



# Perceptual Plasticity for Auditory Object Recognition

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### Specialty section:

This article was submitted to  
Auditory Cognitive Neuroscience,  
a section of the journal  
Frontiers in Psychology

**Received:** 03 March 2016

**Accepted:** 26 April 2017

**Published:** 23 May 2017

### Citation:

Heald SLM, Van Hedger SC and  
Nusbaum HC (2017) Perceptual  
Plasticity for Auditory Object  
Recognition. *Front. Psychol.* 8:781.  
doi: 10.3389/fpsyg.2017.00781

In our auditory environment, we rarely experience the exact acoustic waveform twice. This is especially true for communicative signals that have meaning for listeners. In speech and music, the acoustic signal changes as a function of the talker (or instrument), speaking (or playing) rate, and room acoustics, to name a few factors. Yet, despite this acoustic variability, we are able to recognize a sentence or melody as the same across various kinds of acoustic inputs and determine meaning based on listening goals, expectations, context, and experience. The recognition process relates acoustic signals to prior experience despite variability in signal-relevant and signal-irrelevant acoustic properties, some of which could be considered as “noise” in service of a recognition goal. However, some acoustic variability, if systematic, is lawful and can be exploited by listeners to aid in recognition. Perceivable changes in systematic variability can herald a need for listeners to reorganize perception and reorient their attention to more immediately signal-relevant cues. This view is not incorporated currently in many extant theories of auditory perception, which traditionally reduce psychological or neural representations of perceptual objects and the processes that act on them to static entities. While this reduction is likely done for the sake of empirical tractability, such a reduction may seriously distort the perceptual process to be modeled. We argue that perceptual representations, as well as the processes underlying perception, are dynamically determined by an interaction between the uncertainty of the auditory signal and constraints of context. This suggests that the process of auditory recognition is highly context-dependent in that the identity of a given auditory object may be intrinsically tied to its preceding context. To argue for the flexible neural and psychological updating of sound-to-meaning mappings across speech and music, we draw upon examples of perceptual categories that are thought to be highly stable. This framework suggests that the process of auditory recognition cannot be divorced from the short-term context in which an auditory object is presented. Implications for auditory category acquisition and extant models of auditory perception, both cognitive and neural, are discussed.

**Keywords:** auditory perception, speech perception, music perception, short-term plasticity, categorization, perceptual constancy, lack of invariance, dynamical systems

## INTRODUCTION

Perceptual understanding of the auditory world is not a trivial task. We generally perceive discrete auditory objects, despite highly convolved auditory scenes that occur in the real world. For example, we can effortlessly perceive a siren in the distance and the hum of a washing machine while following a dialog in a movie that is underscored by background music. In part, recognizing these sound objects is aided by the spatial separation of the waveforms (see Cherry, 1953) as well as perceptual organization (see Bregman, 1990). However, each of our two basilar membranes is vibrated by the aggregation of the separate source waveforms striking our eardrums. Moreover, each of the sound objects, beyond being mixed in with an uncertain sound stage of other sound objects, may be distorted by the room, by motion, and further may be physically different from the generator of similar objects (washing machine, siren, or talker) we have encountered in the past. Simply stated, there is an incredible amount of variability in our auditory environments.

In speech, the lack of invariance between acoustic waveforms and their intended linguistic meaning became clear when the spectrograph was used to visually represent acoustic patterns in the spectro-temporal domain. Between talkers, there is variation in vocal tract size and shape that translates into differences in the acoustic realization of phonemes (Fant, 1960; Stevens, 1998). However, even local changes over time in linguistic experience (Cooper, 1974; Iverson and Evans, 2007), affective state (Barrett and Paus, 2002), speaking rate (Gay, 1978; Miller and Baer, 1983), and fatigue (Lindblom, 1963; Moon and Lindblom, 1994) can alter the acoustic realization of a given phoneme. Understanding the various sources of variability and their consequences on speech signals is important as different sources of variability may evoke different adaptive mechanisms for their resolution (see, Nygaard et al., 1995).

Beyond sources of variability that seemingly obstruct identification, there is clear evidence that idiosyncratic articulatory differences in how individuals produce phonemes result in acoustic differences (Liberman et al., 1967). Similar sources of variability hold for higher levels of linguistic representation, such as syllabic, lexical, prosodic, and sentential levels of analysis (cf. Heald and Nusbaum, 2014). Moreover, a highly variable acoustic signal is by no means unique to speech. In music, individuals have a perception of melodic stability or preservation of a melodic “Gestalt” despite changes in tempo (Handel, 1993; Monahan, 1993), pitch height or chroma (Handel, 1989), and instrumental timbre (Zhu et al., 2011). In fact, perhaps with a few contrived exceptions (such as listening to the same audio recording with the same speakers in the same room with the same background noise from the same physical location), we are not exposed to the same acoustic pattern of a particular auditory object twice. The question then becomes – how do we perceptually process acoustic variability in order to achieve a sense of experiential stability and recognizability across variable acoustic signals?

## REGULARITIES IN OUR ENVIRONMENT SHAPE OUR PERCEPTUAL EXPERIENCE

One possibility is that perceptual stability arises from the ability to form and use categories or classes of functional equivalence. It is a longstanding assertion in cognitive psychology that categorization serves to reduce psychologically irrelevant variability, carving the world up into meaningful parts (Bruner et al., 1956). In audition, some have argued that the categorical nature of speech perception originates in the architecture of the perceptual system (Elman and McClelland, 1986; Holt and Lotto, 2010). Other theories have suggested that speech categories arise out of sensitivity to the statistical distribution of occurrences of speech tokens (for a review, see Feldman et al., 2013).

Indeed, it has been proposed that the ability to extract statistical regularities in one’s environment, which could occur by an unsupervised or implicit process, shapes our perceptual categories in both speech (cf. Strange and Jenkins, 1978; Werker and Tees, 1984; Kuhl et al., 1992; Werker and Polka, 1993; Saffran et al., 1996; Kluender et al., 1998; Maye and Gerken, 2000; Maye et al., 2002) and music (cf. Lynch et al., 1990; Lynch and Eilers, 1991, 1992; Soley and Hannon, 2010; Van Hedger et al., 2016). An often-cited example in speech research is that an infant’s ability to discriminate sounds in their native language increases with linguistic exposure, while the ability to discriminate sounds that are not linguistically functional in their native language decreases (Werker and Tees, 1983). Further, work in speech development by Nittrouer and Miller (1997), Nittrouer and Lowenstein (2007) has shown that the shaping of perceptual sensitivities and acoustic to phonetic mappings by one’s native language experience occurs throughout adolescence, indicating that individuals remain sensitive to the statistical regularities of acoustic cues and how they covary with sound meaning distinctions throughout their development. Therefore, it seems that given enough listening experience, individuals are able to learn how multiple acoustic cues work in concert to denote a particular meaning, even when no single cue is necessary or sufficient.

