Encoding of learned importance of sound by magnitude of representational area in primary auditory cortex

Richard G. Rutkowski and Norman M. Weinberger*

Center for the Neurobiology of Learning and Memory and Department of Neurobiology and Behavior, University of California, Irvine, CA 92697-3800

We hypothesized that learning-induced representational expansion in the primary auditory cortex (AI) directly encodes the degree of behavioral importance of a sound. Rats trained on an operant auditory conditioning task were variably motivated to the conditioned stimulus (CS) through different levels of water deprivation. Mean performance values correlated with deprivation level, validating them as a measure of the overall control and, therefore, behavioral importance of the CS. Electrophysiological mapping revealed expanded representations of the CS, compared with other frequencies in experimental subjects, but not in naive or visually trained controls that received noncontingent CS tones. Importantly, representational area showed a significant positive correlation with mean performance levels for only the CS band, with significant effects for relative area in contrast to only modest changes in absolute area. CS representational expansion was asymmetric into high-frequency zones, thus performance level also was significantly correlated with the relative anterior–posterior location of the enlarged representation. An increased representation of low frequencies, related to the acoustic spectrum of the reward delivery equipment, also was discovered in both experimental and control trained subjects, supporting the conclusion that behaviorally important sounds gain representational area. Furthermore, there was a surprising reduction in total AI area for the experimental and control groups, compared with untrained naive subjects, indicating that the functional dimensions of AI are not fixed. Overall, the findings support the encoding of acquired stimulus importance based on representational size in AI.

memory code | plasticity | sound frequency | tonotopic organization

Adult sensory cortex is plastic and can alter its sensory representation in response to experience or injury (1–3). During learning, plasticity may enable the storage of a particular sensory experience or event, allowing the brain to meet the demands of processing an external environment in which stimuli necessary for survival may be continually changing. In the primary auditory cortex (AI), associative learning retunes receptive fields and temporal response properties of cells in a rapid and highly specific manner, thus providing a substrate for a form of physiological memory (4–6). Learning also expands the representational area of a training stimulus in AI maps of animals (7–9) and humans (10, 11). However, the functional significance of such plasticity remains enigmatic, with few investigations finding significant correlations between the degree of map expansion and overall performance level (9, 10). Artificially induced representational expansions in AI also give no apparent changes in frequency discrimination behavior (12).

Importantly, cortical plasticity appears dependent on the behavioral importance of the conditioned stimulus (13), which may initiate and drive cortical reorganization through the release of neuromodulators, including acetylcholine. These bias cellular responses to a particular input (14, 15). The effects of acetylcholine release in AI have been demonstrated by pairing tones of no behavioral importance with either direct iontophoretic application of cholinergic agonists or electrical stimu-

lation of the nucleus basalis, the major source of cortical acetylcholine (16). This cholinergic activation produces dramatic retuning of the characteristic frequency (CF) of cells to the frequency of the paired tone (17–19), resulting in significant expansion of its representation (20).

It remains unclear how strongly performance levels and resulting plasticity may be influenced by the behavioral relevance of a conditioned stimulus (CS). Given the dramatic plasticity during learning, it has been hypothesized that the degree of cortical change, e.g., area of AI that becomes tuned to a CS, may serve as a "memory code" for the acquired behavioral importance of sound (21). The present study investigated this issue by mapping AI of rats trained to perform an operant-conditioning task for water, with performance levels and behavioral relevance directly manipulated by the degree of water deprivation.

