

# Neural population coding of sound level adapts to stimulus statistics

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**Mammals can hear sounds extending over a vast range of sound levels with remarkable accuracy. How auditory neurons code sound level over such a range is unclear; firing rates of individual neurons increase with sound level over only a very limited portion of the full range of hearing. We show that neurons in the auditory midbrain of the guinea pig adjust their responses to the mean, variance and more complex statistics of sound level distributions. We demonstrate that these adjustments improve the accuracy of the neural population code close to the region of most commonly occurring sound levels. This extends the range of sound levels that can be accurately encoded, fine-tuning hearing to the local acoustic environment.**

The auditory system is required to code sounds that vary enormously in level. Accurately assessing the overall level of a sound has important survival value, for example, in judging the distance of a sound source, the urgency of an alarm call or the fitness of a competitor. Furthermore, if sound level is represented accurately, then the levels within an ongoing sound can be better discriminated, aiding analysis and recognition of the sound. At the threshold of hearing (approximately 0 dB sound pressure level (SPL) in humans), the ear drum may move by only a fraction of the width of an atom; some natural environments are characterized by similarly low levels of sound, averaging only a few dB SPL<sup>1</sup>. In comparison, groups of vocal animals can generate sounds of more than 10<sup>9</sup>-fold higher average intensity (90 dB SPL)<sup>1–3</sup>, whereas the upper limit of human hearing is met by sounds that are twelve orders of magnitude higher in intensity (120 dB SPL) than sounds that are just audible. Over this vast range of levels, the auditory system achieves remarkable accuracy in detecting changes in sound level: humans can hear changes in level of about 1 dB across most of the full range of hearing<sup>4–6</sup>.

In order for sound level coding to be achieved using neural firing rates, firing rates must change with level across the full range of hearing. However, the majority of primary auditory nerve fibers have low thresholds to sound stimulation, with firing rates that saturate at low to middle sound levels, giving neural dynamic ranges (the range of levels over which firing rates change) of just 35 dB or so<sup>7,8</sup>. Even by including the smaller population of fibers with higher thresholds and nonsaturating responses, it does not seem that neural firing rates can account for the accuracy of coding over the full range of hearing<sup>9</sup>. As the limited neural dynamic range does not cover the range of levels over which hearing operates (the so-called ‘dynamic range problem’<sup>10</sup>) mechanisms must exist that extend the range of coding beyond that observed in auditory nerve firing rates. To this end, several adjuncts to a rate code for sound level have been considered<sup>9</sup>. However, the means by

which neural responses are normally assessed as a function of sound level bears little resemblance to the demands placed on auditory neurons under natural listening conditions. Traditionally, firing rate versus sound level functions are obtained using sounds separated by long silent intervals, randomized in presentation order, such that consecutive sounds can vary enormously in level<sup>11–14</sup>. Conversely, although natural sound levels can vary extensively over the long term, over short time periods, within a given environment, they more often fluctuate over a relatively limited range<sup>1</sup>.

