Examining The Effects of Vowel Training on Neural Response Sensitivity in Ferret Auditory Cortex

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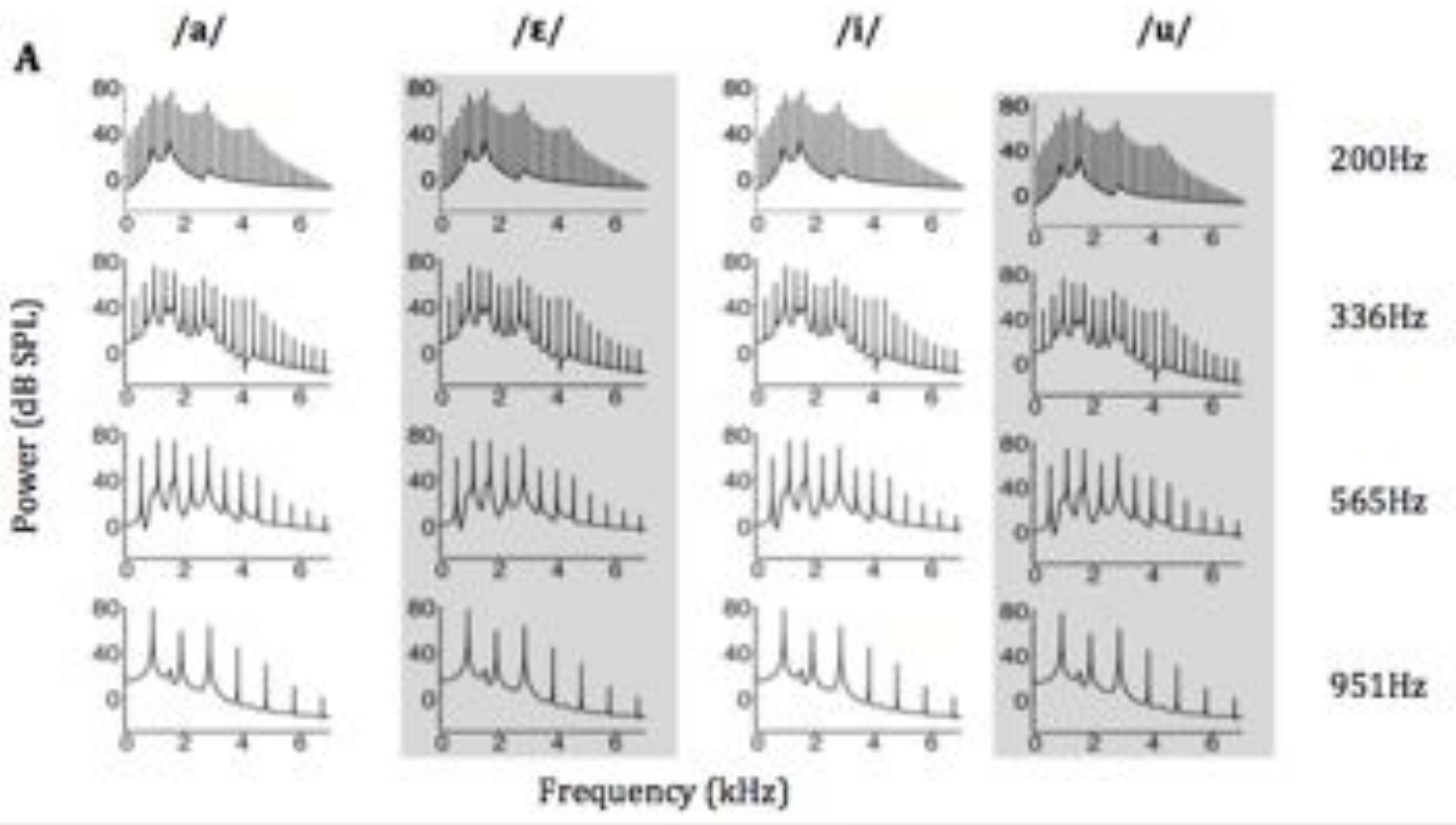
INTRODUCTION

We investigated learning-induced changes in auditory cortex by examining neural responses in animals trained to identity vowel sounds.
In order to measure pitch, timbre and location sensitivity we used a set of artificial vowel sounds, formed from band-pass filtered click-trains, presented in Virtual Acoustic Space (VAS).
Our stimulus set included 64 artificial vowels, which covered a 3-dimensional parameter matrix of 4 pitches, 4 timbres (vowel identities) and 4 spatial locations.

