**Cortical efficient coding shapes behavioral performance.**

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The efficient coding hypothesis has been one of the most influential ideas in computational neuroscience (Barlow, 1961), yet few, if any, studies have been able to link directly the predictions from efficient coding of neuronal response properties to perception. In natural environments, the statistics of background sounds can change dramatically. Changes in the dynamic range (ie. contrast) of acoustic inputs pose a particular challenge to the auditory system, which is composed of neurons with limited dynamic range. The efficient coding hypothesis predicts that as acoustic contrast changes, neurons in the auditory system adapt to match the dynamic range of their response to that of the stimulus distribution. In this study, we show that efficient cortical encoding of sound contrast shapes auditory perception.

Previous work in the auditory cortex demonstrated contrast-driven changes in neural gain, showing that neurons in the auditory pathway adapt to efficiently encode stimulus information (Rabinowitz et al., 2011; Rabinowitz et al., 2013; Cooke et al., 2018; Lohse et al., 2019). At a behavioral level, there is evidence that psychophysical sensitivity to changes in volume (Lohse et al., 2019) and changes in stimulus location (Dahmen et al., 2010) are modulated by the contrast of these two stimulus dimensions. However, previous neural and behavioral experiments were performed in separate subjects: as such, it is unclear whether adaptation in auditory cortex is necessary for task performance. Therefore, we had three goals: 1) To create a normative framework based on efficient neural encoding to understand how neuronal adaptation affects stimulus encoding; 2) To assess whether behavioral perception in environments with different acoustic contrast is consistent with efficient neuronal adaptation, as predicted by our model; and 3) To test whether activity in auditory cortex is necessary for the behavioral task and predictive of individual behavioral performance.

To address these questions, we developed a formal framework based on efficient coding (Mlynarski & Hermundstadt, 2018, 2019) to predict behavioral detection of targets given changes in background sound-level contrast. The model predicted contrast-dependent changes in sensitivity to targets and asymmetric adaptation to each contrast background (Figure 1a). Next, to directly test the role of efficient coding in auditory behavior, we trained mice to detect targets in different contrast backgrounds. We found that mouse behavior followed the model predictions (Figure 1b). We also found that mice were unable to perform the target-in-noise detection task when auditory cortex was inactivated, but were able to perform a simple detection task, establishing a specific role of auditory cortex in extracting targets from background sounds. Finally, simultaneous neural recordings found that the neural code in auditory cortex (Figure 1c) is predictive of individual differences in behavior and asymmetrically adapts to each contrast, but also that variability in neural gain is predictive of individual variability in task performance in a contrast-dependent manner. Combined, our results identify a novel relationship between efficient neuronal coding and acoustic behavior, and provide a normative framework that links efficient coding theory, neuronal adaptation, and behavioral performance.

Understanding how our nervous system transforms stimulus inputs to create perception is a key goal of sensory neuroscience. Our work demonstrates that sound percepts are shaped by efficient codes in the auditory pathway, showing that neuronal adaptation to stimulus statistics predictably modulates neuronal representations to impact behavioral performance. We anticipate that this phenomenon generalizes to many sensory systems, and that our unique approach combining normative modeling with simultaneous neural and behavioral recordings provides a general framework for exploring the role of efficient adaptation in shaping perception. Additionally, by identifying the relationship between neuronal function and behavior, these results highlight potential mechanisms for improving the perception of sounds in noise, which is a common deficit after hearing loss and for users of hearing aids and cochlear implants. We therefore expect that our paper will be of interest not only to the systems neuroscience community, but also to clinical audiences.