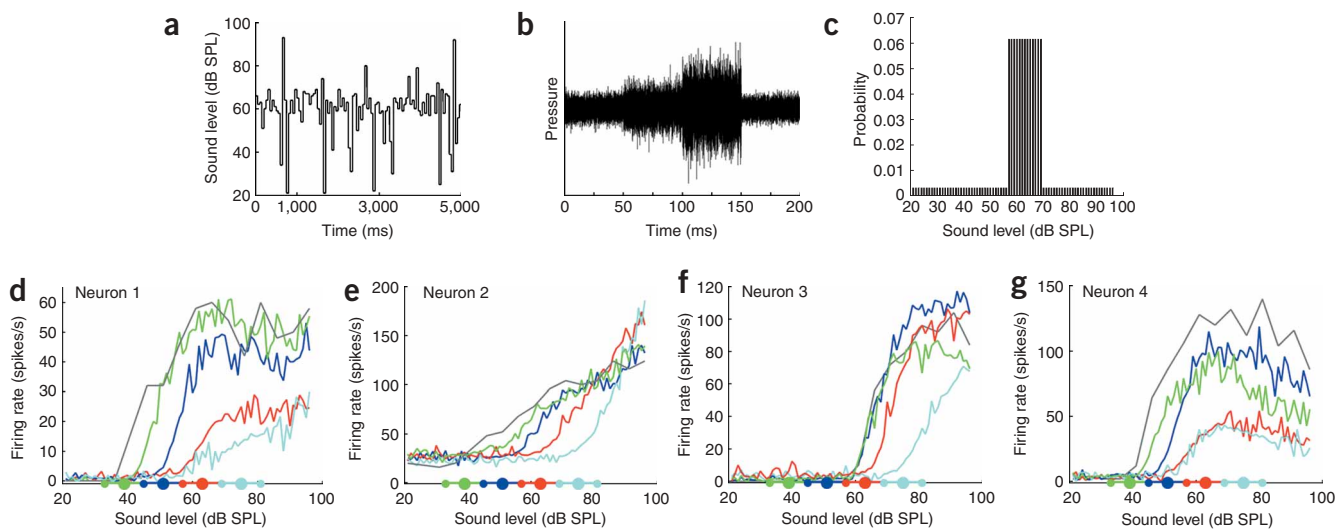
Neurons throughout the auditory system are subject to adaptive processes, causing a change in response over time during sustained input to the neuron. A possible function of these adaptive processes is to tailor the neural code to match the local sensory environment. We hypothesize that the neural code for sound level is flexible enough to take account of the time-varying distribution of natural sound levels, such that coding is context-dependent, allowing an efficient representation of auditory stimuli. We have examined the ability of auditory neurons in the inferior colliculus, the major midbrain nucleus in the ascending auditory pathway, to adjust their coding for sound level to take account of stimulus statistics. Our results show that the responses of inferior collicular neurons are rapidly adjusted according to the statistical distribution of sound levels presented. These adjustments alter the coding properties of the neural population such that coding accuracy is increased near the most commonly occurring sound levels.

## RESULTS

We presented a diotic (identical in each ear) white noise to anesthetized guinea pigs for ~7 min, during which time the sound level was set every 50 ms to a new value drawn randomly from a defined distribution (Fig. 1a,b). The full range of sound levels presented was 21–96 dB SPL. The distribution of sound levels consisted of one or more regions of probable levels, referred to as stimulus ‘high-probability regions’, from

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**Figure 1** Adjustments in responses of inferior collicular neurons to the mean sound level. **(a)** Level variations over 5 s of stimulus with high-probability region centered at 63 dB SPL. **(b)** Stimulus waveform (200 ms shown). **(c)** Level distribution for stimulus with high-probability region centered at 63 dB SPL. **(d–g)** Each panel shows rate-level functions of one neuron for four different sound level distributions, plus the baseline function (gray). Colored functions in all figures obtained with high-probability regions at 39 dB SPL (green), 51 dB SPL (blue), 63 dB SPL (red) and 75 dB SPL (cyan). Filled circles and thick lines on abscissa indicate midpoint and extent of the high-probability region of each stimulus.

which levels were selected with 0.8 overall probability (**Fig. 1c**). The remaining levels were selected with an overall probability of 0.2.

#### Adjustments of neural responses to the mean sound level

We first examined the effect of the mean sound level on neural rate-level functions, using a sound-level distribution with a single high-probability region of width 12 dB (**Fig. 1c**). Neural responses were recorded to level distributions with four different high-probability regions, centered at 39, 51, 63 or 75 dB SPL, referred to hereafter as the 39-, 51-, 63- and 75-dB stimuli. For each level distribution, the mean spike count of the neuron to each sound level was calculated, and the resulting rate-level function was plotted.