## SOUNDS IN A SYSTEM OF CATEGORIES

Individuals are not only sensitive to the statistical regularities of items that give rise to functional classes or categories, but to the systematic regularities *among* the resulting categories themselves. This hierarchical source of information, which goes beyond any specific individual category, could aid in disambiguating a physical signal that has multiple meanings. For both speech and music this allows the categories within each system to be defined internally, through the relationships held among categories of each system. This suggests that individuals possess categories that work collectively with one another as a long-term, experientially defined context to orchestrate a cohesive perceptual world (see Bruner, 1973; Billman and Knutson, 1996; Goldstone et al., 2012). In music, the implied key of a musical piece organizes the interrelations among pitch classes in a hierarchical structure (Krumhansl and Shepard, 1979; Krumhansl and Kessler, 1982).

Importantly, these hierarchical relations become strengthened as a function of listening experience, suggesting that experience with tonal areas or keys shapes how individuals organize pitch classes (cf. Krumhansl and Keil, 1982). These hierarchical relationships are also seen in speech among various phonemic classes, initially described as a featural system (e.g., Chomsky and Halle, 1968) and the distributional constraints on phonemes and phonotactics. For a given talker, vowel categories are often discussed as occupying a vowel space that roughly corresponds to the speaker's articulatory space (Ladefoged and Broadbent, 1957). Some authors have posited that point vowels, which represent the extremes of the acoustic and articulatory space, may be used to calibrate changes in the space across individuals, as they systematically bound the rest of the vowel inventory (Joos, 1948; Gerstman, 1968; Lieberman et al., 1972). Due to the concomitant experience of visual information and acoustic information (rooted in the physical process of speech sound production), there are also systematic relations that extend between modalities. For example, an auditory /ba/ paired with a visual /ga/ often yields the perceptual experience of /da/ due to the systematic relationship of place of articulation among those functional classes (McGurk and MacDonald, 1976). Given these examples, it is clear that within both speech and music, perceptual categories are not isolated entities. Rather, listening experience over time confers systematicity that can be meaningful. Such relationships may be additionally important to ensure stability in a system that is heavily influenced by recent perceptual experience, as stability may exist through interconnections within the category system. Long-term learning mechanisms may remove short-term changes that are inconsistent with the system, while in other cases, allow for such changes to generalize to the rest of the system in order to achieve consistency.

## STABILITY OF PERCEPTUAL SYSTEMS?

Despite clear evidence that listeners are able to rapidly learn from the statistical distributions of their acoustic environments, both for the formation of perceptual categories and the relationships that exist among them, few auditory recognition models include such learning<sup>1</sup>. Indeed, speech perception models such as feature-detector theories (e.g., Stevens and Blumstein, 1981), ecological theories (Fowler and Galantucci, 2005), motor theories (e.g., Liberman and Mattingly, 1985), and interactive theories (TRACE: e.g., McClelland and Elman, 1986; C-CuRe: McMurray and Jongman, 2011) provide no mechanism to update perceptual representations, and as such, implicitly assume that the representations that guide the perceptual process are more stable than plastic. While C-CuRE (McMurray and Jongman, 2011) might be thought of as highly adaptive by allowing different levels of abstraction to interact during perception, this model does not make claims about how the representations that guide perception are established either in terms of the formation of auditory objects or the features that comprise them. For example,

the identification of a given vowel depends on the first (F1) and second (F2) formant values, but some of these values will be ambiguous depending on the linguistic context and talker. According to C-CuRE, once the talker's vocal characteristics are known, a listener can make use of these formant values. The listener can compare the formant values of the given signal against the talker's average F1 and F2, helping to select the likely identification of the vowel. Importantly, for the C-CuRE model, feature meanings are already available to the listener. While there is some suggestion that this knowledge could be derived from linguistic input and may be amended, the model itself has remained agnostic as to how and when this information is obtained and updated by the listener. A similar issue arises in other interactive models of speech perception (e.g., TRACE: McClelland and Elman, 1986; Hebb-Trace: Mirman et al., 2006) and models of pitch perception (e.g., Anantharaman et al., 1993; Gockel et al., 2001).

While some auditory neurobiological models demonstrate clear awareness that mechanisms for learning and adaptation be included in models of perception and recognition (Weinberger, 2004, 2015; McLachlan and Wilson, 2010; Shamma and Fritz, 2014), this is less true for neurobiological models of speech perception, which traditionally limit their modeling to perisylvian language areas (Fitch et al., 1997; Hickok and Poeppel, 2007; Rauschecker and Scott, 2009; Friederici, 2012), ignoring brain regions that have been implicated in category learning, such as the striatum, the thalamus, and the frontoparietal attention-working memory network (McClelland et al., 1995; Ashby and Maddox, 2005). Further, the restriction of speech models to perisylvian language areas marks an extreme cortical myopia of the auditory system, as it ignores the corticofugal pathways that exist between cortical and subcortical regions such as the medial geniculate nucleus in the thalamus, the inferior colliculus in the midbrain, the superior olive and cochlear nucleus in the pons, all the way down to the cochlea in the inner ear (cf. Parvizi, 2009). Previous work has shown that higher-level cognitive functions can reorganize subcortical structures as low as the cochlea. For example, selective attention or discrimination training has been demonstrated to enhance the spectral peaks of evoked otoacoustic emissions produced in the inner ear (Giard et al., 1994; Maison et al., 2001; de Boer and Thornton, 2008). Inclusion of the corticofugal system in neurobiological models of speech would allow the system, through feedback and top-down control, to adapt to ambiguity or change in the speech signal by selectively enhancing the most diagnostic spectral cues for a given talker or expected circumstance, even before it reaches perisylvian language areas. Including the corticofugal system can thus drastically change how extant models, which are entirely cortical, explain top-down, attention modulated effects in speech and music. While the omission of corticofugal pathways and brain regions associated with category learning is likely not an intentional omission but a simplification for the sake of experimental tractability, it is clear that such an omission has large scale consequences for modeling auditory perception, speech or otherwise. Indeed, the inclusion of learning areas and adaptive corticofugal connections on auditory processing requires a vastly different view of perception, in that even the

<sup>1</sup> Although for exceptions, see Tuller et al. (1994), Case et al. (1995), Mirman et al. (2006), Lancia and Winter (2013), and Kleinschmidt and Jaeger (2015).

earliest moments of auditory processing are guided by higher cognitive processing via expectations and listening goals. In this sense, it is unlikely that learning and adaptability can be simply grafted on top of current cortical models of perception. The very notion that learning and adaptive connections could be omitted, however, (even for the sake of simplicity) is in essence, a tacit statement that the representations that guide recognition are more stable than plastic.