Materials and Methods

All procedures were performed in accordance with the University of California, Irvine, Animal Research Committee and the National Institutes of Health Animal Welfare Guidelines. Eleven male Sprague–Dawley rats were water-deprived and trained to bar-press for water during a 10-s CS [mean interstimulus interval = 20 s, range = 10–30 s]. Subjects were trained in an operant chamber (H10-11R, Coulbourn Instruments, Lehigh Valley, PA) fitted with a bar manipulandum (2 cm above floor, 2 cm from right wall), a water cup attached to a retractable lever that delivered water to an opening 9 cm to the left of the bar, a speaker 13 cm above the trough, and a cue light 13 cm above the bar. For experimental animals ($n = 8$), the CS was a 6-kHz pure tone (mean level = 60 dB sound pressure level), and for controls ($n = 3$), it was illumination of the salient cue light. The control group also received noncontingent presentations of the 6-kHz tone, with the same interstimulus interval and mean level presented to the experimental animals. The water reward for both groups was delivered through a 0.1-ml cup attached to a retractable lever and was available for 5 s after any bar press made during CS presentation. Each training session lasted for 1 h, and where necessary, supplemental water was given at least 2 h after the training session to maintain animals within their specified weight range. Each animal was trained for a total of 30 (± 5) days, which sufficiently allowed asymptotic performance levels to be reached.

Two levels of water deprivation were used, i.e., "moderate" (body weight maintained at 85–90% of mean ad libitum weigh, $n = 5$) and "mild" (90–100% of the mean ad libitum weight, $n = 3$). Mean ad libitum weights were obtained daily from three nondeprived, untrained rats of the same age as the trained

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animals. For each deprivation level, subsequent interindividual variability created a divergence of weight and motivation level for the task, leading to a relatively broad continuum of performance values. Water intake was expressed in terms of the percentage difference in weight measured immediately before and after a training session. The overall degree of behavioral importance of the CS was determined from the mean performance level across all training sessions. The performance calculation was based on measures previously used for operant training (22) and involved correcting the hit rate (bar-press rate during CS presentation as a proportion of the total bar-press rate), with the false-positive rate (proportional bar-press rate in absence of CS): performance = hit rate − (false-positive rate × hit rate) × 100. A performance score of 0 indicated no hits, and 100% indicated perfect performance, i.e., no false positives. Chance performance, i.e., hit rate and false-positive rate were equal, gave a score of 25%.

After training, the frequency organization of the right AI was mapped by an experienced experimenter, blind to the previous treatment of the animals, with the rats under general anesthesia (sodium pentobarbital, 50 mg/kg i.p.) as described in ref. 23. A series of calibrated digital photographs of the cortical surface were taken, allowing the position of each recording to be noted. Extracellular recordings of multiunits were obtained with parylene-coated tungsten microelectrodes (1–4 MΩ, FHC, Bowdoinham, ME) from a depth of 400–600 μm (layers III–V). Acoustic stimuli were delivered monaurally through a calibrated speaker placed at the entrance to the left ear canal and were generated by using Tucker–Davis Technologies, Alachua, FL, hardware and software. They consisted of white noise (bandwidth = 1 Hz–50 kHz) and pure tone bursts (1.3–1.7 per s), duration = 100 ms, rise–fall time = 8 ms ($\cos^2$ ramp). AI sites were defined by relative short latency (<20 ms) onset-type responses, with significantly lower thresholds (≤20 dB) for pure tones than noise (20, 23–25). Nonresponsive sites or those that showed either a significantly lower threshold or exclusive response for noise defined the AI border with nonspecific cortex or belt areas, respectively. The boundary between AI and the anterior auditory field was determined by a reversal in the CF representation, as well as changes in bandwidth and latency (23, 25). To estimate the representational area of each CF octave band, Voronoi tessellations were constructed from each complete map, and the area of each polygon was calculated. For all AI sites, anterior–posterior (AP) distances from the most posterior AI site were measured. Each AP distance measurement was then binned into octave bands according to CF, and an average AP distance for each CF octave band was calculated. Unless otherwise stated, group data were statistically compared by ANOVA, with Games–Howell post hoc testing.

Results

Because the aim of the present study was to investigate the relationship between the magnitude of behavioral importance and the degree of plasticity, it was important to validate the performance measures in terms of motivation level to the CS, as imposed by water deprivation. Fig. 1 shows correlations between the mean performance level and the associated mean weight and the mean amount of water consumed during a session, plotted as a percentage of the overall body weight. The performance values calculated were highly correlated with both weight ($r = 0.76$, $P < 0.05$) and mean water consumed ($r = 0.66$, $P < 0.05$), which provides validation that they reflected overall motivation to the CS.

