response to naturally-voiced syllables and syllables that had been spectrally degraded to replicate the signal that would reach the brain after being processed by a cochlear implant. For the overwhelming majority of sites in the posterolateral portion of the superior temporal gyrus (PLST), the amplitude and spatial extent of the responses was greater in response to the natural syllables than the spectrally-degraded stimuli (Nourski et al., 2012). Nourski and colleagues (2013) also reported a rare case study of a patient undergoing invasive monitoring for epilepsy that had also been a cochlear implant user for approximately 20 years. In this patient, speech sounds (which had been spectrally degraded by the cochlear implant) evoked activity in the PLST that was remarkably similar to the natural-speech evoked responses in the normal-hearing patients. The observation that extensive experience with spectrally-degraded speech leads to neural representation in the PLST that closely resembles natural speech suggests that the “speech sensitivity” of this area relies on experience with stimuli of communicative significance, even if the sounds are relatively artificial.

Additional indirect evidence that experience contributes to CV-specific responses comes from studies comparing neuronal responses elicited by natural CVs compared to time-reversed CVs, which contain similar spectral content and acoustic complexity. Preferential responding to natural over time-reversed CVs has been observed in several studies, including in the auditory cortex of marmosets (Wang et al., 1995), the posterior ectosylvian gyrus and ventral part of the auditory cortex in cats (Gourévitch and Eggermont, 2007), the FM-FM area of bats (Esser et al., 1997), and in the forebrain of songbirds (Doupe and Konishi, 1991; Margoliash, 1983). It should be noted, however, that other studies have failed to observe any selectivity for natural over time-reversed CVs, including in the auditory cortex of squirrel monkeys (Glass and Wollberg, 1983a, 1983b), and in the auditory cortex and thalamus of rats and guinea pigs (Huetz et al., 2009; Philibert et al., 2005), while others have reported ambiguous results (e.g., greater onset responses to natural CVs in the cat auditory cortex, but greater sustained responses to time-reversed CVs; Gehr et al., 2000). Bearing these caveats in mind, the idea that selectivity for natural CVs is attributable to their acquired behavioral significance is supported by a study by Wang and Kadia (2001) comparing selectivity for natural over time-reversed marmoset twitter calls in the auditory cortex of marmosets and cats. As in previous studies, the auditory cortex in marmosets exhibited greater firing rates for the natural twitters. In cats, however, for which neither the natural nor the time-reversed marmoset calls have any behavioral relevance, the auditory cortex did not respond differentially between the two call types. Although these findings do

not necessarily rule out potential species-specific or innate mechanisms of CV representation, a recent computational study has found that selectivity for natural over time-reversed CVs can plausibly arise from experience-related short-term plasticity alone (Lee and Buonomano, 2012).

In addition to the neurophysiological studies cited above, a number of developmental studies have provided evidence at the behavioral level that species-typical responses to CVs are influenced by experience (Seyfarth and Cheney, 1997). For instance, Fischer et al. (2000) observed behavioral responses elicited by CVs in a field study of developing baboons. The baboon vocalizations ranged from tonal, harmonically-rich calls, which were typically produced when the caller became distanced from another individual or group (“contact barks”), to noisy, harsh calls, which were typically produced in response to predators (“alarm barks”). In adult baboons, noisy alarm barks reliably provoked strong behavioral responses, whereas the tonal contact barks elicited only a weak response or no response at all. In the infant baboons, adult-like responses to the two call types developed with age: at two and a half months, neither call type elicited a behavioral response; at four months, a similar behavioral response was elicited by either call type; at six months, only the noisy alarm bark elicited a strong behavioral response.

Additional studies have provided behavioral evidence that hemispheric specialization for processing vocal communication emerges through experience. Using a head-orienting task, Böye et al. (2005) found that adult sea lions exhibited a strong right-ear (left hemisphere) preference for CVs, but not HVs. This orienting asymmetry was not observed in infant sea lions, which the authors attributed to a lack of adequate experience with CVs. These observations corroborate an earlier report by Hauser and Andersson (1994) that adult but not infant rhesus monkeys preferentially orient to the right when CVs but not HVs are presented. Similarly, Lemasson et al. (2010) have recently reported that Japanese macaques exhibit a right-orientation bias for vocalizations of familiar but not unfamiliar primates. Although there are limitations to the orienting asymmetry paradigm (Teufel et al., 2010), these studies are consistent with the neurophysiological demonstration by Phan and Vicario (2010) of experience-dependent development of hemispheric specialization in songbirds.