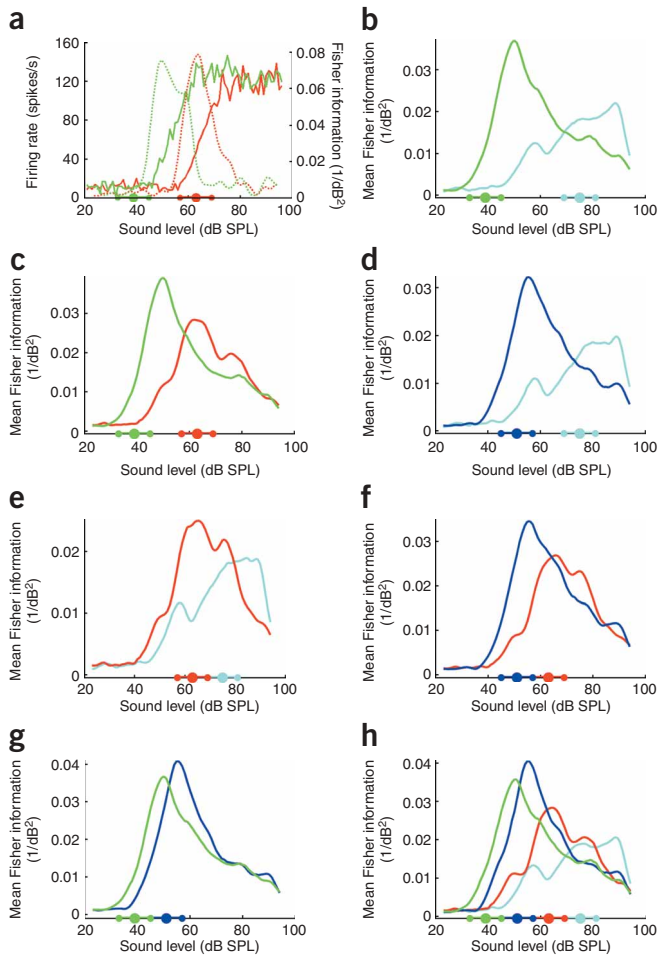
'Baseline' rate-level functions (**Fig. 1d–g**, gray) show the mean spike count to 50-ms noise bursts, separated by 300-ms intervals, at sound levels randomly selected from a flat distribution over 21–96 dB SPL. Sound stimulation of this form is typically used to record rate-level functions of auditory neurons<sup>11–14</sup>. In contrast, when rate-level functions were recorded using the fluctuating noise stimuli, which give each sound level a local statistical context, three observations were commonly made (**Fig. 1d–g**). First, rate-level functions shifted along the abscissa when the position of the high-probability region was changed. This shift resulted in a change in the threshold sound level. The largest change in threshold from the baseline function was approximately 35 dB. Notably, when the high-probability region was positioned below a neuron's baseline threshold, no neuron shifted its threshold to sound levels below its baseline threshold (see **Fig. 1f**). Second, the shifts in rate-level functions often resulted in neurons' thresholds lying within the range of sound levels encompassed by the high-probability region of the stimulus. Third, increasing the mean sound level often reduced the maximum spike rate and the slope of the rate-level functions, particularly over higher sound levels.

#### Adaptation of the population code to the mean sound level

We first investigated whether the adjustments in rate-level functions to different sound-level distributions improve coding of those level

distributions by single neurons. We calculated the Fisher information, a measure of coding accuracy<sup>15</sup>, for rate-level functions of single neurons obtained for different sound-level distributions (**Fig. 2a**). Assuming an optimal decoder, higher Fisher information reflects higher coding accuracy; that is, a more accurate representation of the sound level and thus a higher capacity to discriminate nearby sound levels. An intuitive approximation of Fisher information is the square of the slope of the rate-level function divided by the spike count variance. Thus, Fisher information is high when the spike count variance is low and when the spike count changes steeply with changes in sound level. As the variance in the neural spike counts that we recorded from inferior collicular neurons tended to be low when the spike counts themselves were low, the maximum Fisher information was typically at sound levels just above the threshold of the rate-level function. In some cases, this placed the peak Fisher information close to the high-probability region of the relevant stimulus distribution (**Fig. 2a**), suggesting that the function of the adjustments in rate-level functions might be to improve the accuracy of coding over this region.

However, the rate-level functions of different neurons were diverse, and the peak Fisher information for individual neurons often did not cover the entire high-probability region of the stimulus, nor was it always adjusted to be close to that region. To understand the implications of the adjustments in rate-level functions for sound-level coding, it is necessary to examine responses across populations of neurons. Evidence from many levels and modalities of the vertebrate nervous system suggests that information is represented by the activity of neuronal populations<sup>16</sup>. An estimate of the coding accuracy for the neural population was obtained by summing the Fisher information functions of the individual neurons. This analysis assumes that correlation in spiking noise between neurons is low. Although data concerning such correlations in the auditory system are scarce, correlation in spiking noise is known to be low between auditory nerve fibers<sup>17</sup>, and recent data suggest this to be the case also in the inferior colliculus<sup>18</sup> (see also C.V. Seshagiri & B. Delgutte, *Assoc. for Research in Otolaryngology Abstr.* **685**, 2003).