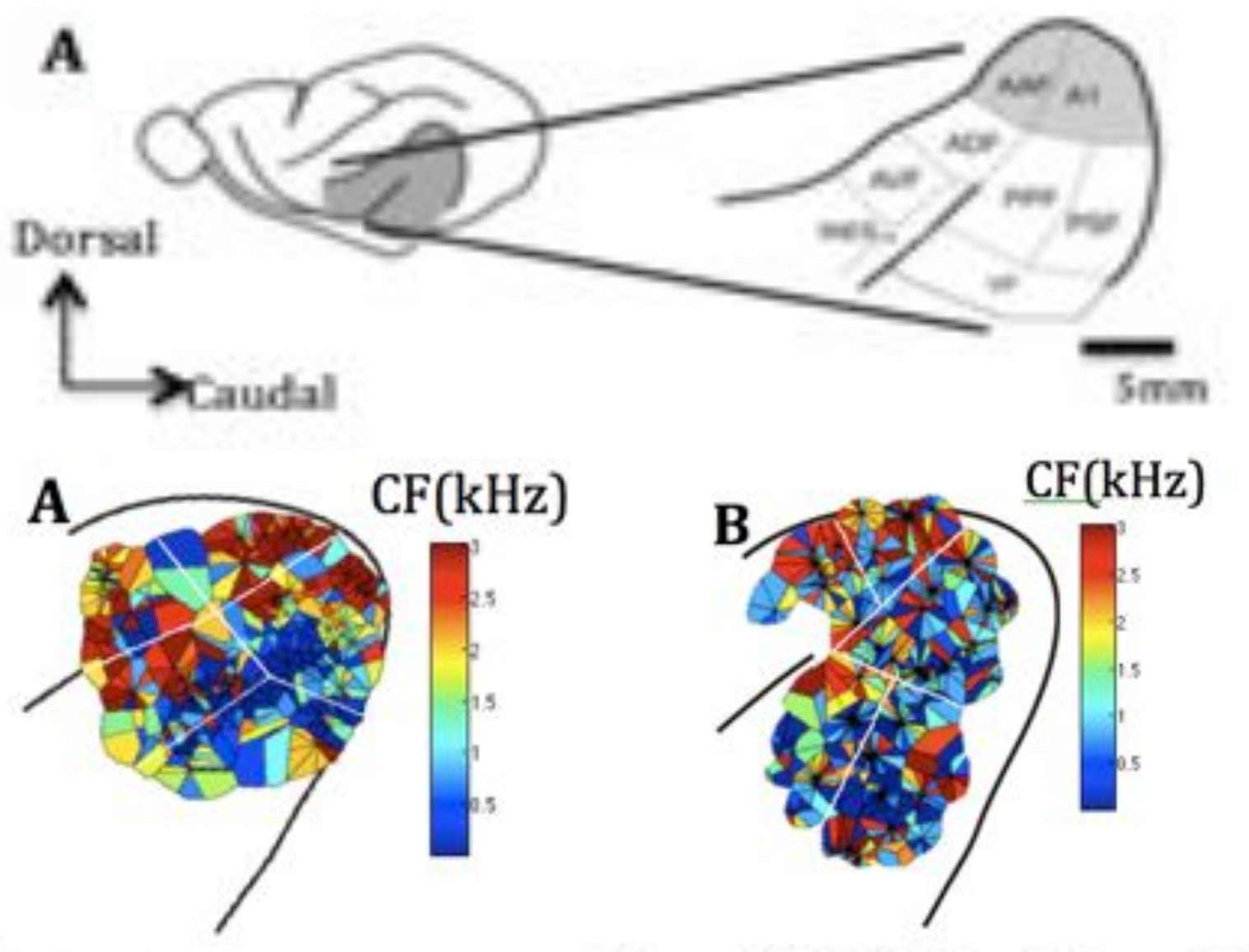


5 naïve ferrets served as control animals for electrophysiological recording.
3 ferrets were extensively trained in vowel discrimination (/ɛ/ and /u/ in a two-alternative forced choice task, under various listening conditions) and subsequently underwent electrophysiological recordings.

Recordings were made in domitor-ketamine anaesthetised ferrets using 16 and/or 32 channel silicon probes (Neuronexus) in either a 16x1, 16x2 or 8x4 configuration.

At each recording site responses to pure tone stimuli of varying frequency and intensity were used to construct frequency response areas from which characteristic frequencies (CFs) were estimated.