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**Figure 1.**

**a,** Normative model of efficient gain control. *Left panel:* A model neuron receives sensory inputs that vary between low (blue solid lines) and high contrast (red solid lines). At each timepoint, the neuron estimates the contrast of the recent stimulus by dynamically adjusting the gain of its nonlinearity (schematic nonlinearities in the rounded inset). To simulate the behavioral task, targets are superimposed on the varying contrast background (blue and red circles), and the spiking responses of the model neuron to target and background are used to compute the discriminability. *Middle panel:* Target from noise discriminability as a function of target volume. The model predicts that thresholds are lower in low contrast and that slopes are steeper. *Right panel:* Model neuron gain as a function of contrast and time from the transition. The model neuron adapts faster after a switch from low to high contrast (red curve) relative to a switch from high to low contrast (blue curve). **b,** Behavioral GO/NO-GO task. *Left panel:* Targets were presented either after a switch from high to low contrast, or after a switch from low to high contrast (black solid lines are waveforms, dashed black lines are the contrast switch, with contrast indicated in red and blue lines above). On target trials, mice were rewarded with water for a correct lick, while on noise trials they were punished for false alarms with a 7s timeout. *Middle panel:* Behavioral performance as a function of contrast and target volume. Consistent with the model, mice had lower thresholds and higher slopes in low contrast. *Right panel:* Behavioral performance as a function of contrast and target time from the contrast switch. Detection performance decreased rapidly in high contrast, but increased slowly in low contrast. **c,** Recordings from auditory cortex concurrently with behavior. *Left panel:* Schematic of a population decoder used to estimate discriminability of target from noise trials in population space. *Middle panel:* neural decoding performance as a function of contrast and target volume. We found that neural thresholds were lower in low contrast, and that neural thresholds and slopes covaried with behavioral thresholds (not pictured). *Right panel:* Neural decoding performance as a function of contrast and target timing. As in behavior, we found that neural performance decreased rapidly immediately after a transition from low to high contrast, but increased slowly after high to low transitions.

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**a,** Experimental setup. Head-fixed mice are presented with sounds from an ultrasonic speaker. During behavior, mice receive water rewards through a lick spout. In a subset of mice, tetrodes were implanted in ACtx to record spiking activity. **b,** GO/NO-GO task design. *Left:* example NO-GO trials. From top to bottom: spectrogram of an example low-to-high contrast trial (colorbar indicates volume in dB SPL); waveform for sample spectrogram; example spectrogram for a high-to-low contrast trial; waveform for example spectrogram; temporally jittered response window to estimate false alarms over time; schematic lick responses in the response window; timeout of 7 seconds delivered after the first lick. Vertical red dashed line indicates the contrast switch after 3 seconds. Black horizontal scale bar indicates 1s. *Right:* example GO trials. From top to bottom: same as in left panel, except the response window immediately follows target presentation and licks within the target window trigger a ~5µL water reward. **c,** Target manipulation example waveforms. *Top:* overlaid trials where target volume differed. Volume is indicated by the amplitude and colorbar, with low volume targets shaded in cyan, and high volume targets shaded in magenta. *Bottom:* overlaid trials where target timing differed. Target timing is indicated by the colorbar, with light magenta targets occurring shortly after the contrast switch, and darker targets occurring at increasing delays. The red vertical dashed line indicates the contrast switch. **d,** Normative model of the task. Left inset shows volume distributions for backgrounds (light lines) and targets (dark lines) in low and high contrast. (1) Spike generation process: a 1-dimensional sensory stimulus consisting of a background that transitions between low and high contrast (light lines) with superimposed targets (solid dots) feeds into a model neuron. The response of the model neuron is governed by a sigmoidal function which then generates stochastic spikes through a Poisson process. (2) Based on the observed spiking, a variance estimator integrates spike counts to estimate the current variance of the stimulus. (3) This estimate is then used to adjust the gain of the model neuron to optimize the estimate of stimulus variance at each time step. (4) The average change in gain of the model after each contrast transition. Dashed lines and dots indicate the time taken to reach half of the range of gain values in each contrast. **e,** Model psychometric functions. Discriminability between model spike rates in response to the background and targets as a function of contrast and target volume. Light dots indicate model discriminability whereas the solid lines indicate logistic fits to the data (see *Methods*). Dashed lines indicate detection thresholds (defined as from the logistic fit). Arrow indicates target mean of 1.50 which is the volume used to assess time courses in **f**. **f,** Model target discrimination as a function of time and contrast. Dashed vertical line indicates the time where the background contrast changes. **g,** Model predictions for the effects of contrast on psychometric thresholds, slopes, and adaptation times.

