SI APPENDIX TEXT

Validation of catch trials

On four electrodes, we trained monkey B to perform frequency discrimination on 2 subsets of stimuli before using the full stimulus set: one with both stimuli in the pair of equal amplitude and one in which the higher frequency stimulus always was at a much lower amplitude. High performance was achieved on all four electrodes for these two subsets (Fig. S7). However, catch trials revealed that the animal was biased toward more intense stimulus in the first set but toward less intense stimuli in the second set. These results are consistent with the hypothesis that catch trials reveal the animal's reliance on intensive cues and indicate that the 30-µA amplitude difference was sufficient to overcome the 100-Hz frequency difference such that the higher frequency stimulus felt less intense than the lower frequency one. When the animal was faced with the full set (which comprised stimuli from the first two), the animal was able to perform the task correctly regardless of amplitude differences on only two of the four electrodes (Fig. S7).

Learning during task transfer

All the data described above reflect monkey B's asymptotic performance, sometime after weeks of training on each electrode and standard frequency. Next, we examined how the animal's performance evolved during training. We found that, on some electrodes, the animal appeared unable to overcome the amplitude confound over the course of up to 6000 trials (Fig. S9*B*). On other electrodes, the animal relied on intensity cues at first, but learned over an extended period to discriminate frequency independent of amplitude (example 1). On yet other electrodes, the animal's performance was initially high but somewhat amplitude-dependent and became, relatively rapidly, independent of amplitude (example 3). We found that the majority of electrodes yielded good performance immediately (above criterion of 75% at all amplitude differences) or never yielded good performance (the animal did not learn to perform above criterion at all amplitude differences within 6000 trials)(Fig. S9*B*).

Adaptation index

We developed an adaptation Index to quantify the relative contributions of slowly adapting and rapidly adapting signals to the multi-unit responses to skin indentations at each electrode (Fig. S3), as has been previously done (1, 2). For this calculation, we normalized neural responses during sustained indentation and indentation offset to their respective grand means across electrodes. The adaptation index was then computed by dividing the normalized offset response by the sum of the normalized sustained and normalized offset responses for each electrode separately. An index of 0 denoted a pure SA1-like response, an index of 1 a pure RA-like response.

SI APPENDIX TABLES AND FIGURES

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Frequency discrimination stimulus set 1: constant pulse amplitude, full stimulus set for detailed psychometric curves				
Standard stimulus frequency (Hz)	Standard stimulus amplitude (µA)	Comparison stimulus frequency (Hz)	Comparison stimulus amplitude (µA)	Phase duration (µs)
20	50, 60, 70, 80	16, 18, 22, 23, 26 29	50, 60, 70, 80	400
50	50, 60, 70, 80	30, 35, 40, 45, 55, 60, 65, 70	50, 60, 70, 80	400
100	50, 60, 70, 80	50, 75, 150, 200, 300	50, 60, 70, 80	200
200	50, 60, 70, 80	100, 150, 250, 300, 350, 400	50, 60, 70, 80	200
Frequency discrimination stimulus set 2: with constant pulse amplitude, reduced stimulus set. Row 1: subset 1, row 2: subset 2, row 3: mixed subset (in Fig. S7)				
Standard stimulus frequency (Hz)	Standard stimulus amplitude (µA)	Comparison stimulus frequency (Hz)	Comparison stimulus amplitude (µA)	Phase duration (µs)
70, 80, 90, 100, 110, 120, 130, 170	50, 60, 70, 80	Always equal to standard frequency + 100	Always equal to standard amplitude	200
70, 80, 90, 100, 110, 120, 130, 170	80	Always equal to standard frequency + 100	50	200
70, 80, 90, 100, 110, 120, 130, 170	50, 60, 70, 80	Always equal to standard frequency + 100	50, 60, 70, 80	200
Catch trials in reduced stimulus set for frequency discrimination (interleaved in frequency discrimination stimulus set 2)				
Standard stimulus frequency (Hz)	Standard stimulus amplitude (µA)	Comparison stimulus frequency (Hz)	Comparison stimulus amplitude (µA)	Phase duration (µs)
70, 80, 90, 100, 110, 120, 130, 170	50	Always equal to standard frequency	80	200
Frequency discrimination stimulus set 3: variable pulse amplitude				
Standard stimulus frequency (Hz)	Standard stimulus amplitude (µA)	Comparison stimulus frequency (Hz)	Comparison stimulus amplitude (µA)	Phase duration (µs)