**Figure 2** Adjustments in neural responses improve population coding accuracy near the mean sound level. **(a)** Rate-level functions of one neuron for stimuli with high-probability regions at 39 and 63 dB SPL, and corresponding Fisher information functions (dotted lines). **(b–h)** Population Fisher information. In this and all figures, the total population Fisher information has been divided by the number of neurons in the population to facilitate comparison between plots. **(b)** High-probability regions at 39 and 75 dB SPL ( $n = 34$  neurons); **(c)** 39 and 63 dB SPL ( $n = 35$ ); **(d)** 51 and 75 dB SPL ( $n = 50$ ); **(e)** 63 and 75 dB SPL ( $n = 42$ ); **(f)** 51 and 63 dB SPL ( $n = 54$ ); **(g)** 39 and 51 dB SPL ( $n = 38$ ); **(h)** all four sound level distributions ( $n = 31$ ).

sound level variance of pure tones has been reported in the cat<sup>19</sup>. However, the effect of sound level variance on neural rate-level functions and on the accuracy of the code for sound level has not been examined. We therefore investigated the effect of extending the range of common sound levels in the distribution by comparing responses to sound-level distributions with high-probability regions 12 dB and 24 dB in width, centered at 63 dB SPL (**Fig. 3a**).

The rate-level functions of some neurons varied with the width of the high-probability region (**Fig. 3b**). However, changes in rate-level functions with increasing width of the high-probability region were typically not marked (**Fig. 3c**). Despite this, the Fisher information curve for the population of neurons was slightly wider when neural responses had adjusted to the wider (24 dB) range of common sound levels (**Fig. 3d**). For both widths, the region of highest coding accuracy was positioned just above the midpoint of the high-probability region; the adjustments of neural responses to the wider high-probability region resulted in a marked increase in Fisher information at the edges of the region of high coding accuracy. The high-probability region was widened on both sides by 6 dB, and the resulting Fisher information curve widened by a similar magnitude. No change was observed in the Fisher information curve when the width of the high-probability region was increased for the stimulus centered at 51 dB SPL (data not shown), possibly because the wider range of (lower) sound levels in this stimulus extended the distribution significantly below the neurons' baseline thresholds.

### Adaptation to stimulus bimodality

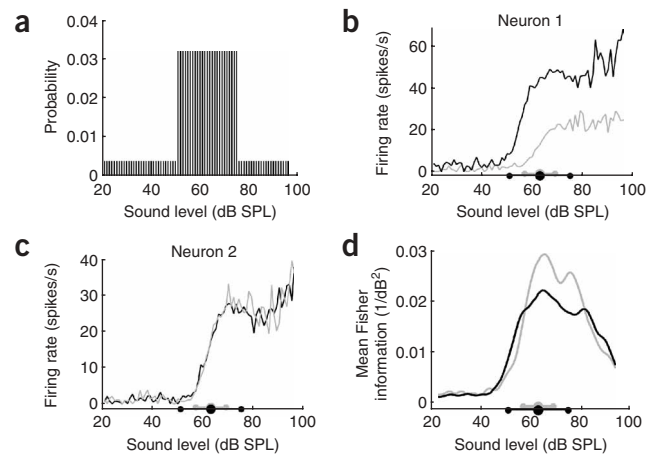
Finally, we examined how inferior colliculus neurons encode stimuli with more complex sound level distributions. In 'bimodal' stimuli, sound levels were selected from a distribution with two high-probability regions, centered at 51 and 75 dB SPL or at 39 and 63 dB SPL (**Fig. 4a**).