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**a,** Schematic of GO/NO-GO paradigm.Task details as in Figure 1 and Methods. **b,** Behavioral performance for the contrast in which each mouse was first trained relative to the first session of task exposure (n=10 mice were first trained in low contrast, whereas n=11 mice were first trained in high contrast). Dots indicate a session, while the traces indicate a running average using a 7 day window. Blue dots and traces indicate sessions in which mice detected targets in low contrast (ie. after high-to-low contrast transitions), while red dots and traces indicate sessions in which mice detected targets in high contrast (ie. after low-to-high contrast transitions). **c,** Psychometric functions averaged for n=21 mice in low and high contrast. Error bars indicate ±SEM over mice at individual target SNRs, while the solid lines are logistic function fits to the average performance per contrast. **d,** Psychometric thresholds per contrast. Each dot represents a mouse, lines connect performance of individual mice on low and high contrast sessions. Bars indicate the average threshold over mice, while error bars in black indicate threshold ±SEM over mice. **e,** Behavioral psychometric functions for n=4 mice tested using the same target volumes in each contrast. Dots with error bars indicate average performance ±SEM over mice as a function of contrast and target volume. Overlaid, dark-colored curves indicate psychometric fits to the averages, with the black dot indicating the average threshold. Light-colored lines indicate the psychometric curves of individual mice. Black, dashed horizontal line indicates chance (0.5) performance. **f,** Psychometric thresholds per contrast. Each dot represents a mouse, lines indicate where mice participated in both low and high contrast sessions. Bars indicate the average threshold over mice, while error bars in black indicate threshold ±SEM over mice. **g,** Psychometric slopes per contrast. Presentation as in **f**. **h,** Behavioral performance as a function of contrast and target time relative to the switch in contrast for n=21 mice. Dots with error bars indicate average performance ±SEM over mice. Solid curves indicate exponential function fits to the average over mice. Black, dashed vertical line indicates the contrast switch. Horizontal lines at the top of the plot indicate significant changes in performance between the first target presentation time and subsequent target presentation times, as assessed by Wilcoxon Sign-rank tests with false discovery rate correction for multiple comparisons. **i,** Average time constant of exponential fits in low and high contrast. Presentation as in **g**. Unless otherwise noted, blue markers indicate data where targets were presented in low contrast and red indicates data where targets were presented in high contrast. . In all plots: ns, not significant; †p<0.1, \*p<0.05, \*\*p<0.01, \*\*\*p<0.001, \*\*\*\*p<0.0001.