5. The effects of learning and memory in shaping neural responses to conspecific vocalizations

Experience and learning are closely-related concepts. Whereas the term “experience” can encompass the entire range of events that an organism is exposed to, herein we use the terms “learning and memory” to refer to the more specific instances of experience in which organisms identify contingent relationships among events (i.e., associative learning). Evidence in birds indicates that species-typical behavioral responses to CVs develop more rapidly when the CVs are part of a specific, contingent relationship than when they are merely experienced by the birds. For example, bobwhite quail chicks require at least 240 minutes of passive experience with the maternal bobwhite call in order to acquire a preference for that call (Lickliter and Hellewell, 1992). However, when playback of the maternal call is made contingent upon the chicks’ own vocalizations, a single 5-minute session is sufficient to induce a preference for the call (Harshaw and Lickliter, 2007). The

roles of experience and learning can sometimes be difficult to distinguish. As noted above, in marmosets that had surgical modifications of the vocal tract, diminished neurophysiological responses were observed following 5–15 months of experience with the altered calls (Cheung et al., 2005). However, the vocal tract modification altered not only the spectral content of the calls, but also reduced their communicative efficacy. Thus, as suggested by the authors, the lack of reward for successful communicative interchanges with conspecifics might have been a key factor in producing the suppressed responses. In this section, we review several studies in which neural responses in vocalization-sensitive brain regions are shown to be influenced specifically by training.

5.1. Songbirds

Gentner and Margoliash (2003) trained adult starlings to discriminate between two sets of conspecific songs using either a two-choice or go/no-go task. In the two-choice task, birds were rewarded for pecking the key corresponding to the correct song set, whereas in the go/no-go task they were only rewarded for pecking a key in response to the correct song set (S+). After reaching asymptotic performance of approximately 90% correct responses, neurophysiological responses in area CM were measured in responses to the learned songs and an additional set of novel songs. In birds trained under both the two-choice and go/no-go paradigms, the overall evoked response magnitude was greater for the learned song sets than the novel songs. For birds trained in the two-choice task, the response magnitude elicited by songs from each set (“peck left” and “peck right”) were approximately equal. However, for birds trained in the go/no-go paradigm, the songs that had been rewarded (S+) elicited significantly greater responses than songs from the unrewarded set (S-), though the unrewarded songs elicited greater responses than the novel, unlearned songs. Moreover, the responses elicited by the rewarded songs in birds trained in the go/no-go task were greater than the responses elicited by either song set in the birds trained on the two-choice alternative task, even though both sets had been rewarded. A similar study by Thompson and Gentner (2010) found that area NCM exhibited similar selectivity for learned over unlearned songs, with the exception that the selectivity for learned songs was manifest in the form of relatively suppressed firing rates. These outcomes support the idea that selectivity for CVs, at least in areas CM and NCM in the songbird brain, is closely tied to the behavioral relevance of CVs.

Like songbirds, parrots learn their vocalizations from a tutor, and the auditory association areas CM and NCM that are typically differentially responsive to CVs are homologous in songbirds and parrots. Eda-Fujiwara et al. (2012) took advantage of the ability of budgerigars, a parrot species, to mimic human vocalizations in addition to learning their own CVs. In their experiment, an experimental group of budgerigars were trained to discriminate two Japanese words that were vocalized by another budgerigar. Following training, neuronal activation in response to the learned words was measured by expression of the immediate early gene *ZENK* in areas CM and NCM. Neuronal activation in both areas was significantly greater in trained birds than untrained control birds that were exposed to the same stimuli. Neuronal activation in untrained birds exposed to the budgerigar-spoken words did not differ from a third group of birds exposed to silence. There were no differences in neural activation in the hippocampus among the three groups, suggesting that the training-induced

changes were specific to areas of the brain that are typically involved in representing CVs. Finally, the degree of neuronal activation in area CM and in the dorsal portion of NCM was positively correlated with behavioral accuracy during discrimination training. The observation that, through training, these areas became robustly responsive to auditory stimuli that would not normally be encountered by budgerigars in the wild provides further support for the idea that selectivity for CVs may be shaped by their learned behavioral significance.