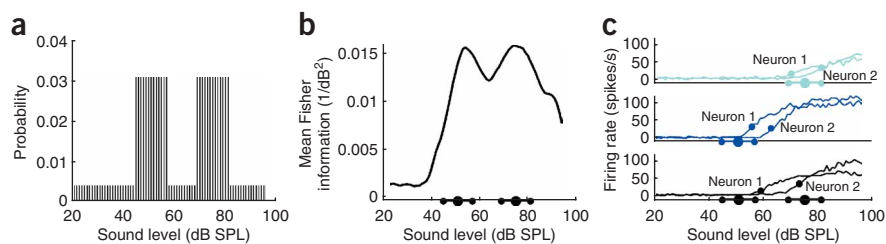
We compared the population Fisher information for neurons adjusted to pairs of different sound-level distributions (**Fig. 2b–g**). Within each comparison, the Fisher information was obtained for exactly the same population of neurons. Across all these paired comparisons, adjustments of rate-level functions to a given distribution improved sound-level coding just above the midpoint of the high-probability region of that distribution. For example, comparing the Fisher information curve for the 39-dB stimulus to that for the 75-dB stimulus (**Fig. 2b**), the most commonly occurring sound levels in the 39-dB stimulus were coded best by responses adjusted to that stimulus. Conversely, for the 75-dB stimulus, the most commonly occurring levels were coded best by responses adjusted to the 75-dB stimulus. Finally, we calculated the population Fisher information for 31 neurons from which responses to all four sound level distributions were obtained (**Fig. 2h**).

### Adaptation to stimulus variance

Natural environments may present the auditory system not only with changes in the mean sound level but also with changes in the extent of sound level fluctuations<sup>1</sup>. Adaptation of inferior collicular neurons to

**Figure 3** Neural adjustments to stimulus variance. **(a)** Level distribution for stimulus with wider (24 dB) high-probability region (compare to **Fig. 1c**). **(b,c)** Each panel shows rate-level functions of one neuron for two widths of the high-probability region of the stimulus, 12 dB (gray) and 24 dB (black). **(d)** Population Fisher information for stimuli centered at 63 dB SPL, with high-probability regions of width 12 dB and 24 dB ( $n = 25$ ).





**Figure 4** Neural adjustments to stimulus bimodality. **(a)** Level distribution for bimodal stimulus centered at 51 and 75 dB SPL. **(b)** Population Fisher information for bimodal stimulus shown in **a** ( $n = 46$ ). **(c)** Rate-level functions from two neurons, from one animal. Filled circles on functions indicate point of each neuron's maximum Fisher information. Top and center: responses to unimodal stimuli; bottom: responses to bimodal stimulus shown in **a**.

Individual rate-level functions did not show any obvious tendency to adjust to both high-probability regions in response to bimodal stimuli. However, when the population Fisher information for bimodal stimuli was compared with that for the corresponding unimodal stimuli, we found that the region of highest coding accuracy was adjusted so as to incorporate both high-probability regions. In the case of the 51- to 75-dB SPL stimulus, two regions of high accuracy were apparent in the population Fisher information, with a dip in accuracy between them; these regions of high accuracy corresponded to the louder ends of each of the two high-probability regions (**Fig. 4b**). This double-peaked Fisher information curve appeared to result, largely, from some neurons positioning the thresholds of their rate-level functions near one of the high-probability regions, and others positioning their thresholds near the other high-probability region, thereby dividing the neural population's resources. These divisions were observed within animals (**Fig. 4c**). Rate-level functions of neurons with high baseline thresholds tended to shift to the louder high-probability region; rate-level functions of neurons with low baseline thresholds tended to shift to the quieter high-probability region (data not shown). Most sound levels presented at high probability within a bimodal stimulus were coded less accurately than the same sound levels presented at high probability within a unimodal stimulus. However, most sound levels presented at high probability within a bimodal stimulus were coded more accurately than the same sound levels presented at low probability within a unimodal stimulus. These results indicate that the neural population did not simply adapt to the mean sound level (which lay between the two high-probability regions of the bimodal stimuli) but rather could apportion its coding resources so as to take account of a more complex stimulus distribution.

### Time course of neural adaptation

The time course of neural coding adjustments was examined by plotting rate-level functions separately for consecutive 5-s segments of the 63-dB (12-dB width) stimulus. For most neurons, rate-level functions were adjusted rapidly to a final, stable position, reproducible in response to subsequent stimulus segments. The time taken for the rate-level function to stabilize was assessed by calculating the root-mean-squared (r.m.s.) difference between the rate-level function from each 5-s segment and the average rate-level function from the final 50 s of the stimulus (**Fig. 5a,b**). Single exponential decay functions were fitted to the r.m.s. data for each neuron (**Fig. 5b**).