75, 105, 135, 165	For each stimulus, one of the following sets of individual pulse amplitudes was randomized, then repeated with the frequency-appropriate inter-pulse interval to complete a 1-s long stimulus: [44 to 72, in increments of 2] , [58 to 86, in increments of 2], [72 to 100, in increments of 2]. Average pulse train amplitudes were 58, 72, or 86.	Always equal to standard frequency + 90	For each stimulus, one of the following sets of individual pulse amplitudes was randomized, then repeated with the frequency-appropriate inter-pulse interval to complete a 1-s long stimulus: [44 to 72, in increments of 2] , [58 to 86, in increments of 2], [72 to 100, in increments of 2]. Average pulse train amplitudes were 58, 72, or 86.	200
Detection task				
Standard stimulus frequency (Hz)	Standard stimulus amplitude (μA)	Comparison stimulus frequency (Hz)	Comparison stimulus amplitude (μA)	Phase duration (μs)
100	10, 25, 40, 55, 70	0	0	200
Amplitude discrimination task (previously performed experiment, results published in (5))				
Standard stimulus frequency (Hz)	Standard stimulus amplitude (μA)	Comparison stimulus frequency (Hz)	Comparison stimulus amplitude (μA)	Phase duration (μs)
50, 100, 250, 500	70	50, 100, 250, 500	40, 50, 60, 80, 90, 100	200

Table S1. Stimulus parameters for each experiment. Each trial in the discrimination task consisted of a standard stimulus and a comparison stimulus. In an experimental block, every combination of amplitudes was used and the standard frequency was paired with every comparison frequency. For example, with the 50-Hz standard stimulus, 4 different standard stimuli (50Hz at 50, 60, 70, and 80 μA) were tested against 32 different comparison stimuli (8 different frequencies at 4 different amplitudes each), at both presentation orders, yielding 256 unique trials in a block (4 standards * 32 comparisons * 2 possible orders).

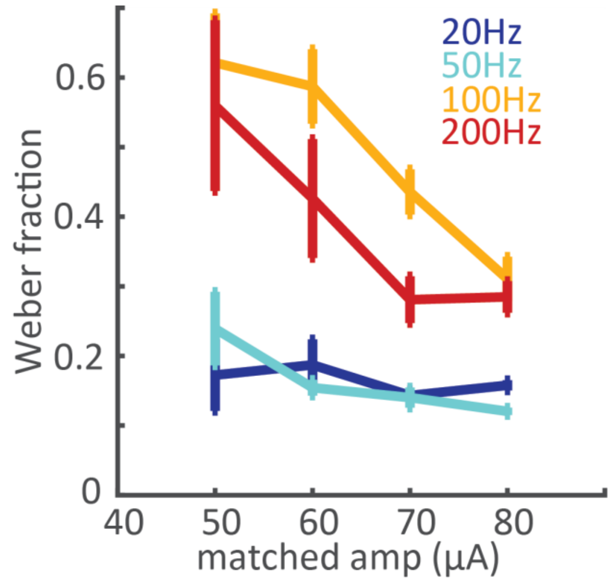

Fig. S1: Weber fraction as a function of amplitude. Performance at each standard frequency is shown in a different color. Error bars show the standard error of the mean across the extensively tested electrodes from the three monkeys (2 electrodes from monkeys A and B for the 20-Hz standard, 5 from monkeys A and B for the 50- and 200-Hz standards, 8 electrodes the three monkeys for the 100-Hz standard). Weber fractions were independent of amplitude in the lower frequency range, but decreased with amplitude for frequencies above 100 Hz.