5.2. Humans and other mammals

Using event-related potentials, Kraus and colleagues have shown that a number of forms of short-term and long-term auditory training influence cortical and subcortical responses evoked by speech features (Chandrasekaran and Kraus, 2010; Kraus and Banai, 2007). For example, individuals with music training have enhanced representation of native speech syllables (Musacchia et al., 2007), vocally-expressed emotion (Strait et al., 2009), and linguistic pitch contours, which is correlated with the extent of musical training (Wong et al., 2007). Similarly, short-term auditory training programs in children have been shown to improve the representation of speech syllables and pitch contours (Russo et al., 2005; Song et al., 2008). While these studies demonstrate training-induced malleability of neural representations of speech, only more recent studies using neuroimaging techniques have been able to identify specific brain regions that are susceptible to these influences.

Using fMRI, Leech et al. (2009) recently reported that training human subjects to recognize and categorize complex artificial sounds led to differential activation of a speech-sensitive cortical area, the left posterior superior temporal sulcus (pSTS). The task consisted of a video game in which subjects had to learn the relationship between a visually-presented alien and its corresponding sound category. After approximately five hours of experience with the game, passive exposure to the training sounds resulted in significantly decreased deactivation of the pSTS relative to pretraining exposure to the sounds. Further, the difference between pretraining and posttraining activation in this area was significantly correlated with behavioral accuracy in categorizing the sounds. The finding that artificial, spectrotemporally-complex sounds produce changes in pSTS activation following training suggest that responses to speech in this area may be related to expertise with speech sounds. This conclusion was further supported by a subsequent study showing that this area was strongly activated bilaterally by both speech and music in individuals with musical expertise (violinists), but only by speech in a control group of experts (actors) without extensive musical training (Dick et al., 2011). A comparable pattern of results was observed in the left planum temporale and an anterior portion of the left superior temporal gyrus. Taken together, these studies provide evidence that the “speech selectivity” of these regions may reflect expertise with spectrotemporally-complex stimuli rather than an innate, domain-specific bias for speech processing.

As reviewed above, cells in the auditory cortex of marmosets frequently exhibit increased overall firing rates for natural over time-reversed marmoset calls, whereas cells in the cat auditory cortex fail to make this distinction (Wang and Kadia, 2001). Schnupp et al. (2006) tested whether learned behavioral significance was sufficient to induce selectivity for natural

marmoset calls in the auditory cortex of adult ferrets by training them to discriminate marmoset twitter calls (S+) from other natural sounds (S-) in a go/no-go paradigm. Whereas no significant difference in the overall firing rate elicited by natural versus reversed calls was observed in control animals, there was a small but significant decrease in firing rate elicited by the natural calls compared to the reversed calls in the trained subjects. However, the degree of this effect was so small that the authors suggested that it was of little physiological significance. On the other hand, the information contained in the temporal spike patterns increased substantially following training. Thus, the learned significance of the HVs was evident in temporal pattern codes, but only weakly in the overall firing rate. The latter observation indicates that the auditory cortex does not inevitably exhibit greater selectivity, as evidenced by increased firing rate, for complex sounds of acquired behavioral significance. It should be noted, however, that the adult ferrets used in this study presumably had well-established neural representations of their own CVs, which could have interfered with expansion of the representation of the natural marmoset call as defined by overall firing rate. However, additional studies surrounding this topic are needed to make this determination.

Collectively, the studies reviewed in Sections 4 and 5 have uniformly shown that neural representations of CVs are susceptible to the influences of experience, learning, and memory. These findings are consistent across a number of species, including songbirds, humans, and other mammals. In some of these studies, neural regions that typically represent CVs came to respond to non-CV sounds according to their acquired behavioral significance, including HVs and artificial, complex sounds. These observations are consistent with the notion that CVs acquire distinctive neural representation through domain-general mechanisms for representing complex auditory objects that are of importance to the animal.