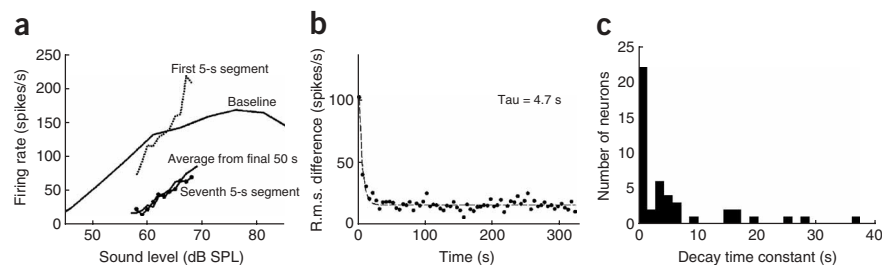
The time taken for neural responses to stabilize varied between neurons (**Fig. 5c**), with a median time constant of 3.2 s ( $n = 50$ ). Most neurons' rate-level functions

clearly differed from their baseline function within the first 5 s of presenting the stimulus (**Fig. 5a**); for 20/50 neurons, the rate-level function from the first 5 s was already very similar to the average function from the final 50 s, such that the r.m.s. data showed no apparent decay. The rate-level function of only one neuron did not stabilize but was continually adjusted throughout the 7 min of stimulus presentation.

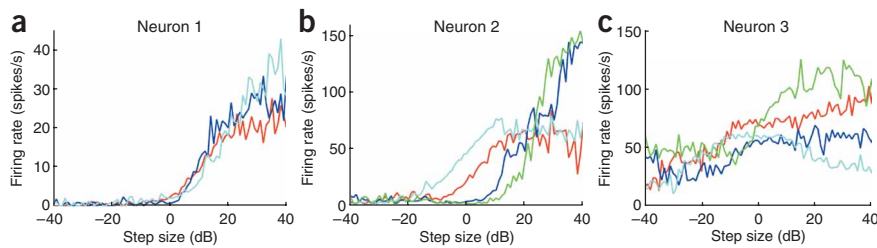
### Neural sensitivity to changes in sound level

Our data demonstrate the extent to which a neuron's stimulation history influences its response to the current stimulus. Thus, the neuron's response will be a function of the current sound level and past sound levels. One of the simplest possible functions that might provide for the shifting rate-level functions is one in which neural responses are determined not by the absolute sound level, but by the difference between the current and immediately preceding sound level (the 'step size'), regardless of the sound level distribution. For this reason, we examined whether firing rate versus step size functions were invariant with sound level distribution (**Fig. 6a-c**).

We found that few neurons' firing rates were dependent on step size in a manner independent of the distribution of sound levels. The rate versus step size functions of such neurons were broadly aligned across different sound level distributions, although never invariant (**Fig. 6a**). However, for most neurons, rate versus step size functions differed considerably in threshold and shape between sound level distributions (**Fig. 6b,c**), as did the rate-level functions. Thresholds of individual neurons to step size varied by up to 30 dB between different sound level distributions (**Fig. 6b**), and, for some distributions, firing rates were relatively insensitive to step size (**Fig. 6c**). Thus, a simple dependence of neural responses on level step size, such that responses were invariant with the sound level distribution, did not account for the neural adaptation we observed.



**Figure 5** Time course of neural adaptation. **(a)** Rate-level functions of one neuron for high-probability region of stimulus only, from 5-s segments of stimulus, compared with average function from final 50 s of stimulus and baseline function. **(b)** Same neuron as **a**: root-mean-squared (r.m.s.) differences between rate-level function from each 5-s segment and average function from final 50 s of stimulus. Times on abscissa: segment number multiplied by the 5-s segment duration, minus 2.5 s. Dashed line: single exponential decay;  $\tau = 4.7$  s. **(c)** Histogram of  $\tau$  values for all neurons for which  $\tau < 40$  s ( $n = 46/51$  neurons).



**Figure 6** Responses of inferior collicular neurons to changes in sound level. (a–c) Each panel shows firing rates of a neuron during the current 50-ms epoch of the stimulus, as a function of the difference in sound level between the current epoch and the previous 50-ms epoch, for different sound-level distributions.