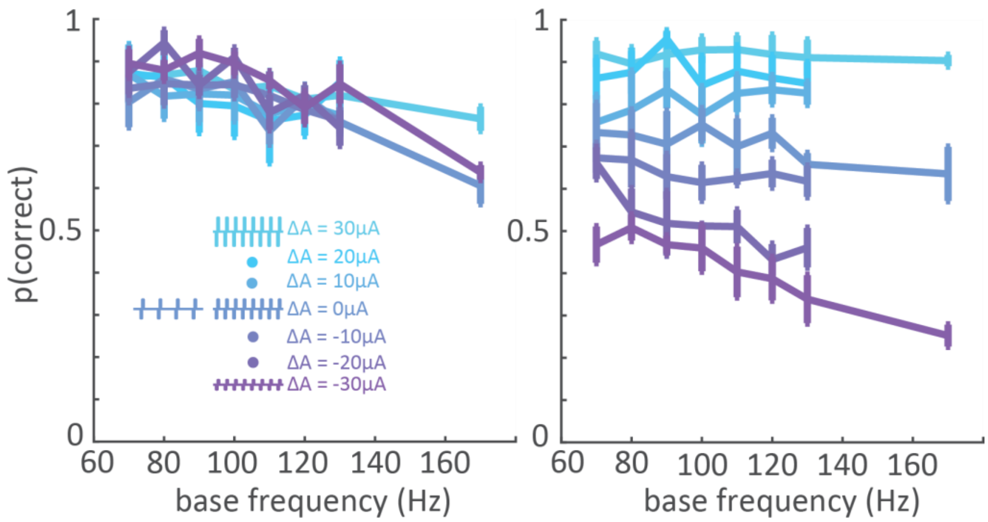

Fig. S2: Frequency discrimination performance as a function of base frequency for the 4 electrodes with the lowest spread (averaged across 4 electrodes) and the 4 electrodes with the greatest spread (average across 4 electrodes). The difference between base and comparison frequencies was always 100 Hz. Performance decreased slightly at higher frequencies, as expected. Error bars show the standard error of the mean across electrodes.

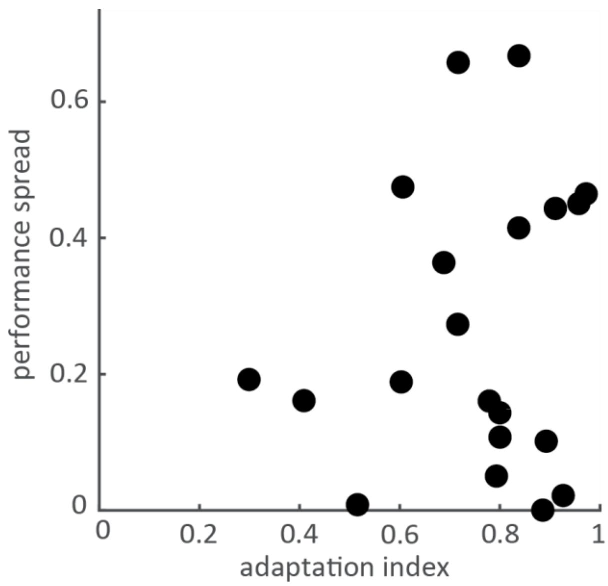

Fig. S3: Susceptibility to amplitude differences vs. adaptation index. Susceptibility is gauged by the difference in performances at the two amplitude difference extrema (purple and cyan in Fig. 4). A lower spread indicates a greater ability to distinguish the effects of frequency and amplitude. There is no apparent relationship between performance at an electrode and the adaptation properties of the corresponding neural response (how "RA-like" it is). Adaptation index values could only be computed for 20 of the 25 electrodes shown in Fig. 4 because the signal quality was too poor at the other 5 electrodes to record the responses of neurons.