The notion that our representations are more stable than plastic may also be rooted in our experience of the world as perceptually stable. In music, relative perceptual constancy can be found for a given melody despite changes in key, tempo, or instrument. Similarly, in speech, a given phoneme can be recognized despite changes in phonetic environment and talker. This is not to say that listeners are “deaf” to acoustic differences between different examples of a given melody or phoneme, but that different goals in listening can arguably shape the way we direct attention (consciously or unconsciously) to variability among auditory objects. In this sense, listening goals organize attention, such that individuals orient toward cues that reflect a given parsing, and away from cues that do not (cf. Goldstone and Hendrickson, 2010). More recent work on change deafness demonstrates that changes in listening goals alter a participant’s ability to notice a change in talker over a phone conversation (Fenn et al., 2011). More specifically, the authors demonstrated that participants did not detect a surreptitious change in talker during a phone conversation, but could detect the change if told to explicitly monitor for it. This suggests that listening goals modulate how we parse or categorize signals, in that these listening determine how attention is directed toward the acoustic variance of a given signal.

Perceptual classification or categorization here should not be confused with categorical perception (cf. Holt and Lotto, 2010). *Categorical perception*, classically defined in audition, refers to the notion that a continuum of sounds that differ along a particular acoustic dimension are not heard to change continuously, but rather as an abrupt shift from one category to another (e.g., Liberman et al., 1957). As such, categorical perception suggests that despite changes in listening goals, individuals’ perceptual discrimination of any two stimuli is inextricably linked to the probability of classifying these stimuli as belonging to different categories (e.g., Studdert-Kennedy et al., 1970). Categorization, conversely, refers to a particular organization of attention, wherein cues that are indicative of between-category variability are emphasized while cues that reflect within-category variability are deemphasized (Goldstone, 1994). Indeed, even within the earliest examples of categorical perception (a phenomenon that, in theory, completely attenuates within-category variability), there appears to be some retention of within-category discriminability (e.g., Liberman et al., 1957). English listeners can reliably rate some acoustic realizations of phonetic categories (e.g., “ba”) as better versions than others (e.g., Pisoni and Lazarus, 1974; Pisoni and Tash, 1974; Carney et al., 1977; Iverson and Kuhl, 1995). Additionally, a number of studies have shown that not only are individuals sensitive to within-category variability, but also this variability affects subsequent lexical processing (Dahan et al., 2001; McMurray et al., 2002;

Gow et al., 2003). In music, the perception of pitch chroma categories among absolute pitch (AP) possessors is categorical in the sense that AP possessors show sharp identification boundaries between note categories (e.g., Ward and Burns, 1999). However, AP possessors also show reliable within-category differentiation when providing goodness judgments within a note category (e.g., Levitin and Rogers, 2005). Graded evaluations within a category are further seen in musical intervals, where sharp category boundaries indicative of categorical perception are also generally observed at least for musicians (Siegel and Siegel, 1977). There is also evidence that within-category discrimination can exceed what would be predicted from category identification responses (Zatorre and Halpern, 1979). Indeed, Holt et al. (2000) have suggested that the task structure typically employed in categorical perception tasks may be what is driving the manifestation of within category homogeneity that is characteristic of categorical perception. Another way of stating this is that listening goals defined by the task structure modulate the way attention is directed toward acoustic variance.

While there is clear evidence that individuals possess the ability to attend to acoustic variability, even within perceptual categories, it is still unclear from the demonstrations reported thus far whether listeners are influenced by acoustic variability that is attenuated by disattention due to their listening goals. More specifically, it is unclear whether the representations that guide perception are influenced by subtle, within-category acoustic variability, even if it appears to be functionally irrelevant for current listening goals. Even though there is ample evidence that perceptual sensitivity to acoustic variability is attenuated through categorization, this variability may nevertheless be preserved and further, may be incorporated into the representations that guide perception. In this sense, putatively irrelevant acoustic variability, even if not consciously experienced, may still affect subsequent perception. For example, Gureckis and Goldstone (2008) have argued that the preservation of variability (in our case, the acoustic trace independent of the way in which the acoustics relate to an established category structure due to a current listening goal) allows for perceptual plasticity within a system, as adaptability can only be achieved if individuals are sensitive (consciously or unconsciously) to potentially behavioral relevant changes in within-category structure. In this sense, without the preservation of variability listeners would fail to adapt to situations where the identity of perceptual objects rapidly change. Indeed, there is a growing body of evidence supporting the view that the preservation of acoustic variability can be used in service of instantiating a novel category. In speech, adult listeners are able to amend perceptual categories as well as learn novel perceptual categories not present in their native language, even when the acoustic cues needed to learn the novel category structure are in direct conflict with a preexisting category structure. Adult native Japanese listeners, who presumably become insensitive to the acoustic differences between /r/ and /l/ categories through accrued experience listening to Japanese, are nevertheless able to learn this non-native discrimination through explicit perceptual training (Lively et al., 1994; Bradlow et al., 1997; Ingvalson et al., 2012), rapid incidental perceptual learning (Lim and Holt, 2011),

as well as through the accrual of time residing in English-speaking countries (Ingvalson et al., 2011). Further, adult English speakers are able to learn the non-native Thai pre-voicing contrast, which functionally splits their native /b/ category (Pisoni et al., 1982) and to distinguish between different Zulu clicks, which make use of completely novel acoustic cues (Best et al., 1988).

Beyond retaining an ability to form non-native perceptual categories in adulthood, there is also clear evidence that individuals are able to update and amend the representations that guide their processing of native speech. Clarke and Luce (2005) showed that within moments of listening to a new speaker, listeners modify their classification of stop consonants to reflect the new speaker's productions, suggesting that linguistic representations are plastic in that they can be adjusted online to optimize perception. This finding has been replicated in a study that further showed that participants' lexical decisions reflect recently heard acoustic probability distributions (Clayards et al., 2008).