Fig. 2 A and B shows representative maps of AI recorded from a naive (untrained) and a trained experimental rat, respectively. For the naive rat, the tonotopic organization of low to high CFs is clearly seen to progress from posterior to anterior, in agreement with previous reports (20, 23–25). The mean total area

calculated for naive AI (6 mm^2) also agrees with most previous studies (24, 25). The trained experimental animals showed a similar tonotopic organization, with surprisingly no significant difference in mean area for the CS band (4.1–8 kHz), compared with naive animals (Student's t test; $t = -0.12$, $P = 0.91$). However, in some regions, the tonotopic gradient was compressed as a result of CS representations being found in more anterior locations. Also, an increased number of sites exhibited either significantly lower thresholds for, or exclusive responses to, white noise, thus making them more belt-like. The compressed gradient and increased responses to noise contracted the mean AI area to 3.3 mm^2, a reduction of ≈50% from that of naive rats, and contributed to a pronounced relative expansion of the CS representational area.

Fig. 1. Validation of performance levels as measures of CS importance. The plots highlight significant linear correlations between mean performance level and mean weight (A), expressed as a percentage of the mean weight of undeprived animals, and mean water intake (B), expressed as the mean percentage difference in body weight measured before and after each training session.

Fig. 2. Examples of the effects of training on representational area. Organization of CFs in AI for a representative untrained naive (A), and a trained experimental (B) rat. Each "×" indicates an electrode penetration, with colored polygons indicating the estimated AI area representing the CF according to the color bar shown below the maps; D, dorsal; A, anterior. Cortical area representing CFs within the CS octave band, i.e., 4.1–8 kHz, is highlighted by outlined polygons and vertical hatching. Points not surrounded by color indicate sites physiologically classified as non-AI (see *Materials and Methods*). (Scale bar: 1.0 mm.) (C) Learning curves for three animals showing low (blue squares), mid (black diamonds), and high (red triangles) levels of motivation level. (D) Corresponding distributions of relative representational area (percent of total AI area) for each animal, together with mean naive areas (gray line), are shown. Vertical bars on naive area distribution indicate ± SEM; dashed circle and light gray box highlight the CS bin.

Fig. 3. Summary of linear correlation coefficients between mean performance and absolute area (*A*), relative area (*B*), and relative AP distance (*C*) for each CF band. Scatter plots of significant correlations are shown to the right of each bar chart. Dashed circles highlight the CS band. *, $P < 0.05$; **, $P < 0.01$.

Fig. 4. Findings for visually trained control subjects. (*A*) Fast Fourier transform analysis for a recording of a bar press and subsequent water delivery, with the CS training tone (6 kHz) presented in the background. The microphone was placed between the bar and the water trough, in a position that approximated that of the animal's head. The recording also was made in the presence of the CS so that the relative acoustic power from each source could be compared at this particular head position and location in the test chamber. Significant power may be noted in the 0.1- to 2-kHz band ($\approx$70 dB) in addition to the CS at 6 kHz ($\approx$60 dB), confirming the possibility of reinforcement for the 0.1- to 2-kHz as well as the CS band. The lower power for the CS frequency is consistent with its original calibration at the location where the recording was made. (*B*) AI recorded from a control animal trained to a visual stimulus and which received random presentations of the 6-kHz pure tone used in training experimental subjects (labeling as described for maps shown in Fig. 2). (*C*) A comparison of mean total areas of AI for experimental (Exp, red), control (Con, blue), and untrained naive (Nai, gray) rats. *, $P < 0.05$. Vertical bars indicate $\pm$ SEM.

Fig. 2*C* highlights the effects of differential motivation on learning in three rats. The mean performance levels exhibited by each rat were significantly different from that of the other two subjects ($F = 31.4$, $P < 0.01$), with the least-deprived rat exhibiting the worst and most variable performance and the most-deprived rats showing the highest and most consistent levels of performance. By reaching maximal performance after $\approx$10 sessions, the most-deprived subject also displayed the steepest learning curve, indicating that the CS imparted the largest degree of behavioral control in this animal. Fig. 2*D* shows the corresponding distributions of cortical area for each CF band, expressed as percent of the total AI area. The highest-performing animal clearly shows the largest CS area, with the mid- and low-performing animals exhibiting smaller CS areas. All three animals exhibited significant differences from each other (χ^2 range = 67–94, χ^2, $P < 0.001$, df = 5), with increasing performance level leading to larger relative CS representation.