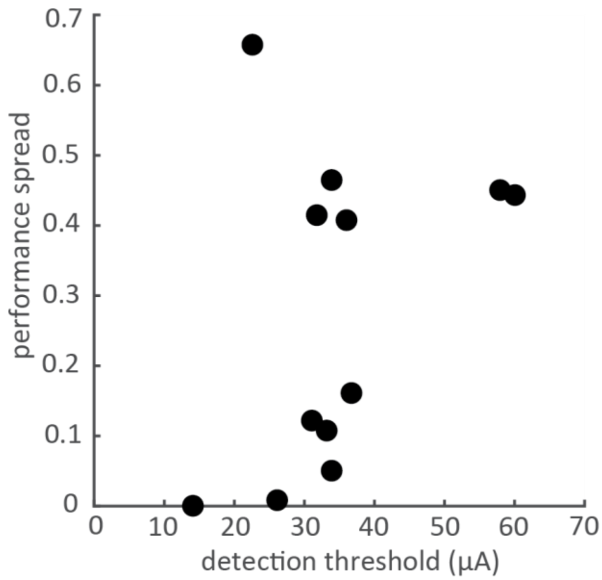

Fig. S4: Susceptibility to amplitude differences in the frequency discrimination task vs. detection threshold (measured at 100-Hz). The threshold is the minimum amplitude at which the animal detects the stimulus 75% of the time. Animals performed the detection task after all frequency discrimination experiments were complete to avoid any confusion due to task changes. The detection task was performed for 12 electrodes of the 25 electrodes shown in Fig. 4, 6 of which were selected from among low-spread electrodes (left side of Fig. 4) and 6 of which were selected from among high-spread electrodes (right side).