Perceptual flexibility also can be demonstrated at a higher level, presumably due to discernible higher-order structure. Work in our lab has demonstrated that individuals are able to rapidly learn synthetic speech produced by rule that is defined by poor and often misleading acoustic cues. In this research, no words ever repeat during testing or training, so that the learning of a particular synthesizer is thought to entail the redirection of attention to the most diagnostic and behaviorally relevant acoustic cues across multiple phonemic categories in concert (see Nusbaum and Schwab, 1986; Fenn et al., 2003; Francis et al., 2007; Francis and Nusbaum, 2009) in much the same way as learning new phonetic categories (Francis and Nusbaum, 2002). Given these studies, it appears that the process of categorization in pursuit of current listening goals does not completely attenuate acoustic variability.

Beyond speech, the representations that guide music perception also appear to be remarkably flexible. Wong et al. (2009) have demonstrated that individuals are able to learn multiple musical systems through passive listening exposure. This "bimusicality" is not merely the storage of two, modular systems of music (Wong et al., 2011); though it is unclear whether early exposure (i.e., within a putative critical period) is necessary to develop this knowledge. In support of the notion that even adult listeners can come to understand a novel musical system that may parse pitch space in a conflicting way compared to Western music, Loui and Wessel (2008) have demonstrated that adult listeners of Western music are able to learn a novel artificial musical grammar. In their paradigm, individuals heard melodies composed using the Bohlen–Pierce scale – a musical system that is strikingly different from Western music, as it consists of 13 equally spaced notes within a three-octave range as opposed to 12 equally spaced notes within a two-octave range. Nevertheless, after mere minutes of listening to 15 Bohlen–Pierce melodies that conformed to a finite-state grammar, listeners were able to recognize these previously heard melodies as well as generalize the rules of the finite-state grammar to novel melodies.

Even within the Western musical system, adults display plasticity for learning categories thought to be unlearnable in adulthood. A particularly salient example of adult plasticity

within Western music learning comes from the phenomenon of AP – the ability to name or produce any musical note without the aid of a reference note (see Deutsch, 2013 for a review). AP has been conceptualized as a rare ability, manifesting in as few as one in every 10,000 individuals in Western cultures (Bachem, 1955), though the mechanisms of AP acquisition are still debated. While there is some research arguing for a genetic predisposition underlying AP (e.g., Baharloo et al., 1998; Theusch et al., 2009), with even some accounts claiming that AP requires little or no environmental shaping (Ross et al., 2003), most theories of AP acquisition adhere to an early-learning framework (e.g., Crozier, 1997). This framework predicts that only individuals with early note naming experience would be candidates for developing AP categories. As such, previously naive adults should not be able to learn AP. This early-learning argument of AP has been further explained as a "loss" of AP processing without early interventions, either from music or language (i.e., tonal languages), in which AP is emphasized (cf. Sergeant and Roche, 1973; Deutsch et al., 2004). In support of this explanation, infants appear to process pitch both absolutely and relatively, though they switch to relative pitch cues when AP cues become unreliable (Saffran et al., 2005).

Yet, similar to how even "irrelevant" acoustic variability within speech is not completely attenuated, there is mounting evidence that most individuals (regardless of possessing AP) retain the ability to perceive and remember AP, presumably through implicit statistical learning mechanisms. For example, non-AP possessors are able to tell when familiar music recordings have been subtly shifted in pitch (e.g., Terhardt and Seewan, 1983; Schellenberg and Trehub, 2003), even if they are not able to explicitly name the musical notes they are hearing. These results suggest that the perception of AP is not an ability that is completely lost without the knowledge of explicit musical note category labels or with more advanced development of relative pitch abilities. As such, it is possible that adult listeners might be able to learn how musical note categories map onto particular absolute pitches. In support of this idea, most studies examining the degree to which AP can be trained in an adult population find *some* improvement after training, even after a single training session (Van Hedger et al., 2015). A few studies have even found improvements in absolute note identification such that post-training performance rivals that of that an AP population who learned note categories early in life (Brady, 1970; Rush, 1989). These findings not only support the notion that most adults retain an ability to perceive and remember AP to some degree, but also that AP categories are, to an extent, trainable into adulthood.

Despite these accounts of AP plasticity within an adult population, one might still argue that the adult learning of AP categories represents a fundamentally different phenomenon than that of early-acquired AP, even if the behavioral note classifications from trained adults are, in some extreme cases, indistinguishable from that of an AP population who acquired note categories early in life. One reason to support this kind of dissociation between adult-acquired and early-acquired AP relates to the putative lack of plasticity that exists within an AP possessor who acquired note categories early in life. Specifically, note categories within an early-acquired AP

population are thought to be highly stable once established (Ward and Burns, 1999), only being alterable in very limited circumstances, such as through physiological changes to the auditory system as a result of aging (cf. Athos et al., 2007) or pharmaceutical interventions (e.g., Kobayashi et al., 2001). However, recent empirical evidence has demonstrated that even within this early-acquired AP population, there exists a great deal of plasticity in note category representations that is tied to particular environmental experiences. Wilson et al. (2012) reported reductions in AP ability as a function of whether an individual plays a “movable *do*” instrument (i.e., an instrument in which a notated “C” actually belongs to a different pitch chroma category, such as “F”), suggesting that nascent AP abilities might be undone through inconsistent sound-to-category mappings. Dohn et al. (2014) reported differences in note identification accuracy among AP possessors that could be explained by whether one was actively playing a musical instrument, suggesting that AP ability might be “tuned up” by recent musical experience.

Both of these studies speak to how particular regularities in the environment may affect overall note category accuracy within an AP population, though they do not speak to whether the *structure* of the note categories can be altered through experience once they are acquired. Indeed, one of the hallmarks of AP is not only being able to accurately label a given pitch with its note category (e.g., C#), but also provide a goodness rating of how well that pitch conforms to the category (e.g., flat, in-tune, or sharp). Presumably, this ability to label some category members as better than others stems from either a fixed note-frequency association established early in life, or through the consistent environmental exposure of listening to music that is tuned to a very specific standard (e.g., in which the “A” above middle C is tuned to 440 Hz). Adopting the first explanation, plasticity of AP category structure should not be possible. Adopting the second explanation, AP category structure should be modifiable and tied to the statistical regularities of hearing particular tunings in the environment. Our previous work has clearly demonstrated evidence in support of this second explanation – that is, the structure of note categories for AP possessors is plastic and dependent on how music is tuned in the current listening environment (Hedger et al., 2013). In our paradigm, AP possessors assigned goodness ratings to isolated musical notes. Not surprisingly, in-tune notes (according to an  $A = 440$  Hz standard) were rated as more “in-tune” than notes that deviated from this standard by one-third of a note category. However, after listening to a symphony that was slowly flattened by one-third of a note category, the same participants began rating similarly flattened versions of isolated notes as more “in-tune” than the notes that were in-tune based off of the  $A = 440$  Hz standard. These findings suggest that AP note categories are held in place by the recent listening environment, not by a fixed and immutable note-frequency association that is established early in life. Overall, then, the past decade or so of research on AP has highlighted how this ability can be modified by behaviorally relevant environmental input that extends well into adulthood.