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**Figure 3.**

**a,** Setup schematic for muscimol application in behaving mice. *Bottom*: legend indicating colors used for each background condition. **b,** Behavioral psychometric functions during muscimol or saline application for n=4 mice. Dark solid lines and filled circles indicate average performance after saline injection. Dark dashed lines and open circles indicate average performance after muscimol injection. Light solid and dashed lines are psychometric curves from individual sessions. Error bars indicate ±SEM. across sessions. **c,** Behavioral performance metrics as a function of contrast and pharmacological intervention. Open circles indicate performance in individual sessions. Colored bars indicate average performance across sessions. Bars with low transparency and solid outlines are averages after saline application, while high transparency bars with dashed outlines are averages after muscimol application. Clockwise from the upper left, are plots of the max response rate, false alarm rate, psychometric threshold, and the maximum slope of the psychometric curve. **d,** *Left*: Example stimulus spectrogram for the target-in-noise detection task with the corresponding waveform below. The scale bar indicates 1 second, and the colorbar indicates the volume for each time-frequency bin (silence is black). *Right*: psychometric performance for n=2 mice in the target-in-noise task, with target volume on the abscissa and probability of responding on the ordinate. Filled circles and dark solid lines indicate average performance after saline injection and psychometric fits to the average. Red open circles and dark dashed lines indicate average performance after muscimol injection and psychometric fits to the average. Light red solid and dashed lines are psychometric curves from individual sessions. Errorbars indicate ±SEM across sessions. **e,** *Left*: Example stimulus spectrogram for the target-in-silence detection task with the corresponding waveform below. Time scale and volume scale as in **d**. *Right*: psychometric performance for n=2 mice (same mice as in **d**) in the target-in-silence task, with target attenuation relative to the highest volume target from the target-in-noise task on the abscissa and probability of responding on the ordinate. Black filled circles and dark solid lines indicate average performance after saline injection and psychometric fits to the average. Open circles and dark dashed lines indicate average performance after muscimol injection and psychometric fits to the average. Light grey solid and dashed lines are psychometric curves from individual sessions. Errorbars indicate ±SEM across sessions. **f,** Behavioral performance metrics as a function of task type (detection in noise or detection in silence) and pharmacological intervention. Formatting and metrics as in c (with the exception of response rate at threshold). Dark and light red bars indicate performance in the detection-in-noise task, with application of saline or muscimol. Dark and light grey bars indicate performance in the detection-in-silence task, with application of saline or muscimol. In all plots: ns*p*>0.1; †*p*<0.1, \**p*<0.05, \*\**p*<0.01, \*\*\**p*<0.001, \*\*\*\**p*<0.0001.

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**a,** Experimental setup for chronic ACtx recordings from behaving mice. **b,** Example spiking responses to targets and noise in low contrast during behavior. The top portion of the plot is a spike raster ordered by target volume. Colored bars indicate the target volume, grey bars indicate noise only trials. The bottom portion of the plot contains spike rates for each target condition, averaged over trials and smoothed with a 2ms standard deviation Gaussian kernel. *Inset:* Closed circles and the solid blue line indicate the area under the ROC curve (AUC) when discriminating noise from target responses across trials (activity was averaged from 0-100ms post target to compute AUC). Circle colors indicate the presented volume. The dashed horizontal line indicates chance performance (0.5). Error bars are the bootstrapped 95% confidence interval of the AUC value (see *Methods*). **c,** Neurograms of populations of simultaneously recorded neurons during a low contrast and high contrast session from the same mouse. Neurons are plotted along the ordinate, while target volume is plotted along the abscissa. Within each plot, the shade indicates the neural response to each target volume, with the average response to noise alone subtracted. White indicates no change in firing rate, blue/red indicate increases in firing rate relative to the noise response, and cyan indicates suppression below the noise response. Asterix indicates the responses of the neuron in panel **b**. **d,** Discriminating targets from noise using population responses. *Left:* schematic of coding direction analysis. In high dimensional neural space, noise trials are represented as a gray point-cloud, while target responses are represented as a blue point-cloud. The coding direction (CD) is the vector defining the average difference between these two point-clouds as indicated by the arrow. *Right:* trial distributions of projections along the coding direction for one session (session CA118-200707, as plotted in **c**. The blue distribution is the average projection value in a 40ms window after presentation of 20 dB SNR targets (indicated by arrow in panel **e**. The gray distribution is the average projection value in the same window during noise only trials. The vertical red line is the criterion which yielded the highest performance in predicting target presence across all trials. **e,** Example neurometric and psychometric curves. *Left:* Low contrast curves. Light blue circles and solid lines indicate psychometric performance and a logistic fit, respectively. Dark blue circles and solid lines indicate neurometric performance from the session plotted in the left panel of **c**. The horizontal dashed line indicates chance performance (0.5). The arrow indicates the neural performance computed from the distributions and criterion plotted in **d**. *Right:* High contrast curves from the same mouse for the session plotted in the right panel of **c**. **f,** Average psychometric and neurometric functions across mice. Light circles indicate average behavioral performance, dark red and blue circles indicate average neural performance. Light solid curves indicate logistic fits to average behavioral performance, while vertical lines indicate the fit thresholds. Dark solid lines indicate fits and thresholds for the neural data. The dashed vertical line indicates chance performance. Shades of blue and red indicate averages over low and high contrast respectively. **g,** Relationship between behavioral and neural thresholds. Each circle represents the average behavioral and neural threshold for each mouse for each contrast (as indicated by the circle fill color). Grey lines and shaded areas indicate the linear regression fit across contrasts, ±95% confidence interval. The solid black line indicates unity. Inset text indicates the significance of linear fits between all data points (black), low contrast data points only (blue), or high contrast data points only (red). **H,** Relationship between behavioral and neural slopes. Appearance as in **g**. **i,** Population decoder performance in each contrast transition, as a function of target presentation relative to the transition (indicated by the dashed vertical black line at 0s). Ticks on the abscissa indicate average target time from the transition in milliseconds. Solid lines and circles indicate the percent correct performance of a target decoder after a switch to low contrast (blue) or high contrast (red). Errorbars indicate ±SEM over sessions. Horizontal lines indicate significant changes in performance between the first target presentation time and subsequent target presentation times, as assessed by Wilcoxon Sign-rank tests with false discovery rate correction for multiple comparisons. The span of the lines indicates the target times being compared, while the color of the lines indicates whether the test was performed within high contrast (red) or low contrast (blue). **j,** Adaptation time constants of exponentials fitted to the average neural decoder performance for each mouse in each contrast. Blue and red circles indicate the adaptation time constants from neural populations for each mouse in low and high contrast respectively. Solid black lines indicate time constants from the same mouse.