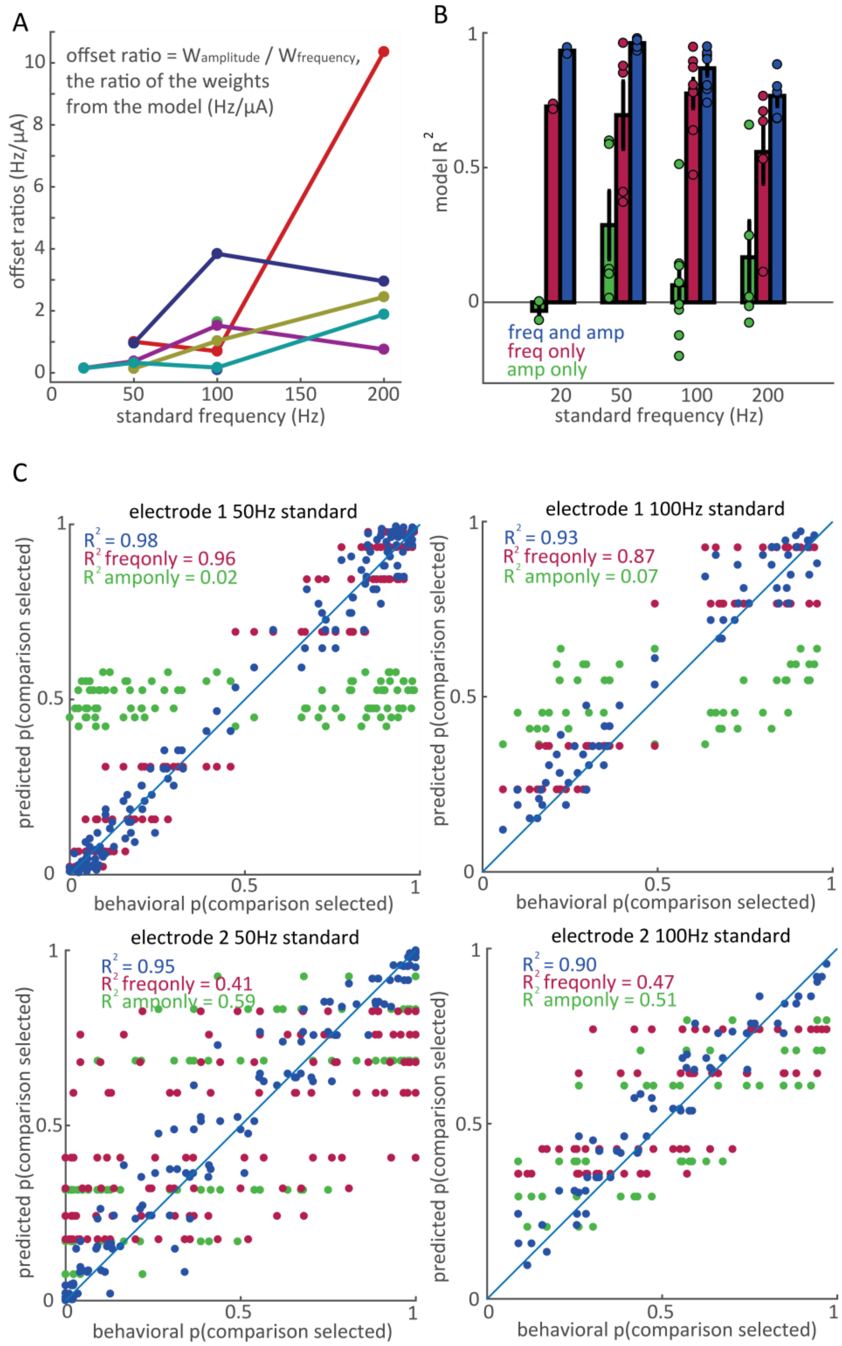

Fig. S5: Contribution of frequency and amplitude to frequency discrimination performance. A| Slopes of equivalent frequency-amplitude tradeoffs (the number of Hz equivalent to a 1μA change), derived from the model fit, for each standard frequency. We refer to these slopes as offset ratios. Different colors denote different electrodes. B| Goodness of fit of the model (R^2 = 1 - *RSS/TSS*, where *RSS* is the residual sum of squares and *TSS* is the total sum of squares) when using amplitude only (green), frequency only (red), or both (blue) as predictors. Bars denote the mean R^2, error bars the standard error of the mean and dots the value for individual electrodes. C| For the same two electrodes and standard frequencies shown in Fig. 3, model predictions for each unique stimulus pair vs. actual performance. Amplitude dominated the animal's choices on the bottom electrode to the point that the reconstruction using amplitude only is superior to the reconstruction using frequency only.