## CROSS-DOMAIN TRANSFER BETWEEN MUSIC AND SPEECH

These accounts of plasticity in auditory perception for both speech and music suggest that both systems may be subserved by common perceptual and learning mechanisms. Recent work exploring the relationship between speech and music processing has found mounting evidence that musical training improves several aspects of speech processing, though it is debated whether these transfer effects are due to general enhancements in auditory processing (e.g., pitch perception) vs. an enhanced representation of phonological categories. Hypotheses like OPERA (Patel, 2011) posit that musical training may enhance aspects of speech processing when there is anatomical *overlap* between networks that process the acoustic features shared between music and speech, when the perceptual *precision* required of musical training exceed that of general speech processing, when the training of music elicits positive *emotions*, when musical training is *repetitive*, and when the musical training engages *attention*. Indeed, the OPERA hypothesis provides a framework for understanding many of the empirical findings within the music-to-speech transfer literature. Musical training helps individuals to detect speech in noise (Parbery-Clark et al., 2009), presumably through strengthened auditory working memory, which requires directed attention. Musicians are also better able to use non-native tonal contrasts to distinguish word meanings (Wong and Perrachione, 2007), presumably because musical training has made pitch processing more precise. This explanation can further be applied to the empirical findings that musicians are better able to subcortically track the pitch of emotional speech (Strait et al., 2009).

Recent work has further demonstrated that musical training can also influence the categorical perception of speech. Bidelman et al. (2014) found that musicians showed steeper identification functions of vowels that varied along a categorical speech continuum, and moreover these results could be modeled by changes at multiple levels of the auditory pathway (both subcortical and cortical). In a similar study, Wu et al. (2015) found that Chinese musicians were better able to discriminate within-category lexical tone exemplars in a categorical perception task compared to non-musicians, though, unlike Bidelman et al. (2014), the between-category differentiation between musicians and non-musicians was comparable. Wu et al. (2015) interpret the within-category improvement among musicians in an OPERA framework, arguing that musicians have more precise representations of pitch that allow for fine-grained distinctions within a linguistic category.

Finally, there is emerging evidence that certain kinds of speech expertise may enhance musical processing, demonstrating a proof-of-concept of the bidirectionality of music-speech transfer effects. Specifically, non-musician speakers of a tonal language (Cantonese) showed auditory processing advantages in pitch acuity and music perception that non-musician speakers of English did not show (Bidelman et al., 2013). While there is less evidence supporting this direction of transfer, this is perhaps not surprising as speech expertise is ubiquitous in a way music

expertise is not. Thus, transfer effects from speech to music processing are more constrained, as one has to design a study in which there (1) exists substantial differences in speech expertise, and (2) this difference in expertise must theoretically relate to some aspect of music processing (e.g., pitch perception).

How can these transfer effects between speech and music be interpreted in the larger context of auditory object plasticity? Given the evidence across speech and music that recent auditory events profoundly influence the perception of auditory objects within each system, it stands to reason that recent auditory experience from one system of knowledge (e.g., music) may influence subsequent auditory perception in the other system (e.g., speech), assuming there is overlap among particular acoustic features of both systems. Indeed, there is some empirical evidence to at least conceptually support this idea. An accumulating body of work has demonstrated that the perception of speech sounds is influenced by the long-term average spectrum (LTAS) of a preceding sound, even if that preceding sound is non-linguistic in nature (e.g., Holt et al., 2000; Holt and Lotto, 2002). This influence of non-linguistic sounds on speech perception appears to reflect a general sensitivity to spectro-temporal distributional information, as the non-linguistic preceding context can influence speech categorization even when it is not immediately preceding the to-be-categorized speech sound (Holt, 2005). While these results do not directly demonstrate that recent experience in music can influence the way in which a speech sound is categorized, it is reasonable to predict that certain kinds of experiences in music or speech (e.g., a melody played in a particular frequency range) may alter the way in which subsequent speech sounds are perceived. As such, future work within this realm will help us understand the extent to which auditory object plasticity can be understood using a general auditory framework.

## NEURAL MARKERS FOR RAPID AUDITORY PLASTICITY

What is most remarkable about the previously discussed examples of perceptual plasticity in both speech and music is that significant reorganization of perception can be achieved within a single experimental session. Indeed, there is clear neural evidence from animal models that the ability to rapidly reorganize maps in auditory cortex is maintained into adulthood (see Feldman and Brecht, 2005 for a review; Ohl and Scheich, 2005). While these maps are thought to represent long-term experience with one's auditory environment (Schreiner and Polley, 2014), they demonstrate high mutability in adults, in that cortical reorganizations may be triggered by task demands as well as the attentional state of the animal (Ahissar et al., 1992, 1998; Fritz et al., 2003, 2010; Fritz J.B. et al., 2005; Polley et al., 2006; for a review see Jääskeläinen and Ahveninen, 2014). In fact, plasticity is not observed when the stimuli are not behaviorally relevant for the organism (Ahissar et al., 1992; Polley et al., 2006; Fritz et al., 2010). Behaviorally relevant experience with a set of tones is known to lead to rapid tonotopic map expansion (Recanzone et al., 1993; Polley et al., 2006; Bieszczad and Weinberger, 2010),

sharper receptive field tunings (Recanzone et al., 1993), and greater neuronal synchrony (Kilgard et al., 2007). Notably, these changes appear to have a direct effect on subsequent performance wherein larger cortical map expansion and sharper receptive field tunings are associated with greater improvements in performance following training (Recanzone, 2003). Further, the changes in spectro-temporal receptive field selectivity and inhibition persist for hours after learning, even during subsequent passive listening (Fritz et al., 2003). More recent work by Reed et al. (2011) suggests that while cortical map expansion may be triggered by perceptual learning, these states do not need to be maintained in order to preserve perceptual performance gains. They argue that the function of cortical map expansions is to identify the most efficient circuitry to support a behaviorally relevant, perceptual improvement. Once efficient circuitry is established, the system is able to preserve enhancement in performance via the discovered circuitry despite any subsequent retraction in cortical map representation.