We recorded 758 acoustically sensitive recording sites, 483 of which were driven by the vowel stimuli. Of these, 312 recordings were from single neurons and 166 were small unit clusters. There was no significant difference between the response properties of single units and small unit clusters (t=0.8901, p=0.3925).

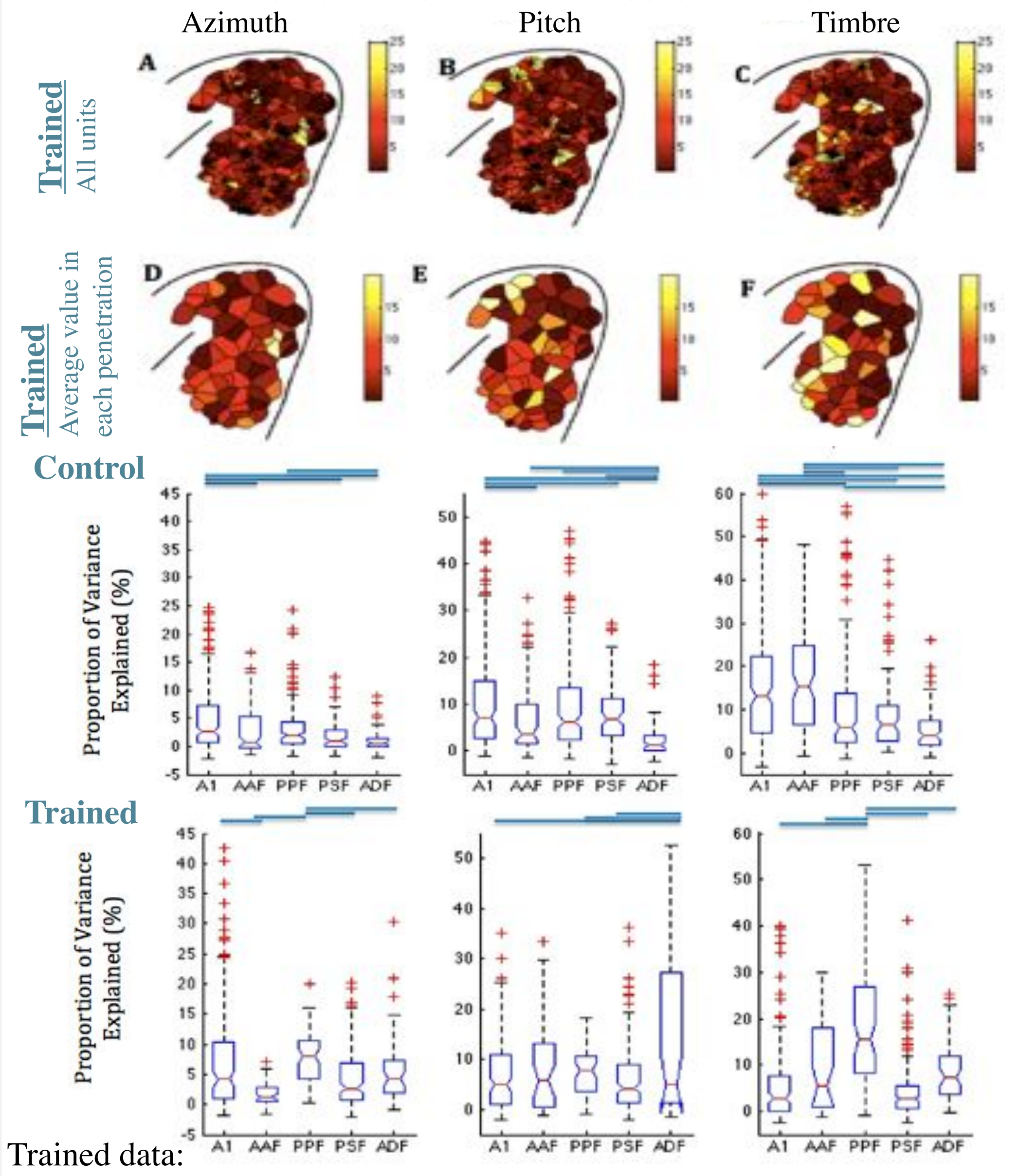


	A1	AAF	PPF	PSF	ADF
Recordings from Naïve Animals					
Probe Placement(n)	*10*	*7*	*11*	*7*	*5*
Units (n)	*189*	*101*	*152*	*96*	*77*
Recordings from Trained Animals					
Probe Placement(n)	*14*	*4*	*5*	*13*	*4*
Units (n)	*133*	*40*	*75*	*185*	*50*