6. Comparison of vocalizations and faces

The visual and auditory systems share much in common in terms of sensory processing strategies (Nelken and Calford, 2011) and experience-dependent plasticity (Rauschecker, 1999). As mentioned above, both sensory systems appear to be organized into dorsal and ventral processing streams that are specialized for processing non-spatial and spatial stimulus attributes, i.e., the “what” and “where” pathways, respectively (Kaas and Hackett, 1999; Poremba et al., 2003; Rauschecker and Tian, 2000; Ungerleider and Mishkin, 1982). This includes the observation that cells in hierarchically-advanced regions of the ventral processing stream exhibit selectivity for more complex objects, such that vocalization- and face-sensitive regions lie anterior to primary sensory areas in the temporal lobe (Fujita et al., 1992; Gross and Sargent, 1992; Kanwisher et al., 1997; Perrett et al., 1988; Petkov et al., 2008; Poremba et al., 2004). These regions in turn project to the prefrontal cortex, where integration of CVs and faces has been observed (Sugihara et al., 2006; Romanski, 2012; Romanski and Averbeck, 2009).

In humans, the fusiform gyrus of the right hemisphere, or fusiform face area (FFA), is preferentially activated by faces over a number of control stimuli, such as houses and scrambled faces (Kanwisher et al., 1997). Initial evidence that the FFA might be activated

by visual stimuli with which subjects have extensive experience came from a study by Gauthier et al. (1999), in which subjects were trained to become experts at categorizing a novel class of visual objects (greebles). Following training, increased activation was observed during categorization of upright versus inverted greebles. Further, passive viewing of greebles produced greater activation of the FFA in the trained experts than in novices. A subsequent study revealed that these results generalized to expertise with birds and cars (Gauthier et al., 2000). In bird experts, passive viewing of birds compared to other familiar objects produced significant activation of the FFA, whereas cars failed to elicit similar activation. In car experts, passive viewing of cars compared with other objects, but not birds, elicited significant FFA activity. A more recent study has similarly reported that FFA activity in radiologists detecting abnormalities in chest radiographs is positively correlated with expertise (Harley et al., 2009). Although there is debate as to whether face selectivity in the FFA depends entirely on experience (Bukach et al., 2006; Kanwisher, 2000; McKone et al., 2007; Tarr and Gauthier, 2000), at minimum, these studies indicate that experience with behaviorally-relevant, non-face stimuli leads to activation in the FFA.

These findings corroborate earlier behavioral evidence that face-specific processing may be driven by experience. Similar to the advantages for discriminating and remembering CVs, there are advantages for processing natural faces at the behavioral level. For example, recognition memory for faces is disrupted to a greater degree by inverted presentation than other classes of images. Diamond and Carey (1986) showed that, in dog experts, memory for inverted images of dogs is similarly disrupted relative to natural images, suggesting that this bias results from extensive experience. Similarly, recent evidence suggests that infants' preference for faces and face-discrimination abilities, initially assumed to be innate, may arise from domain-general perceptual biases and experience (Turati, 2004).

In summary, both behavioral and neural studies have suggested experience and learning play a central role in the distinctive processing of faces. These outcomes provide a visual parallel to the studies in the auditory system reviewed above, indicating that preferential behavioral and neural processing of CVs is closely tied to experience with CVs and their learned behavioral significance. Taken together, these findings support the position that representation of meaningful stimuli is acquired through experience and learning, rather than by domain-specific mechanisms that have evolved to invariantly represent stimuli of ecological significance.

7. Additional factors influencing the neural representation of conspecific vocalizations: arousal, attention, and short-term memory

The majority of studies describing neural regions that are differentially responsive to CVs have employed passive-listening paradigms in which sounds are exposed to subjects with little or no behavioral interaction. It should be noted, however, that neural responses evoked by a given sound may vary depending on the behavioral state of the animal, or the context in which the sounds occur. For instance, it is well known that anesthesia has a major impact on the sound-responsiveness of auditory brain regions, including the primary auditory cortex (Cheung et al., 2001; Gaese and Ostwald, 2001; Howard et al., 2000). Similarly, responses elicited by sounds including CVs in primary and secondary auditory cortices often differ

during wakefulness and sleep (Edeline et al., 2001; Issa and Wang, 2008, 2011). Moreover, whether or not a subject is attending to a sound or performing well during a behavioral task may modulate the evoked response characteristics (Mesgarani and Chang, 2012; Niwa et al., 2012; Otazu et al., 2009; Poremba and Bigelow, 2013; Ryan et al., 1984); however, even the influence of attention will need to be separated from the effects of experience with sounds (Baumann et al., 2008). The influence of attention on neural encoding of CVs may be a strong modulator of the neural processing discussed herein.