## DISCUSSION

Our data demonstrate that although auditory rate-level functions show a restricted dynamic range, the range of sound levels over which the dynamic range lies is mutable. Neural responses were rapidly adjusted in a manner that tended to improve coding of the most probable sound levels by the neural population. There was a slight bias of coding accuracy towards levels louder than those occurring most commonly. This may arise because the brain needs not only to encode the ongoing noise stimulus, or the ambient environment, but also to be prepared for encoding any additional stimuli that may be encountered. Further, although rate-level functions shifted in an approximately parallel manner over some mean sound levels, parallel shifts were not maintained across all mean levels. This suggests that the neural code is not invariant with mean sound level, but rather that it retains some information about overall level, which is consistent with evolutionary demands for some representation of overall level. It is possible that mean sound level-independent representation occurs at stages in the auditory pathway higher than the inferior colliculus, such as auditory cortex.

A number of mechanisms, possibly acting in combination, might underlie the adaptive effects we have described. It is unlikely that the middle-ear muscle reflex is involved, as this reflex is only weakly active in guinea pigs<sup>20</sup>, is inactive in anesthetized animals<sup>21</sup> and predominantly affects transmission of very high intensity, low-frequency sounds<sup>22</sup>. A more likely contributing mechanism is the action of the medial olivocochlear system, which feeds back directly to the receptor hair cells of the inner ear, causing suppression; however, the time constant of action of this efferent system is approximately 100 ms (ref. 23), precluding it from fully accounting for the adaptive effects reported here, which have a time constant of several seconds. A further contributing mechanism is likely to be neural spike-frequency adaptation, or the decline in firing rate over time during a sustained stimulus. Such adaptation may arise through mechanisms intrinsic to the neuron, through synaptic depression or through network interactions. Spike-frequency adaptation is a characteristic of primary auditory nerve fibers<sup>24,25</sup> as well as of higher-level auditory neurons<sup>26</sup>. Thus, it is possible that neural substrates for the changes in coding we observed originate at low levels of the auditory system. Previous studies have shown that rate-level functions to pure tones shift to higher sound levels if the tones are presented in a constant level of background noise. These effects are observed at all levels of the auditory system that have been examined<sup>12–14,27,28</sup>. This phenomenon may share some mechanisms with the shifts in rate-level functions that we observed, although the effect of such changes in rate-level functions on the population coding accuracy for sound level has not been measured. At subcortical levels, noise-induced changes in rate-level functions to tones are thought to result largely from cochlear, or ‘two-tone’, suppression<sup>12,29</sup>.

Two-tone suppression is dependent on nearby frequencies in the background noise suppressing the response to the tone on the basilar membrane. As the relative power of our wide-band stimulus was constant across all frequency components for all sound level distributions, we can discount two-tone suppression as a potential mechanism contributing to the adjustments in coding that we describe. Our data have shown that, despite the diversity of adaptive mechanisms that are likely to shape inferior colliculus responses, the concerted action of such processes seems to function so as to improve the accuracy of the neural code for sound level.

Neural adaptation has been attributed a number of functions. For example, there is evidence that adaptive processes in auditory cortex facilitate novelty detection by single neurons<sup>30</sup>. The adaptation that we have described may be the auditory analogue of gain control processes in the visual system<sup>31–33</sup>. These processes have been suggested to improve coding by adjusting neural responses to the statistics of visual stimuli. An improvement in coding resulting from neural adaptation has recently been demonstrated for single neurons in the blowfly visual system<sup>34,35</sup>. Our study is the first demonstration of neural adaptation, dependent on stimulus statistics, that improves the coding accuracy of a neural population; we have shown that the population code adapts to the mean sound level, the variance and even bimodality. The capacity of the auditory brain to fine-tune to the local acoustic environment allows high accuracy in level discrimination to be maintained over a wide range of sound levels, despite the limited dynamic range of individual neurons.