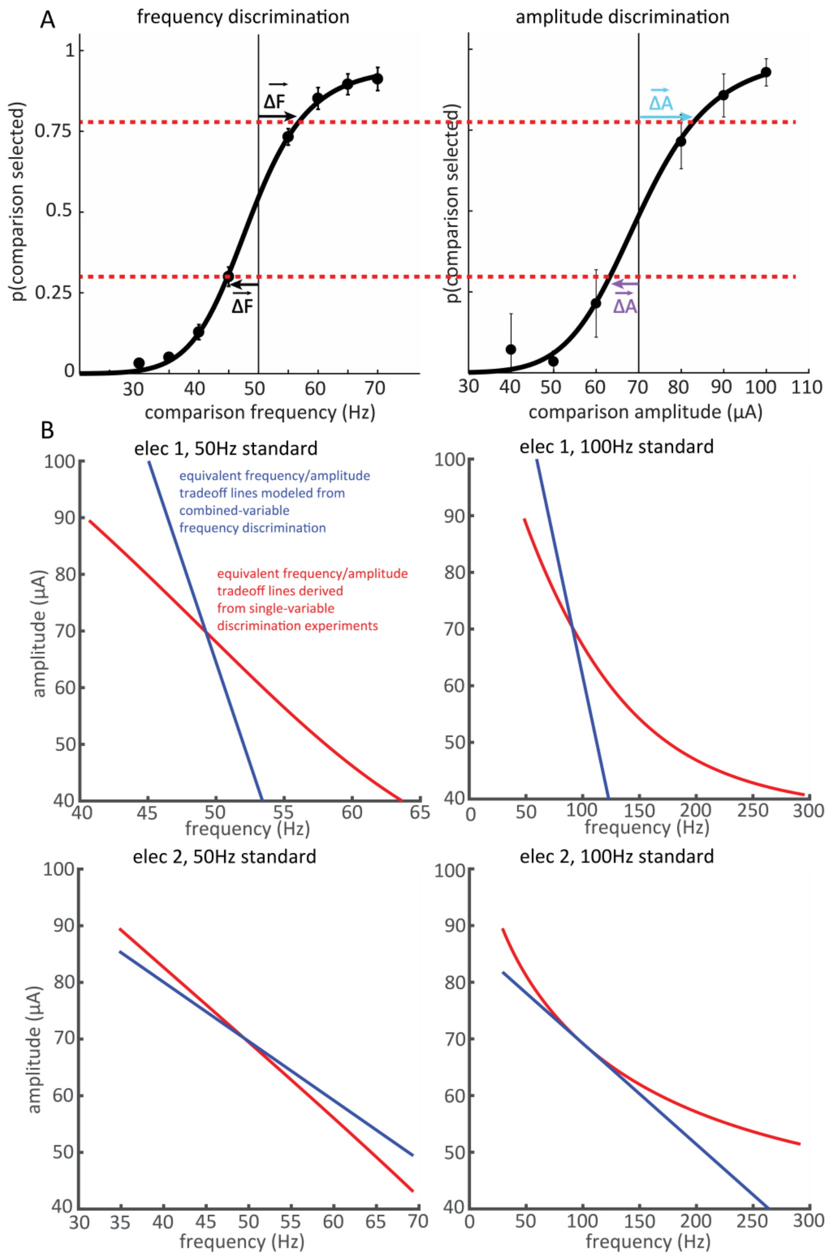

Fig. S6. A| Construction of iso-intensity lines from single-variable discrimination experiments (see *Generating equivalent frequency-amplitude tradeoffs using single-variable discrimination* in methods). Frequency differences in a frequency discrimination task (left) and amplitude differences in an amplitude discrimination task (right) that yield the same discrimination performance are used to obtain perceptual equivalence (red, below). Note that this methodology assumes that differences in amplitude and frequency affect the percept along the same sensory continuum. B| For the two electrodes and standards in Fig. 3, equivalence lines were derived from single-variable discrimination (red) and from the full stimulus (blue, see Fig. S5). At the standard stimulus, the equivalence line predicted from the single-variable experiments has a very different slope than observed equivalence relationship (blue) for electrode 1, but not for electrode 2. The relative importance of frequency is much greater for electrode 1 than what could be expected from the single-variable experiment, indicating that amplitude and frequency affect the elicited sensation along different perceptual axes.

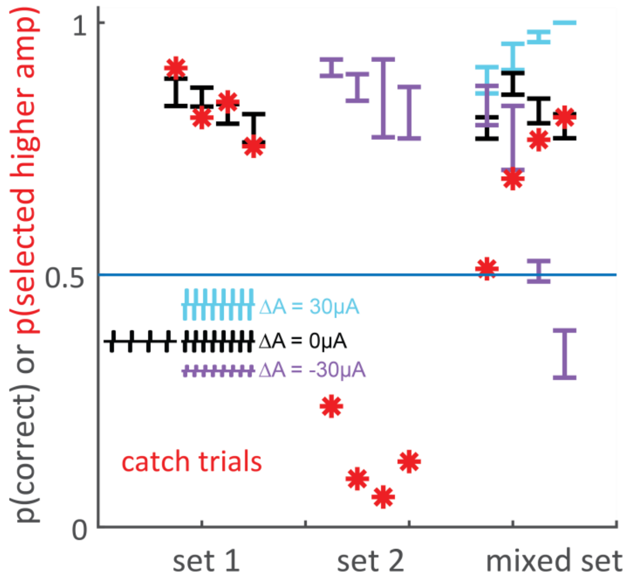

Fig. S7. Catch trials betray the animal's reliance on sensory magnitude. For four electrodes, p(correct) in the frequency discrimination task when amplitudes are matched (subset 1, black), when the higher frequency always has a lower amplitude (subset 2, purple), or when the full set is used (mixed subset, only the -30, 0, and 30 μA differences are shown for the sake of clarity). The ordering of the four electrodes remains the same in each stimulus set. Two of the selected electrodes had low amplitude-related performance spreads and two had higher ones (as can be seen in the mixed set results in this figure). Red asterisks for each electrode in each condition denote the probability of selecting the higher amplitude on catch trials in which stimulus frequencies were equal (so the frequency discrimination task had no correct answer). Catch trials represented less than 5% of total trials in each condition. The probability of selecting the higher amplitude on catch trials was well above 50% for all four electrodes when the animal was trained on the first stimulus set (in which both stimuli always have equal amplitudes in non-catch trials), indicating that the animal was biased toward selecting the more intense stimulus. This is consistent with perceived intensity increasing with increases in frequency. The probability of selecting the higher amplitude on catch trials was well below 50% for all four electrodes when the animal was trained on the second stimulus set (in which the higher frequency always has much lower amplitude on non-catch trials), indicating that the animal was biased toward selecting the less intense stimulus. This suggests that the amplitude difference of 30 μA was sufficient to ensure that the higher-frequency stimulus was the less intense one. The mixed stimulus set therefore contained some trials in which the higher frequency stimulus was more intense, and some trials in which the higher frequency stimulus was less intense, randomly interleaved. To perform well on both types of trials, the animal could not rely on intensity as it could with the first two stimulus sets. On the first electrode in the mixed set, the animal could reliably select the higher frequency stimulus whether it had the higher or lower amplitude, yet the catch trial results indicate the animal's decisions were not biased toward higher or lower intensities. The animal therefore must have been using a non-intensive cue to perform the task. The number of catch trials performed at each electrode and in each condition ranged from 84 to 152. Error bars show the standard error of the mean across training blocks.