Neural sensitivity to pitch, timbre and location were estimated using a 4-way ANOVA with response time, stimulus pitch, timbre and location as factors and spike rate (within a 20 ms bin) as the dependent value (see Bizley et al., 2009). The proportion of variance explained was calculated by using the resulting sum of squares values:

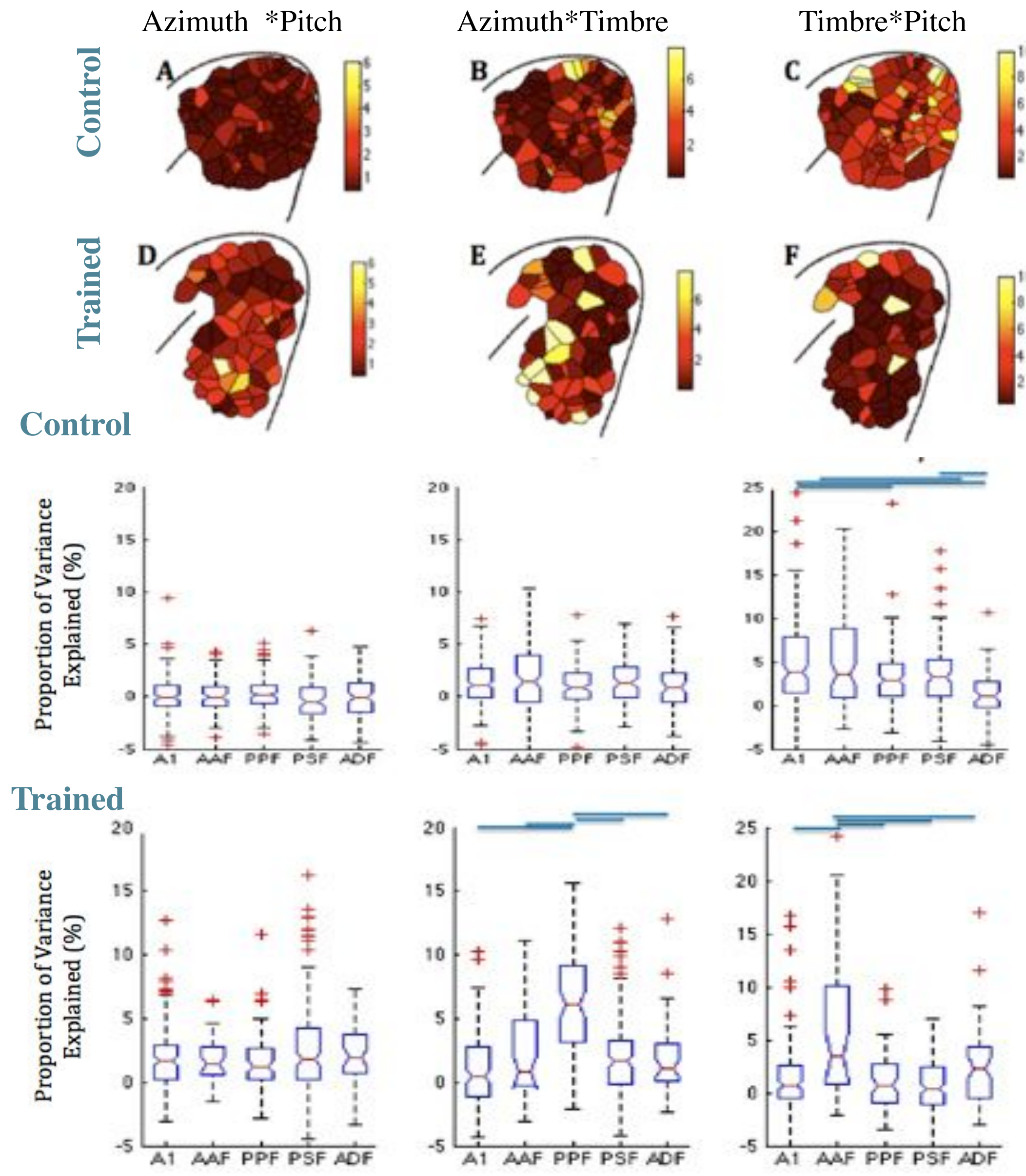
$$\frac{SS_{stim*bin} - SS_{error} \cdot df_{stim*bin}}{SS_{total} - SS_{bin}}$$

Distribution of neural sensitivity to azimuth, pitch and timbre in trained animals