Beyond tonotopic changes, other modes of plasticity in auditory cortex have been found as a consequence of auditory training. For example, experience discriminating spectrally structured auditory gratings (often referred to as auditory spectral ripples) leads to significant changes in the spectral and spectro-temporal receptive field bandwidth of neurons in auditory cortex (Keeling et al., 2008; Yin et al., 2014). These changes, if present in humans, would provide a mechanism that supports the perceptual adaptation to complex sounds, such as phonemes or chord classification (e.g., Schreiner and Calhoun, 1994; Kowalski et al., 1995; Keeling et al., 2008). Besides changes in spectral bandwidth receptivity, auditory training in adult animals can fully correct atypical temporal processing found in auditory cortex due to long-term auditory deprivation, such that normal following capacity and spike-timing precision are found after training (Beitel et al., 2003; Zhou et al., 2012). Crucially, training also appears to induce object-based or category-level processing, in that behaviorally relevant experience engenders complex, categorical representations that go beyond acoustic feature processing (King and Nelken, 2009; Bathellier et al., 2012; Bao et al., 2013; Lu et al., 2017). More specifically, recent work by Bao et al. (2013) has shown that early training leads to neural selectivity for complex spectral features in that trained sounds show greater population level activation relative to untrained sound. Further, while experienced sounds post-training show a reduction in the number of responding neurons, these elicited responses are greater in magnitude. Importantly, the mechanisms guiding plasticity appear to maintain homeostasis within individual receptive fields, in that inhibitory and excitatory synaptic modifications are coordinated such that they collectively sum to zero across a single neuron's receptive field (Froemke et al., 2013). Coordination between inhibitory and excitatory modifications within a receptive field are necessary, as changes in long-term potentiation or long-term depression alone would create destabilized network activity that is either hyper or hypo-receptive (Abbott and Nelson, 2000). Importantly, the balancing of synaptic modification within individual receptive fields is predicted by cognitive theories of selective attention, which suggest that while directed attention

perceptually boosts salient or behaviorally relevant stimuli, it does so at the expense of other stimuli (for a review see, Treisman, 1969).

Neural evidence for rapid perceptual learning in adults has also been found in humans (for reviews, see Jääskeläinen and Ahveninen, 2014; Lee et al., 2014). Specifically, perceptual training of novel phonetic categories appears to lead to changes in early sensory components of scalp recorded auditory evoked potentials (AEPs), which are thought to arise from auditory cortex (Hari et al., 1980; Wood and Wolpaw, 1982; Näätänen and Picton, 1987), suggesting that experience-contingent, perceptual reorganization similarly occurs in humans (e.g., Tremblay et al., 2001; Reinke et al., 2003; Alain et al., 2007, 2015; Ben-David et al., 2011). A recent fMRI and AEP study by de Souza et al. (2013) has shown that rapid perceptual learning is marked not only by a reorganization in sensory cortex but in higher level areas such as left and right superior temporal gyrus and left inferior frontal gyrus. Importantly, their findings suggest that perceptual reorganization due to training is gated by the allocation of attention, implicating behavioral relevance via listening goals as the gating agent in perceptual plasticity. Evidence for this can also be found in the work of Mesgarani and Chang (2012). Using Electrocorticography (ECoG), where electrodes are placed directly on the surface of the brain to record changes in electrical activity from cortex, Mesgarani and Chang (2012) demonstrated that the cortical representations evoked to understand a signal are determined largely by listening goals, such that rapid changes in which talker participants were attending to in multi-talker speech led to immediate changes in population responses in non-primary auditory cortex known to encode critical spectral and temporal features of speech. Specifically, they showed that cortical responses in non-primary auditory cortex are attention-modulated, such that the representations evoked were specific to the talker to which the listener was attending, rather than the external acoustic environment (Mesgarani and Chang, 2012; see also Zion-Golumbic et al., 2013; for review see, Zion-Golumbic and Schroeder, 2012).

As previously mentioned, rapid neural changes in sensory and higher level areas are thought to be the product of the corticofugal system (which includes cortex and subcortical structures such as the inferior colliculus, thalamus, amygdala, hippocampus, and cerebellum), in that bottom-up processes may operate contemporaneously and interactively with top-down driven processes to actively shape signal processing (Suga and Ma, 2003; Slee and David, 2015). Rapid strengthening or diminishing of synapse efficacy can occur within minutes through mechanisms such as long-term potentiation and long-term depression (Cruikshank and Weinberger, 1996; Finnerty et al., 1999; Dinse et al., 2003). As previously mentioned, these alterations appear to be contingent on whether input is behaviorally relevant, especially in the adult animal, suggesting that neural plasticity is gated by top-down or descending systems (Crow, 1968; Kety, 1970; Ahissar et al., 1992; Ahissar et al., 1998; for similar work in adult rats, see Polley et al., 2006) such as the cholinergic and noradrenergic systems that originate from the basal forebrain whose effects are mediated through the regulation of GABA circuits (Ahissar et al., 1996). While there appears to

be receptivity in the speech and music community to modeling putatively top-down interactions operating entirely in cortex (George and Hawkins, 2009; Kiebel et al., 2009; Friston, 2010; Moran et al., 2013; Yildiz et al., 2013), very little work has been done to model corticofugal interactions in achieving behaviorally relevant signal processing, as extant neurobiological models of speech and music traditionally limit modeling solely to cortex. As such, the process of perception that extant models puts forth reflects a myopic view of the neural architecture that supports auditory understanding in a world where behavioral relevance is ever-changing (cf. Parvizi, 2009).

Beyond the notion that rapid cortical changes appear to persist for hours, even after the conclusion of a given task (Fritz et al., 2003; Fritz J. et al., 2005; Fritz J.B. et al., 2005), more recent work has started to examine how such rapid changes may be made more robust through other concurrent but more long-term neurobiological mechanisms that may require off-line processing during an inactive period such as sleep (Louie and Wilson, 2001; Brawn et al., 2010). These long-term mechanisms include dendritic remodeling, changes in receptor and transmitter base levels or axonal sprouting or pruning (Sun et al., 2005). Indeed, it is unlikely that immediate changes in cortex are a product of rapid remodeling of synaptic connections, or dendritic expansion or formation, which are likely components of more long-term mechanisms that support learning. Fritz et al. (2013) have suggested that rapid changes in behavior may be driven by changes in the gain of synaptic input onto individual dendritic spines, which may have the necessary architecture to achieve rapid changes. Recent work by Chen et al. (2011) supports this suggestion, as individual synaptic spines on dendrites of layers II to III of A1 neurons in mice are remarkably variable in their tuning frequencies, in that individual neurons possess dendritic spines that are tuned to widely different frequencies, with tunings that are both broad and narrow. As such, the arrangement and pattern of synaptic spines of A1 neurons appears to provide an ideal substrate for rapid cortical receptive field plasticity.