Three additional measures of AI representation were compared with performance level: mean absolute area (mm^2) and also, mean absolute and relative AP distance (mm and percent of total AP distance of AI, respectively). Absolute measures were useful for comparing the effects noted in previous studies (9, 26), whereas relative measures quantified changes in the context of overall AI size. Fig. 3 highlights specific map changes that significantly correlated with performance level for at least one CF band. For absolute area, a significantly positive correlation with performance level was noted for the CS band ($r = 0.74$, $P = 0.018$; Fig. 3*A*). However, there was a much stronger

correlation for relative area ($r = 0.87$, $P = 0.003$; Fig. 3*B*). Significant negative correlations were found for both absolute and relative areas of the 32.1- to 50-kHz band, indicating concomitant reductions in high-CF representation with expansions of the CS band. Correlations between performance and AP distance also were stronger for relative rather than absolute measures, with significance found only for relative AP position of the CS band ($r = 0.78$, $P < 0.05$; Fig. 3*C*). There was no significant correlation between performance and total AI area ($r = 0.02$, $P = 0.48$).

In addition to relative expansion of CS area, a number of animals appeared to show a marked increase in relative area for 0.1–2 kHz (e.g., low-performing subject in Fig. 2*D*). This increase in 0.1–2 kHz area suggested reinforcement to additional acoustic stimuli that may have acquired some degree of behavioral relevance. The lack of correlation with performance level (Fig. 3 *A* and *B*) may have indicated variability in the coincidence of the low-frequency sounds with each CS trial or reflected an intermittent occurrence from trial to trial. To explore this possibility, we recorded the acoustic environment to which each rat was exposed and identified noise arising from the bar-press and water delivery system at $\leq$2 kHz (Fig. 4*A*). Because these sounds preceded water reward on correct trials, they might be expected to have gained behavioral significance and thus caused representational expansion.

To investigate this possibility, we trained control animals that were moderately water-deprived and conditioned to a visual rather than an auditory stimulus. The controls also received random presentations of the 6-kHz tone, as used with the experimental group. Fig. 4*B* shows a map of AI recorded from a control subject. A reduction in area may be noted, particularly in the posteroventral region, where sites showed either a lower threshold or exclusive response to white noise or were nonresponsive, consistent with similar observations made for the

Fig. 5. Comparisons of mean absolute and relative areas (*A* and *B*, respectively) and mean absolute and relative AP distances (*C* and *D*, respectively) among experimental (Exp), control (Con), and untrained naive (Nai) rats. Pair-wise comparisons for each CF band are shown below each plot. *, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.005; ****, *P* < 0.001. Dashed circles and light gray boxes highlight the CS bin in each plot. Vertical bars indicate ± SEM.

experimental group. Fig. 4*C* compares the mean total AI area in controls with that of experimental and untrained naive groups. As noted for experimental animals, controls showed a significantly smaller total AI area, compared with naive rats ($F = 7.04$, $P = 0.014$ and $P = 0.039$, respectively; Scheffé's test). No significant differences in total AI area were found between the control and experimental groups ($F = 7.04$, $P = 0.98$; Scheffé's test).

Fig. 5 compares mean areas and AP distances among all groups, across all CF bands. Fig. 5*A* highlights the surprising lack of difference in absolute area noted between experimental and naive rats for the CS band. The only significant difference occurred at 32.1–50 kHz, where the experimental group showed a smaller representation ($F = 7.2$, $P = 0.03$). Importantly, the experimental group showed a significantly expanded relative CS representation, compared with controls (Fig. 5*B*; $F = 4.2$, $P = 0.02$). However, both groups showed expansion of relative area for 0.1–2 kHz, with a significant difference found between control and naive animals ($F = 5.8$, $P = 0.015$). The experimental group also showed a significantly anterior representation of the CS band, compared with both naive ($F = 6.0$, $P = 0.001$) and control ($F = 6.0$, $P = 0.004$) subjects (Fig. 5*C*). For relative AP distance, which takes into account absolute AP shift with overall reduction in total AI area, experimental animals displayed significantly more anterior representations of the CS ($F = 9.4$, $P < 0.001$), as well as the 0.1- to 2-kHz ($F = 3.5$, $P = 0.023$) and 8.1- to 16-kHz ($F = 2.6$, $P = 0.031$) bands, compared with naive animals (Fig. 5*D*). Compared with controls, significantly anterior representations were noted only for the CS band ($F = 9.4$, $P = 0.013$).