## METHODS

**Physiological recordings.** Extracellular recordings were made from the right inferior colliculi of urethane-anesthetized guinea pigs, using standard techniques<sup>26</sup> approved by the UK Home Office. Single neuron responses were recorded using glass-coated tungsten microelectrodes (Tucker Davis Technologies System III). White noise (<25 kHz) was presented diotically via sealed, calibrated earphones. Only integer dB values of sound level, between 21–96 dB SPL, were used, giving 76 sound level values in total. For a given sound-level distribution, the level sequence and noise token were the same for all neurons. For baseline rate-level functions, noise bursts were separated by 300-ms intervals; levels were selected randomly from a flat distribution, and each level was presented ten times. For all other stimuli, sound was presented in 5-s segments, separated by <0.4 s. All rate-level functions were plotted from the mean number of spikes occurring during the 50-ms epochs corresponding to a given sound level. We used a standardized neural latency of 8 ms, the minimum latency measured, so we do not assume the operation of a system that can account for differing neural latencies. The first and second 5-s segments of each stimulus were excluded from all analyses, except analyses of the time course of changes in neural responses. For time course analyses, we calculated the r.m.s. difference between the rate-level function from each 5-s segment and the average function from the final 50 s of the stimulus. This analysis was performed for the high-probability region of the stimulus only, because other sound levels were presented too few times within each 5-s segment. We then fitted the r.m.s. data for each neuron with a single exponential decay (Fig. 5b) and obtained a decay time constant. For 20/50 neurons, the r.m.s. data were better fitted by a flat line than by an exponential decay (*F*-test, *P* < 0.05 to accept exponential fit), indicating that the rate-level function had already, within the first 5 s, reached the position occupied in the final 50 s of the stimulus; the time constant of these neurons was designated 0 s. The time constant of one neuron was >600 s, indicating that the rate-level function had not stabilized within the time of recording.

**Measuring the Fisher information of the neural population.** The population Fisher information function  $F(s)$  was used to measure the accuracy with which sound level  $s$  was encoded by the spike counts of the recorded neural population when  $s$  was presented in a given sound level distribution. In the limit of a large number of neurons, the reciprocal of the Fisher information equals the variance of the representation of  $s$  by the neural population. The square root of this variance is proportional to the just-noticeable difference, another common measure of coding accuracy. Correlation in spike count of neuron pairs due to shared stimulus history was small for all stimuli. The mean correlation coefficient averaged over sound levels, for all neuron pairs and all stimuli, was 0.056 (s.d. across pairs = 0.13). Furthermore, there is some suggestion that correlation in intrinsic spiking noise between inferior collicular neurons is low<sup>18</sup> (see also C.V. Seshagiri & B. Delgutte, *Assoc. for Research in Otolaryngology Abstr.* **685**, 2003). Thus, it is reasonable to approximate the Fisher information by assuming that the neurons generate spikes independently, giving

$$F(s) = \sum_a f_a(s)$$

where  $f_a(s)$  is the Fisher information function of each neuron  $a$ , for the sound level distribution of interest. The Fisher information function of a neuron is calculated from the probability  $P_a[r | s]$  of neuron  $a$  giving  $r$  spikes when sound level  $s$  is presented. Hence,

$$f_a(s) = \sum_r P_a[r | s] \left( \frac{d \ln P_a[r | s]}{ds} \right)^2$$

where the differential was performed by a five-point centered numerical algorithm.

To obtain  $P_a[r | s]$  for the stimulus with the level distribution of interest, the number of spikes was counted during each 50-ms epoch, with a standardized 8-ms neural latency.  $F(s)$  was also calculated using each neuron's measured latency, rather than the 8-ms latency; this had no qualitative effect on the results. For each sound level,  $s$ , a histogram was constructed of the number of epochs in the stimulus containing  $r$  spikes. This gave an  $R \times 76$  matrix, where  $R$  is the maximum number of spikes in any epoch. For the high-probability region of the stimulus, only a random sample of the epochs was used so that the average number of epochs per dB was the same in the high-probability region as elsewhere. For the unimodal stimuli, the number of epochs used for each sound level averaged at 23.5. Owing to the sampling, each neuron's Fisher information function is the median of 20 functions, where each function was obtained using a different sample. The matrix was convolved with a Gaussian kernel with 0.5 spikes standard deviation and 4 dB standard deviation, in order to remove spurious fluctuations. Finally, the matrix was converted into a probability matrix of spike count given sound level,  $P_a[r | s]$ , by normalizing the sum of each sound level column to 1.

In addition,  $F(s)$  was calculated using an approximation of the single neuron Fisher information  $f_a(s) = y_a'(s)^2 / \sigma_a(s)^2$ , where  $y_a'(s)$  is the differential of the spline fit to the rate-level function, and  $\sigma_a(s)$  is the spline fit to the standard deviation as a function of sound level, for neuron  $a$ . The splines were fitted using the BARS algorithm<sup>36</sup>. This alternative method had no qualitative effect on the results.

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#### COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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