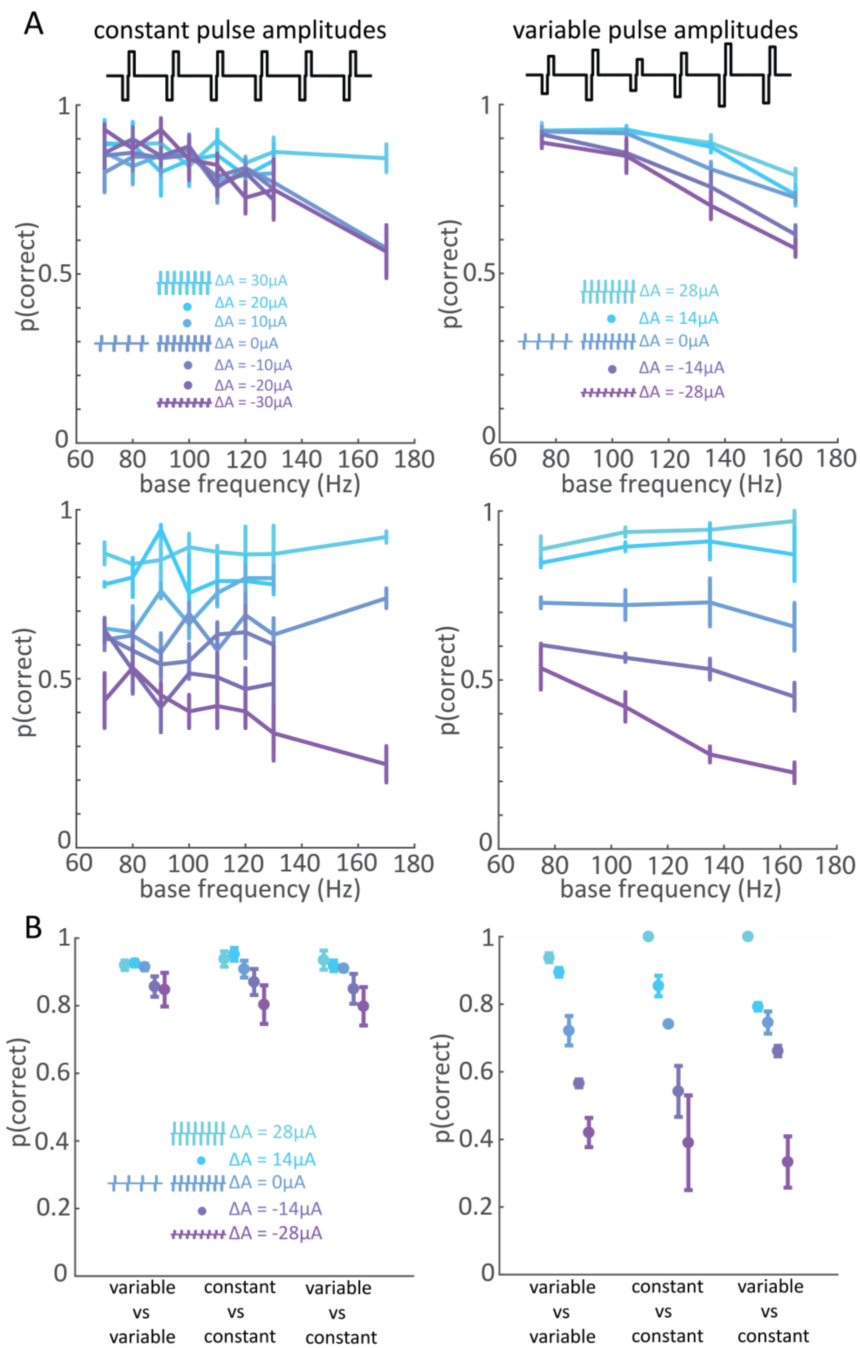

Fig. S8: Varying individual pulse amplitude has a negligible effect on frequency discrimination performance. This figure extends Fig. 6. A| Monkey B's performance vs. base frequency in the constant-amplitude experiment (left column) and the variable-amplitude experiment (right column) for the 4 electrodes with weak amplitude bias (top row) and the 2 electrodes with strong amplitude bias (bottom row). The frequency difference was always 100 Hz for the constant-amplitude experiment and 90 Hz for the variable-amplitude experiment due to hardware constraints (see Methods). B| Performance when stimulus pulse trains were both variable-amplitude, were split, or were both constant-amplitude, for the 4 electrodes with weak amplitude bias (left) and the two with strong amplitude bias (right). Changing the spatial distribution of the ICMS-induced activity on a pulse-by-pulse basis had little to no effect on the animal's ability to discriminate frequency. The top right panel in A and the left panel in B are taken from Fig. 6. Error bars in A and B show the standard error of the mean across electrodes.