Fig. 6 highlights map plasticity associated with increasing CS importance relative to the mean AI representation in trained controls. To enable comparisons at different levels of CS control, the experimental animals were pooled into one of three groups based on performance level, i.e., low (40–50%, $n = 2$), inter-
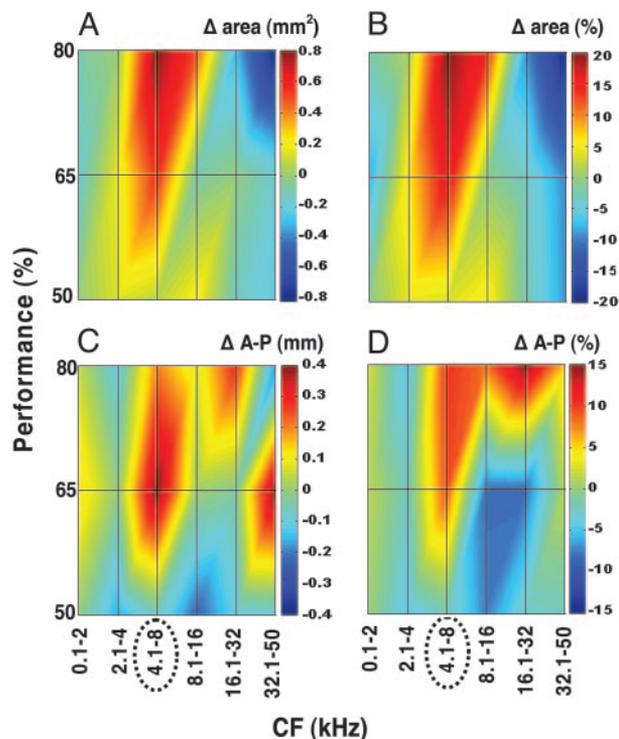
Fig. 6. Overall associative effects of learned importance and schema of mechanism. (*A–D*) Filled contour plots displaying differences in absolute and relative area (*A* and *B*, respectively) and absolute and relative AP distance (*C* and *D*, respectively) between experimental and control rats, with respect to increasing performance level. Linear interpolation between each CF–performance combination was used, with coloring scaled according to the bars shown to the right of each plot. For area, warm colors indicate relative expansion, and cold colors show contraction. For AP distance, warm colors highlight anterior shifts in the mean location of the CF band representation, and cold colors indicate posterior shifts. Dashed circles highlight the CS band. (*E*) Schematic summary of a probable mechanism underlying the map reorganization observed. In both experimental and control animals, training led to an apparent reduction in absolute AI area, compared with untrained naive subjects. In experimental animals, learned behavioral importance of the CS led to gradual retuning of units, with CFs greater than the CS frequency. This retuning gave the observed pattern of an anterior expansion for not only the CS representation (hatched green area), but also for subsequently higher-CF representations. (*F*) The apparent anterior directionality in recruitment might be underpinned by an existing low-frequency bias of tuning curves in AI. A shallower slope on the low-frequency edge may lead to an asymmetrical activation of cells (highlighted by black lines), with CFs higher than the CS frequency (black circle). Because these cells are already activated by the CS, they might show more rapid and efficient retuning than those with CFs lower than the CS frequency.