**Diagram

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**a,** Schematic of the generalized-linear-nonlinear model. 1) Schematic of a spectro-temporal receptive field (STRF). 2) Example stimulus spectrogram of low and high contrast. 3) The gray trace is the filter response when convolving the STRF with the spectrogram. The black trace is the observed spike rate during the same stimulus period. 4) Schematized nonlinearities fit separately to low and high contrast periods in a gain control (GC) model or fit to all data in a static model. **b,** Example background-locked responses from a well-tuned cortical unit across the trial duration. The top portion of the plot is a spike raster sorted by the frozen noise scenes (Scene 1-5) of the background. The bottom portion of the plot is a PSTH of the observed spiking, binned every 25ms (black trace). The colored traces are the GC model predictions in each contrast (red trace uses the red nonlinearity in **d**, blue trace uses the blue nonlinearity in **d**). **c,** STRF for this example neuron. STRF values are indicated by the colorbar. **d,** Estimated nonlinearities for this example neuron. Points indicate the mean observed firing rate (ordinate), binned according to observed filter prediction values (abscissa). Solid lines indicate exponential function fits to the underlying points. Each line is a fit to the test set in 10 cross-validation runs (see *Methods*). **e,** Correlation coefficients between the observed trial-averaged spike rate and the model prediction for the static model and the gain control model. Each dot is the average correlation across 10 cross-validation folds for each neuron, where black dots are high stimulus locking neurons with low noise-to-signal ratios (NR < 100) and grey dots are neurons with low stimulus locking (NR > 100). For the remaining figures, only neurons with NR < 100 are included. The solid red line indicates unity. The red “x” indicates the median correlation for each model. **f,** Gain control in auditory cortex during the task. Each histogram is the distribution of gain values in high and low contrast across neurons with NR below 100, recorded during behavior. Dashed vertical lines indicate the median of each distribution. **g,** Relationship between gain and behavioral threshold. Each circle represents the average gain and behavioral threshold for each mouse for each contrast (as indicated by the circle fill color). Gain values were averaged over target selective neurons. Grey lines and shaded areas indicate the linear regression fit across contrasts, +- the 95% confidence interval. **h,** Relationship between gain and behavioral slope. Appearance as in **g**.