Historically, studies of the neural circuitry underlying short-term memory have focused on visual stimuli. Typically, single- or multi-unit recordings are conducted while the subject performs a delay task in which a sample stimulus is presented, followed by retention interval, after which one or more test stimuli are presented. These studies have revealed a prominent role for the prefrontal cortex in short-term memory, where changes in firing rate are often observed during the retention interval (Shafi et al., 2007; Fuster and Alexander, 1971). Further, test stimuli that “match” the sample stimulus are often associated with enhanced responses (e.g., Miller et al., 1996). Recordings in the temporal lobe, on the other hand, show that matching test stimuli are more commonly associated with suppressed responses (Miller et al., 1993; Nakamura and Kubota, 1995). Although neurophysiological investigations of auditory short-term memory are relatively sparse, the existing evidence suggests that many of the same memory-related phenomena reported in the visual literature are also observed during auditory short-term memory (Poremba and Bigelow, 2013). For example, Plakke et al. (2013) reported that matching sounds elicited elevated firing rates in prefrontal neurons during an auditory short-term memory task. Using the same paradigm, Ng (2011) found that neurons in the dorsal temporal pole exhibited suppressed firing rates when matching sounds were presented. Neurophysiological as well as neuropsychological studies also suggest a role for the auditory cortex in short-term memory (Gottlieb et al., 1989; Ku mierek et al., 2007; Sakurai, 1990, 1994), suggesting that memory-related modulation of sound-evoked activity may be widespread in auditory cortical pathways.

In summary, neural responses to sounds including CVs are not “fixed” across behavioral states; rather, they are strongly modulated by arousal and attention, and also depend on stimulus presentation history and the behavioral context in which sounds are presented. Although our current understanding of the neural substrates of these phenomena is incomplete, these influences should be taken into consideration when investigating the neural representation of CVs.

8. Relationship to human language development

Any information about the mechanisms underlying human language development may be beneficial to animal work utilizing vocalizations, as some relevant components of these processes may be similar across species. The debate over language development has spanned decades but has heated up in the past 25 years even as the timeline of language learning has become well mapped. The relative contributions of experience versus ‘innateness’ are still debated, but support for a more experience-based explanation of language acquisition has taken precedence (Spencer et al., 2009; Werker and Vouloumanos, 2001). Saffran and colleagues originally showed that experience might play a greater role in

language acquisition than previously thought, suggesting that infants separate and segment speech using statistical learning methods as they determine which syllables are commonly found together and which syllables are infrequently grouped (Saffran et al., 1996). This general set of hypotheses regarding the learning of language has now been expanded by other recent findings (McMurray, 2007; Samuelson et al., 2011). Language development's reliance on speech exposure (Huttenlocher et al., 1991) is also supported by studies of feral children who do not develop language without early speech experience; this is similar to the studies of songbird learning manipulations discussed in section 4.1.

Word-learning is an essential stepping stone to understanding speech, as well as for garnering meaning from one's environment. The processes by which children learn and navigate their environments early in life can also be the same processes that account for the development of vocabulary (Saffran et al., 1996). Studying shape bias is a popular method of studying word learning in children, and research in this area suggests that attention, which modulates and pervades many types of learning both in early childhood and adulthood, is an essential factor for children to develop into effective word learners (Saffran et al., 1996; Samuelson et al., 2011). The shape bias refers to a child's ability to hear a novel name for a novel object, and then to generalize that name to other novel objects, which are similar to the original object presented. This research suggests that what children are really learning is the association between the object and the context that adults will use to name that object. By forming that association and by paying attention to novel objects, children can focus on the relevant features of the object that need to be recognized and categorized in the future (Smith and Samuelson, 2006; Spencer et al., 2009).