mediate (50–60%, $n = 3$), and high (60–85%, $n = 3$). At every performance level, the representational measure for each CF band was averaged, and the corresponding mean value for

control animals was subtracted. Fig. 6 *A* and *B* shows the differences between experimental and control groups for absolute and relative area, respectively. The 0.1- to 2-kHz expansion, common to both groups, thus is eliminated. The group differences are mainly on the CS band, where enlargements correlated with increasing performance level at the progressive expense of high-CF representations. A widening of the expansion zone also may be noted at the highest performance level in both plots, with increases in the representation of 8.1–16 kHz occurring in addition to those observed for the CS band. These expansions correspond with contractions in the 16.1- to 32-kHz and 32.1- to 50-kHz areas, indicating a gradual retuning of high-CF representations toward the CS frequency. Fig. 6 *C* and *D* plot experimental–control differences in absolute and relative AP locations, respectively. The CS band is again dominant, with progressively anterior shifts in relative position associated with increasing performance level. Neighboring high-CF bands (8.1–16, 16.1–32, and 32.1–50 kHz) also appeared to show anterior shifts in relative position with increasing performance. In combination with the observed erosion in their representation, these high-frequency anterior shifts suggest a retuning toward the CS frequency, which initially occurs in high-CF cells closely bordering those with lower CFs. Additional recruitment associated with improved performance levels might be possible through the retuning of cells with even higher CFs, leading to further anterior shifts of the CS and remaining higher-CF representations.

Fig. 6*E* depicts a summary of the possible sequence of reorganization underlying the observations made. AI is initially reduced in area due to general (non-CS) experience-dependent changes in response properties, e.g., units close to the AI border becoming more belt-like. The subsequent learning of CS importance correlates with a retuning of mainly high-CF cells toward the CS frequency, leading to an anterior expansion of the CS representation.

Discussion

This study supports the hypothesis that acquired behavioral importance of a CS is encoded in AI and that such encoding is accomplished (at least in part) by the magnitude of representational area. The serendipitous findings that noise produced by the water delivery device apparently caused an expansion in the 0.1- to 2-kHz band also supports this hypothesis. The CS tone, the representation of which expanded only for the experimental group, was the designated stimulus whose importance was manipulated by the experimenters, but the equipment noise was nonetheless an additional signal for water reward and thus likely gained behavioral importance, as indicated by expansion of the 0.1- to 2-kHz representation in both experimental and control groups. Expansion for 0.1–2 kHz may have been smaller than for the CS because of unsuccessful bar presses in the absence in the CS, i.e., false-positive responses, so that bar presses were less reliable predictors of reward than the CS. In any case, the data suggest that AI tracks the relative acquired importance of sounds, regardless of spectral properties.

Absolute AI area also was reduced in both the experimental and control groups to a similar extent and showed no correlation with mean performance levels. This observation therefore appears to reflect a general training phenomenon, unrelated to acquired CS significance. Furthermore, as the experimental group exhibited a CS-specific increase in relative area, the effect is genuine rather than due to any putative artifact of compromised cortical state, differential depth of anesthesia, or failure to correctly classify recording sites as AI on functional grounds. Rather, the reduced absolute area appeared related to a change in response properties at sites approaching the AI border, where neurons became exclusively responsive to or showed lower thresholds for noise than for pure tones. Such an increase in belt-type responses (23–25) might be plausible, given the expo-

sure to a richer and more complex acoustic environment outside of the vivarium through training-related and general laboratory experience. The reduction in AI size also is consistent with recent work in rat primary somatosensory cortex, which demonstrated contraction of primary whisker representations by as much as 46% after experience in an environment that encouraged more naturalistic somatosensory activity (27). Moreover, larger primary sensory cortex in experience-restricted animals is hypothesized to reflect relative sensory deprivation (28).