The notion that there are multiple learning mechanisms operating at different time scales concurrently is present in some cognitive learning models (e.g., complementary learning systems, McClelland et al., 1995; Ashby and Maddox, 2005; Ashby et al., 2007). While these models have been important in accounts of learning and memory, they have not been widely incorporated in models of speech and music perception. This omission along with the extreme cortical myopia found within models of speech and music perception reflect an overly simplified, perhaps misguided understanding of the neural mechanisms that underlie perception, as the addition of such mechanisms may drastically alter the processes to be modeled. More explicitly, an important consequence of viewing the perceptual process as highly adaptive is that putatively uninformative variability is no longer something for the system to overcome, but part of the information the system uses to grant perceptual constancy. In this way, it may be our ability to adapt to variable experiences that allows one to assign behaviorally relevant meaning and achieve perceptual stability.

A somewhat different approach to understanding perceptual representations and learning, however, can be found in neural dynamical system models (Laurent et al., 2001; Rabinovich et al., 2001). These models treat a given interpretation for an object as one of many paths through a multidimensional feature space in service of a given listening goal. In essence, the patterns of neural activity in these kinds of systems can form stable trajectories (reflecting different classifications) that are distinct but mutable with experience. These models do not have “stored memories” separate from the processing activity itself within neural populations, so that auditory objects would be represented by the pattern of neural activity over time within the processing network, with different spectro-temporal patterns having different stabilities. This is entirely consistent with Walter Freeman’s work on brain oscillations showing that after rabbits learn a set of odor objects, learning a new odor subsequently alters oscillatory patterns associated with *all* previously learned odors (Freeman, 1978). These types of models do not require a separate stable “representation” for a given object such that different neurons or different network subparts are disjunctively representative of different objects, but instead dynamically create a percept from stable patterns of neural activity arising from the interaction with neural populations. Given that this marks a theoretical shift in ideas about perceptual representation from a traditional neuron doctrine (Barlow, 1972) or cell assembly idea (e.g., Hebb, 1949) in which specific neurons are identified with psychologically distinct objects to the idea that these representations emerge in the patterns of neural activity within a network (see Yuste, 2015), it is unclear how such a framework may be applied to the neural receptive field tuning data just reviewed. One possibility is that changes in behaviorally relevance or training via exposure may shift the activity pattern in a population of neurons from one stable trajectory to another and that mechanisms such as cortical magnification may allow for the most efficient pattern to be found (see, Reed et al., 2011). Models of this sort may provide a different way of conceptualizing short-term and long-term changes in tunings by unifying the impact of experience, not on the formation of representations in memory, but through the dynamic interaction of neural population responses that are sensitive to changes in attention and context.

## RELiance ON RECENT EXPERIENCE AND EXPECTATIONS

The evidence cited earlier that receptive fields change as a result of behaviorally relevant experience and that such changes persist after learning, highlights that perceptual constancy may indeed arise through a categorization process that results in attenuation of goal-irrelevant acoustic variability in service of current listening goals. However, such variability may be preserved outside of the veil of perceptual constancy and be incorporated, if lawful, into the representations that guide perception (Elman and McClelland, 1986). Indeed, individuals are faced with continual changes in how phonetic categories are acoustically realized over time at both a community level (Watson et al., 2000; Labov, 2001)

and at an idiosyncratic level (Bauer, 1985; Evans and Iverson, 2007). As such, neural representations must preserve aspects of variability outside of processes that produce forms of perceptual constancy.

Work by Tuller et al. (1994), Case et al. (1995) have put forth a non-linear dynamic model of speech perception. In their model, perception is viewed as a dynamical process that is highly context-dependent, such that perceptual constancy is achieved via attraction to “perceptual magnets” that are modified non-linearly through experience. Crucial to their model, listeners remain sensitive to the fine-grain acoustic properties of auditory input as recent experience can induce a shift in perception. Similar to Tuller et al. (1994), Kleinschmidt and Jaeger (2015) have proposed a highly context-dependent model of speech perception. In their model, perceptual stability in speech is achieved through recognition “strategies” that vary depending on the degree to which a signal is familiar based on past experience. This flexible strategic approach based on prior familiarity is critical for successful perception, as a system that is rigidly fixed in acoustic-to-meaning mappings would fail to recognize (perhaps by misclassification) perceptual information that was distinct from past experience, whereas a system that is too flexible might require a listener to continually start from scratch. However, from this view, perceptual constancy is not achieved through the activation of a fixed set of features, but through listening expectations based on the statistics of prior experience. In this way, perceptual constancy arising from such a system could be thought of as an emergent property that results from the comparison of prior experience to bottom-up information from (i) the signal and (ii) recent listening experience (i.e., context).

Within a window of recent experience, what kinds of cues convey to a listener that a deviation from expectations has occurred? Listeners must flexibly shift between different situations that may have different underlying statistical distributions (Qian et al., 2012; Zinszer and Weiss, 2013), using contextual cues that signal a change in an underlying statistical structure (Gebhart et al., 2009). One particularly clear and ecologically relevant contextual cue comes from a change in source information – that is, a change in talker for speech, or instrument for music. For example, when participants learn novel words from distributional probabilities of items across two unrelated artificial languages (i.e., that mark words using different distributional probabilities), they only show reliable transfer of learning across both languages when the differences between languages are contextually cued through different talkers (Weiss et al., 2009). This is presumably because without a contextual cue to index the specific language, listeners must rely on the *overall* accrued statistics of their past experience in relation to the sample of language drawn from the current experience, which may be too noisy to be adequately learned or deployed. More recent work has demonstrated that the kind of cueing necessary to parse incoming distributional information into multiple representations can come from temporal cues as well. Gonzales et al. (2015) found that infants could reliably differentiate statistical input from two accents if temporally separated. This suggests that even in the absence of a salient perceptual distinction between two sources of information (e.g.,

speaker), listeners can nevertheless use other kinds of cues to meaningfully use variable input to form expectations that can constrain recognition. Indeed, work by Pisoni (1993) has demonstrated that listeners track attributes of speech signals that have been traditionally thought to be unimportant to the recognition process (e.g., a speaker's speaking rate, emotional state, dialect, and gender) but may be useful in forming expectations that guide and constrain the recognition process. To be clear, these results suggest that experience with the different statistics of pattern sets, given a context cue that appropriately identifies the different sets, may subsequently shape the way listeners direct attention to stimulus properties highlighting a possible way in which top down interactions (via cortical or corticofugal means) may reorganize perception.