The process of forming associations is critical in early word learning and also the environment of the child, including social interactions, may be important. In conversation, words often function to direct a listener to a specific region of space with what we say often reflected in where we look. Spatial constancy of the objects presented to the children also affects how well new words are learned (Samuelson et al., 2011; Smith et al., 2003). Social interaction, often between parent and child, assists not only the learning of new words, but also the perception and production of speech (Cousillas et al., 2008). Language learning in children is fostered by a social environment in which interaction promotes attention on the part of the child, and learning is grounded in general processes such as association dependent upon experience. Social interaction is critical for language learning not only in children, but also in other species such as songbirds. Social deprivation has devastating effects on the acquisition of language in humans and even, in the case of songbirds, leading to perceptual abnormalities within the auditory pathway (Cousillas et al., 2008; Kuhl, 2004). In general, these additional processes such as social interactions and attention can modulate the quality and quantity of experience, learning, and memory that can occur for CVs.

9. Summary and future research directions

We have been discussing whether CVs are “special” and whether they deserve special status when studying auditory processing. There is ample evidence that CVs hold special significance in terms of behavioral meaning (Section 1) and neural representation (Section 2). However, the available evidence reviewed herein is consistent with the notion that this

special status may be acquired through experience, learning, and memory, rather than through innate, domain-specific mechanisms for processing CVs. This tentative conclusion is not unexpected in light of a large body of research describing the auditory system as inherently plastic (Figure 1; Table 1) and capable of augmenting the neural representation of behaviorally-relevant acoustic features. Moreover, these observations are consistent with studies in the visual system suggesting face-selective neural regions and face-specific behavioral processing rely at least in part on experience. Together, these findings are difficult to reconcile with the idea that domain-specific neural modules have evolved to exclusively represent ecologically-salient stimuli such as CVs and faces, regardless of experience or developmental history.

These advances notwithstanding, there are still a great many questions surrounding the emergence of species-typical behavioral processing and neural representation of CVs. Many of these questions surround early auditory development, including the possibility of an early “sensitive period” for acquiring species-typical behavioral and neural responses to CVs (Braun et al., 2003; Kuhl, 2010; Nakahara et al., 2004; Phan et al., 2006; Wang, 2004; Ziabreva et al., 2003). In this regard, it is worth noting that self-vocalizations alone have been shown to be sufficient to induce at least some forms of behavioral and neural sensitivity to CVs in several bird species (Gottlieb, 1991; Phan and Vicario, 2010). Moreover, several studies have documented prenatal sensitivity to auditory stimulation (Harshaw and Lickliter, 2011; Lickliter and Stoumbos, 1992), including the observation that human infants’ behavioral and neural responses to speech sounds are influenced by prenatal maternal speech (Byers-Heinlein et al., 2010; DeCasper and Fifer, 1980; DeCasper and Spence, 1986; May et al., 2011; Minagawa-Kawai et al., 2011; see also Seebach et al., 1994). Thus, developmental studies should be mindful of these influences when seeking to identify the variables underlying the emergence of species-typical representation of CVs.

In adults, additional studies of auditory expertise could be useful for addressing the specificity of regions that are typically selective for CVs. For example, as pointed out by Chartrand et al. (2008), studies of auditory perception in musicians and bird experts could provide parallels to studies in the visual system showing that objects with which subjects have expertise activate face-selective areas (Section 6). In the same way, extensive training with complex artificial stimuli could induce activity in regions that typically represent CVs. As reviewed in Section 5, there is already some evidence that this is the case. Another potentially interesting avenue of research in animals would be to compare the behavioral and neural responses elicited by CVs and other behaviorally-relevant vocalizations with which subjects have extensive experience, such as those of predators. Additional opportunities for future research include direct comparisons of the effects of auditory exposure versus associative learning, and investigations of potential differences in the degree to which experience, learning, and memory affect representation of CVs among different brain regions, as well as among different species.

If experience and learning play important roles in making communication sounds “special”, then their influence and modulating effects need to be taken into consideration when using them as stimuli in experiments and in their comparison to other non-communication sounds. Comparisons between stimuli are particularly important in imaging and neurophysiological