The finding of representational expansion is not only consistent with but also links studies that have induced and correlated it with performance or stimulus importance through classical conditioning, discrimination training, or direct neurochemical means (4, 9, 13, 21). AI may enlarge a particular representation to optimize signal to noise and subsequent processing of a behaviorally important input (27). However, not all studies have shown expansion. Cats trained on a frequency-discrimination task showed no apparent changes in training-frequency representations in AI (26), findings that conflict with a previous frequency-discrimination experiment in owl monkeys (9). The discrepancy may have arisen from the cat study limiting the overall area of analysis in AI to a 3-mm-wide band, which might have excluded neighboring sites where cells had retuned toward the training frequencies. Furthermore, comparisons of absolute area between experimental and naive animals were made. In the present investigation, such a comparison yielded no significant difference (Figs. 1*D* and 5*A*). The present findings also demonstrate that relative, rather than absolute, changes provide a more sensitive measure of plasticity, as well as a stronger correlation with performance level (Figs. 1*F* and 5*B*). However, neither of the previous studies reported relative areas and, therefore, may not have identified more significant reorganization. Furthermore, features more closely associated with the learned importance of the CS were uncovered by subtraction of the mean control map from that of each experimental animal (Fig. 6*A–D*), which removed the general effects of the training experience *per se*.

The observation of relative expansion in combination with a change in mean position appears to be consistent with magnetoencephalogram recordings in humans, which have shown that tactile discrimination training causes a significant shift in the location of the N-20 dipole in primary somatosensory cortex related to an asymmetrical representational enlargement (10, 11). The anterior directionality in expansion observed in the current study may have arisen from two nonexclusive processes. Tuning curves commonly display an asymmetry in steepness between the high- and low-frequency edges, with the low-frequency edge exhibiting a shallower slope, compared with the high-frequency edge (Fig. 6*F*; refs. 20, 24, and 29–32). This asymmetry may largely result from upward spread of masking in the cochlea (33). Therefore, given a CS at a particular frequency and level, the spatial distribution of activity in and around the CS band will be asymmetrical and biased toward cells with CFs greater than or equal to CS frequency. Because the CS already lies in the response areas of these cells, they may be more easily recruited than those in lower-frequency bands (Fig. 6*F*). A second possible mechanism might involve active competition between inputs encoding the CS and those encoding the low-frequency sounds from the bar-press and water-delivery system. In this case, expansion of the CS area into low-CF regions (leading to a more symmetrical enlargement) may have been prevented by competition from the low-CF representation of sounds that were reinforced by water delivery. Furthermore, comparatively less reinforcement of high-CF areas may have reduced their competitiveness, making them more amenable to retune toward the CS frequency. Such competitive processes have been widely described in previous experiments demonstrat-

ing training, injury-related, and developmental plasticity (34–36).

By validating the performance measured, the present findings support a neural code for acquired stimulus importance based on representational expansion within a sensory map. Studies involving more complex learning, e.g., perceptual discrimination, support that this code may be multifaceted, with the exact coding facet that correlates with stimulus importance dependent on the stimulus domain requiring attention. For example, although a significant representational expansion was noted in primary somatosensory cortex in response to learning a tactile temporal discrimination task, only changes in the temporal response properties of cells were found to correlate with the overall performance level (37). Also, frequency discrimination has been shown to produce representational expansion along with increased unit response latency and tuning sharpness. In this case, only representational expansion was found to correlate with performance (9). The emergent code also may be constrained by modality-specific cytoarchitectonics, neurochemistry, and physiology, leading to differences in the types of plasticity expressed in different sensory cortices (3).

Several other issues are raised by the current findings. For example, this study used extensive training (30 sessions). The developmental rate of the selective expansion of the CS frequency band needs to be determined; it might occur quite rapidly, because CS-specific receptive field shifts have been observed after a single brief training session (3). In addition, that training in both experimental and control subjects produced a reduction in the absolute size of AI opens several lines of inquiry. For example, are other modalities similarly affected? Simultaneous analysis of at least two different sensory modalities would shed light on this issue. Furthermore, the changes observed in AI indicate a possible influence from additional plasticity occurring in surrounding fields. Such interfield effects, which may have significantly contributed to both the expansion of representation and the shrinkage of AI as functionally defined, also await investigation. The resultant coding strategy allowing primary sensory cortices to track the current behavioral significance of stimuli also may be updated with changes in environmental challenges. Extinction and retraining to a different frequency might reveal this property in AI.

By examining map changes resulting from a simple form of behavior, the present work not only uncovers a fundamental rule by which primary sensory cortex might be operating but also demonstrates the importance of directing and assessing behavior in terms of a relevant and meaningful factor, treating it as an adjustable independent variable against which to measure neuronal plasticity.

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