Work by Magnuson and Nusbaum (2007) has shown that attention and expectations alone may influence the way listeners tune their perception to context. Specifically, they demonstrated that the performance costs typically associated with adjusting to talker variability, were modulated solely by altering the expectations of hearing one or two talkers. In their study, listeners expecting to hear a single talker did not show performance costs in word recognition when listeners were expecting to hear two talkers, even though the acoustic tokens were identical. Related work by Magnuson et al. (1995) showed that this performance cost is still observed when shifting between two familiar talkers. This example of contextual tuning illustrates that top-down expectations, which occur outside of statistical learning, can fundamentally change how talker variability is accommodated in word recognition. This finding is conceptually similar to research by Niedzielski (1999), who demonstrated that vowel classification differed depending on whether listeners thought the vowels were produced by a speaker from Windsor, Ontario or Detroit, Michigan – cities that have different speech patterns but are close in distance. Similarly Johnson et al. (1999) showed that the perception of “androgynous” speech was altered when presented with a male vs. female face. Linking the domains of speech and music, recent work has demonstrated that the pitch of an identical acoustic signal is processed differently depending on whether the signal is interpreted as spoken or sung (Vanden Bosch der Nederlanden et al., 2015).

Kleinschmidt and Jaeger (2015) has offered a computational approach on how such expectations may influence the perception of a signal. Specifically, they posit that until a listener has enough direct experience with a talker, a listener must supplement their observed input with their prior beliefs, which are brought online via expectations. However, this suggests that prior expectations are only necessary until enough direct experience has accrued. Another possibility, supported by Magnuson and Nusbaum (2007), is that prior expectations are able to shape the interpretation of an acoustic pattern, regardless of accrued experience, as most acoustic patterns are non-deterministic (ambiguous). More specifically, Magnuson and Nusbaum (2007) show that when a many-to-many mapping between acoustic cues and their meanings occurs that this requires more cognitive, active processes, such as a change in expectation that may then direct attention to resolve the recognition uncertainty (cf. Heald and Nusbaum, 2014). Taken together, this suggests that auditory

perception cannot be a purely passive, bottom-up process, as expectations about the interpretation of a signal clearly alter the nature of how that signal is processed.

If top-down, attention driven effects are vital in auditory processing, then deficits in such processing should be associated with failures in detecting signal embedded in noise (Atiani et al., 2009; Parbery-Clark et al., 2011), poorer discrimination among stimuli with subtle differences (Edeline et al., 1993), and failure in learning new perceptual categories (Garrido et al., 2009). Indeed, recent work by Perrachione et al. (2016) has argued that the neurophysiological dysfunctions found in dyslexic individuals, which include deficits in these behaviors, arises due to a diminished ability to generate robust, top-down perceptual expectations (for a similar argument see also, Ahissar et al., 2006; Jaffe-Dax et al., 2015).

If recent experience and expectations shape perception, it also follows that the ability to learn signal and pattern statistics is not solely sufficient to explain the empirical accounts of rapid perceptual plasticity within auditory object recognition. Changes in expectations appear to alter the priors the observer uses and may do so by violating the local statistics (prior context), such as when a talker changes. Further, there must be some processing by which one may resolve the inherent ambiguity or uncertainty that arises from the fact that the environment can be represented by multiple associations among cues. Listeners must determine the relevant associations weighing the given context under a given listening goal in order to direct attention appropriately (cf. Heald and Nusbaum, 2014). We argue that the uncertainty in weighing potential interpretations puts a particular emphasis on recent experience, as temporally local changes in contextual cues or changes in the variance of the input can signal to a listener that the underlying statistics have changed, altering how attention is distributed among the available cues in order to appropriately interpret a given signal. Importantly, this window of recent experience may also help solidify or alter listener expectations. In this way, recent experience may act as a buffer or an anchor against which the current signal and current representations are compared to previous experience. This would allow for rapid adaptability across a wide range of putatively stable representations, such as note category representations for AP possessors (Hedger et al., 2013), linguistic representations of pitch (Dolscheid et al., 2013), and phonetic category representations (Liberman et al., 1956; Ladefoged and Broadbent, 1957; Mann, 1986; Evans and Iverson, 2004; Huang and Holt, 2012).

It is important to consider exactly how plasticity engendered by a short-term window relates to a putatively stable, long-term representation of an auditory object. Given the behavioral and neural evidence previously discussed, it does not appear to be the case that auditory representations are static entities once established. Instead, auditory representations appear to be heavily influenced by recent perceptual context. Further, these changes persist in time after learning has concluded. However, this does not imply that there is no inherent stability built into the perceptual system. As previously discussed, perceptual categories in speech and music are not freestanding entities, but rather are a part of a constellation of categories that possess meaningful

relationships with one another. Stability may exist through interconnections that exist in the category systems. Long-term neural mechanisms may work to remove rapid cortical changes that are inconsistent with the system, while in other cases, allow such changes to generalize to the rest of the system in order to achieve consistency.

## CONCLUSION

The present paper has addressed the apparent paradox between experiencing perceptual constancy and dynamic perceptual flexibility in auditory object recognition. Two critical factors in this issue are the problem of acoustic variability and the reliance of listeners on recent experience. Specifically, we have argued that the process of achieving plasticity in audition necessarily entails that one must retain the ability to perceive acoustic variance independent of current listening goals. This is because a system that completely attenuates putatively “irrelevant” variance, by definition, has a single representational structure and assesses incoming perceptual information through a fixed lens. This would necessarily prevent individuals from flexibly adapting to behaviorally relevant changes in their environment. This view also suggests that learning is an important part of the recognition process, as listeners must be able to rapidly learn from and adapt to changes in the statistical distributions of their acoustic environments. A goal for future research should be to examine the degree to which perceptual learning is influenced by listening goals and expectations. More specifically, while perceptual

constancy may be goal driven, we have argued that perceptual learning may occur to some extent outside of perceptual constancy. In addition to maintaining sensitivity to acoustic variance, we have argued that a reliance on *recent* experience is necessary for individuals to flexibly adapt to changes in their environment. Recent experience provides a window through which the given signal and current representations are compared to previous knowledge, in that it contains meaningful cues as to when one should switch to an alternate sound-to-meaning mapping. Future work should examine the neural and cognitive mechanisms that underlie this process. Further, extant models of speech and music perception should be updated to reflect the importance of variability and short-term experience in the instantiation of both perceptual flexibility and constancy.

## AUTHOR CONTRIBUTIONS

SH and SVH wrote the first draft of the manuscript. HN provided comments on the draft, and all authors revised the manuscript to its final form.

## ACKNOWLEDGMENTS

This work was supported by the Multidisciplinary University Research Initiatives (MURI) Program of the Office of Naval Research through grant, DOD/ONR N00014-13-1-0205.

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**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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