studies in helping to determine which components of the auditory system may be contributing during sound processing. The amount of experience with the sounds, associations that these sounds may have gained, developmental trajectory of the experience, social pairings, etc., should be considered when drawing conclusions, or the assumptions even tested when possible. If communication signals are primarily learned about or driven by experience, then are all presentations of communication stimuli equal across experiments? Although this possibility exists in human experiments too, the number of subjects can be increased to help control for differences in their experience levels. In animal studies, one possibility is that for some experiments, housing parameters may play a role particularly if some animals are housed in pairs or individually. However, a study of lab-housed animals suggests that communication processing may be normal in these animals as cross-habituation was observed when the monkey calls were functionally equivalent, but acoustically distinct (Gifford et al, 2003). Associations between the sounds and meanings may not be as strong, although CVs are most likely the most frequently heard auditory stimulus. However, these possibilities should be considered and tested when possible. On the plus side, there are several studies showing that different types of sounds in non-human primates elicit different behavioral and neural responses (Poremba et al., 2004; Ng et al., 2009), but future controlled testing of sounds with a similar frequency range to vocalizations and consideration of the amount of experience with the sounds will need further consideration. In addition, we must study whether the neural processes underlying associative conditioning also underlie learning of CVs and the relationship between conditioning, experience, and memory encoding.

Another caveat to studying CVs in a variety of situations is to be careful in our testing of why these sounds are occurring. The study of Blumberg and colleagues provides cautionary evidence (Blumberg and Alberts, 1990). Although it was assumed that when rat pups became separated from their dams they made specialized cries that brought the dam to them. They discovered that under hypothermic conditions these cries were instead a byproduct of temperature regulation, which induces increased breathing. Yes, the rat dams are alerted by the calls and retrieve the rat pups, but the meaning and mechanism behind the pup “call” may be different than what human researchers had assumed. Hypotheses derived from other studies suggest that the rat pups may eventually learn to make this isolation call when separated and further study needs to ascertain when its production changes from an unconditioned response to a conditioned one with the stimulus being the colder temperatures away from the dam (Hofer and Shair, 1993). At some point as we continue investigating CVs in animals, we must be concerned with what meaning is meant to be conveyed by the subject making the CVs, what may be interpreted by the listener, and how that may change or develop over time.

One advantage of the view that the neural representation of CVs is not consigned to an innate, modular “black box” is that the underlying mechanisms can be better delineated and understood. More direct comparisons to the study of human language become possible as we systematically determine which mechanisms exist in animals and which may be lacking, under-developed, or missing completely. Understanding where and how auditory objects are encoded and communicative signals are processed in animals may delineate the precursor neural framework for the evolution of language; it may also reveal species’ differences in

communication systems and the lack of a sophisticated language system in animals. Ultimately, defining the neural circuits and cellular interactions necessary for encoding CVs and auditory objects as well as for auditory associative learning, recognition, and short-term memory, will lead to a better understanding of the etiology underlying auditory aphasia like word deafness, potentially leading to treatments for learning disabilities (Goll et al., 2010), and shedding light on communicative disorders.

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- Learning, memory, and experience instantiate communication sounds as unique representations
- Conspecific vocalizations acquire neural representations through domain-general mechanisms
- Exposure to sounds during development is crucial for later communication processing
- Conspecific vocalization processing may be modulated by associate conditioning

Figure 1.

Associative conditioning, short-term and recognition memory, and experience/context-dependent plasticity have been demonstrated throughout the auditory pathway as evidenced by studies using neurophysiological recording techniques from single-unit to electroencephalograms. Illustrated above is the basic mammalian ascending auditory pathway depicting major structures and connections. The color coding depicts different types of neural plasticity: associative conditioning is represented in blue, short-term and recognition memory in red, and experience/context-dependent plasticity in green; see Table 1 for references of examples of each type of finding. A. Auditory information enters through the ear and is translated into neuronal signals via hair cells located in the cochlea. B. Auditory information is then relayed via the auditory portion of the vestibulocochlear nerve into the cochlear nuclei. The first signs of experience-dependent plasticity are observed at this early stage of auditory processing, in the dorsal (DCN) and ventral (VCN) cochlear nuclei. C. The superior olivary complex (SO) receives primary projections from the cochlear nuclei, also implicated in auditory-related experience-dependent plasticity. D. Auditory information is then sent to the inferior colliculus (IC) where the signal can be transmitted between the left and right IC. Neurons in the IC have also been suggested to demonstrate plasticity evoked during auditory associative conditioning, see caveat in Table 1 caption. E. The IC projects to the medial geniculate nucleus (MGN). The MGN has been identified in a breadth of research for its role in auditory conditioning, and is thought to be an area which

is influenced by, or plays a role in, establishing associative learning involving auditory stimuli. F. Auditory information reaches primary auditory cortex (A1) and associative auditory cortices, which are not differentiated within the figure. Across mammalian species, A1 is implicated in the perception of sound, and all three forms of plasticity have been demonstrated in both primary and associative cortices. Although the prefrontal cortex (PFC) as well as the amygdala and other limbic regions are not shown, they do exhibit plasticity in relation to audition, with the amygdala being heavily implicated in auditory conditioning and the PFC playing a role in auditory short-term and recognition memory. A1: primary auditory cortex; DCN: dorsal cochlear nucleus; IC: inferior colliculus; MGN: medial geniculate nucleus; SO: superior olive; VCN: ventral cochlear nucleus.