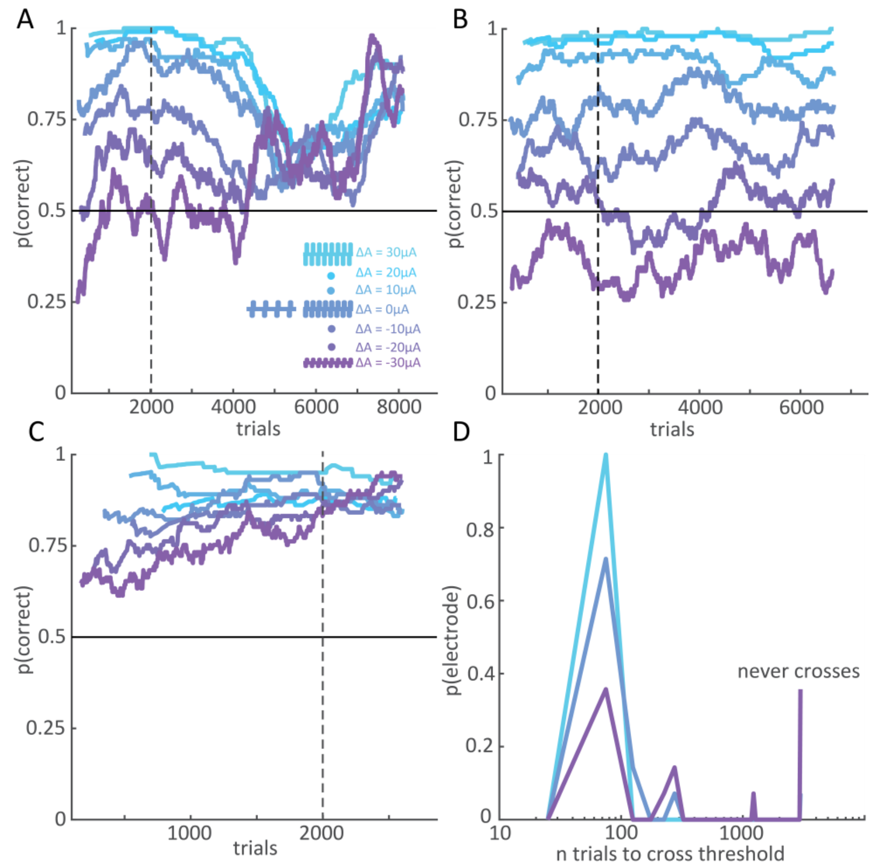

Fig. S9: Learning rate. A| Performance over time for an electrode at which the monkey first relied on intensity before learning to judge frequency independently. B| Example of an electrode at which the animal continued to rely on intensity. C| Example of an electrode at which the animal immediately performed well at all amplitude differences. D| Probability histogram of the number of trials of each condition required to achieve performance above a 75% threshold at amplitude differences of -30, 0, and 30 μA (for the 17 electrodes tested with the reduced stimulus set). When amplitudes were matched or the higher frequency had a higher amplitude, performance was above threshold immediately for all electrodes. When the lower frequency had a higher amplitude, at the vast majority of electrodes performance was either above threshold after little training, or never reached threshold. There were only a few electrodes for which performance in this condition was initially low but eventually met criterion performance.

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