Table 1
Neurophysiological studies describing plasticity in the auditory system

These are example studies listed within each category and are not meant to be an exhaustive listing.

Auditory Structure	Form of Plasticity		
	Associative Conditioning ^a	Short-term, Recognition Memory ^b	Experience, Contextual Dependence ^c
Prefrontal Cortex	Baeg et al., 2001; Gilmartin and McEchron, 2005; Ono et al., 1984; Pirch et al., 1983, 1985; Watanabe 1992	Artchakov et al., 2007, 2009; Bodner et al., 1996; Fuster et al., 2000; Joseph and Barone, 1987; Kikuchi-Yorioka and Sawaguchi, 2000; Plakke et al., 2013; Russ et al., 2008	Fritz et al., 2010; Plakke, 2010; Plakke et al., 2013
Amygdala	Blair et al., 2001, 2003; Maren et al., 1991; Quirk et al., 1997		McEchron et al., 1995
Auditory Association Cortex	Bao et al., 2001; Diamond and Weinberger, 1984, 1986; Kraus and Disterhoft, 1982; Polley et al., 2006	Mazzoni et al., 1996; Ng, 2011	Esser and Eiermann, 1999; Kayser et al., 2008; Schreiner and Cynader, 1984
Primary Auditory Cortex	Bakin and Weinberger, 1996; Edeline et al., 1993; González-Lima and Scheich, 1986; Kilgard and Merzenich, 1998a; Ohl and Scheich, 1996; Recanzone et al., 1993; Weinberger, 2004*	Gottlieb et al., 1989; Sakurai, 1990, 1994	Ahissar et al., 1992; Brosch et al., 2005; Condon and Weinberger, 1991; David et al., 2003; Fritz et al., 2003; Kayser et al., 2008; Niwa et al., 2012; Ryan et al., 1984; Ulanovsky et al., 2003; Yin et al., 2008
Medial Geniculate Nucleus	Edeline, 1990, 1999*; Edeline and Weinberger, 1991a, 1991b, 1992; Gabriel et al., 1975; Lennartz and Weinberger, 1992; McEchron et al., 1996; O'Connor et al., 1997		Bäuerle et al., 2011; Calford, 1983; Kitzes and Buchwald, 1969; Komura et al. 2001, 2005; Ryan et al., 1984
Inferior Colliculus	Brainard and Knudsen, 1993; Gao and Suga, 1998, 2000; Ji et al., 2001		Finlayson and Adam, 1997b; Kitzes and Buchwald, 1969; Ryan et al., 1984
Superior Olive			Finlayson and Adam, 1997a, 1997b; Park et al., 2008; Ryan et al., 1984
Cochlear Nuclei	Edeline et al., 1990; Oleson et al., 1975; Woody et al., 1992, 1994		Buchwald and Humphrey, 1972; Kaltenbach et al., 1998; Webster et al., 1965; Worden and Marsh, 1963

^a Classical and operant conditioning

^b Short-term memory, working memory, recognition memory

^c Active versus passive listening, attention, stimulus presentation history, stimulus-specific adaptation, co-presentation of stimuli

* Review article

Please note that the associative conditioning listed for the inferior colliculus and cochlear nucleus may be the result of feedback from higher auditory regions and more studies combining lesions and recording need to be done to verify these results. However, these same type of confirmatory studies with lesions, either permanent or temporary, in upper divisions of the auditory system with recording in the lower structures during acquisition should be done for all regions showing plasticity to determine the origination of plasticity and the sources of feedback or interactions as this may also be occurring in the medial geniculate nucleus (e.g., Poremba and Gabriel, 2001) or auditory cortex as well, perhaps modulated by the type of learning.