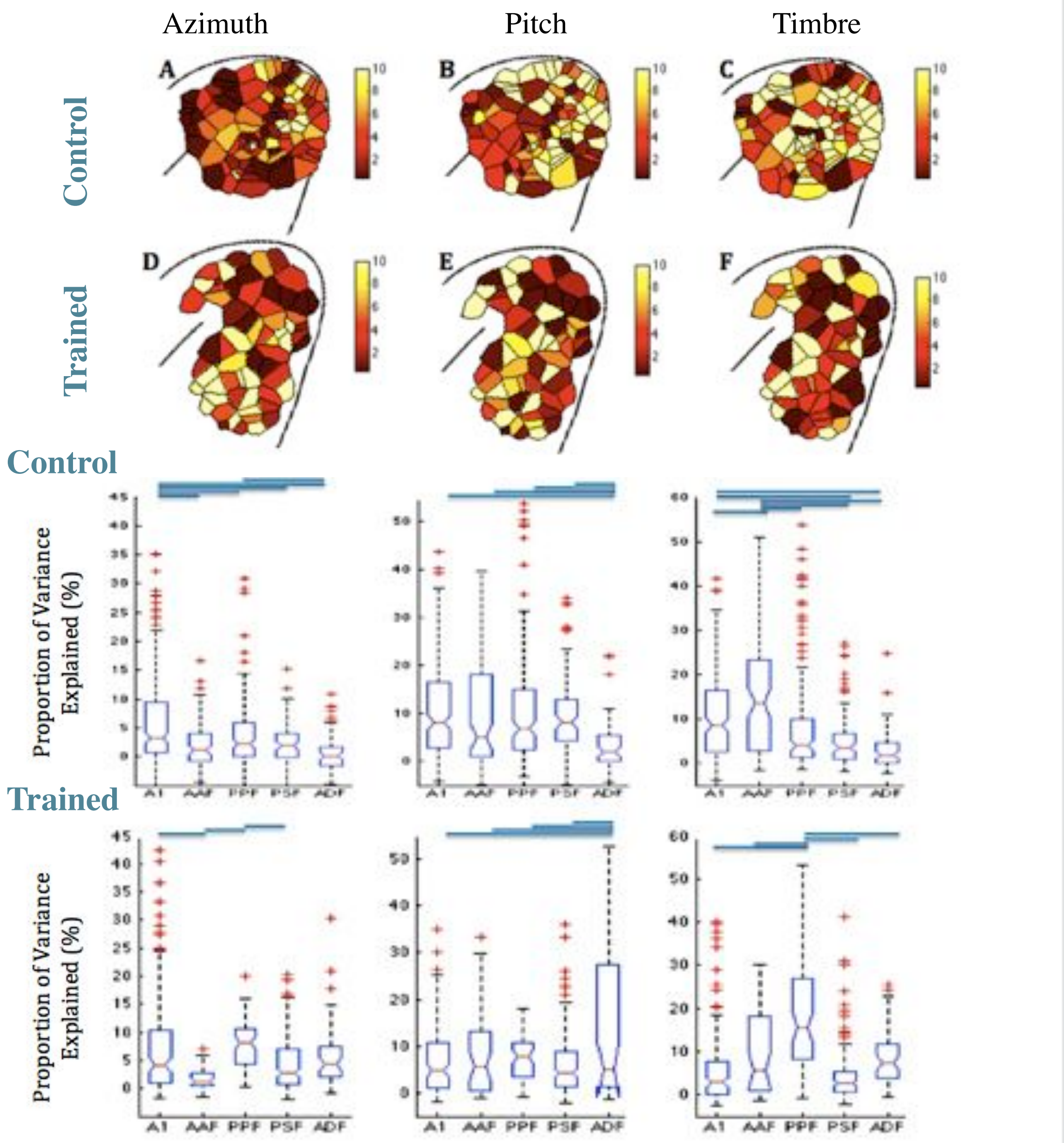
Trained data:
Azimuth and timbre sensitivity both varied significantly across cortical fields (Kruskal–wallis test, *p* <0.0001 and *p* <0.0001 respectively). Field PPF had significantly greater timbre and azimuth sensitivity (all significant pairwise differences are shown by the blue lines in each plot, *Post hoc* pairwise comparisons *p* <0.05). The distribution of sensitivity across cortical fields was significantly different between control and trained animals and is discussed further below.

Distribution of neural sensitivity to stimulus interactions in control and trained animals



There were significant cortical field effects of the proportion of variance explained by azimuth*timbre and timbre*pitch (Kruskal–Wallis test, *p* <0.0001). *Post-hoc* comparisons (*p* <0.05) show field PPF had significantly greater azimuth*timbre combination sensitivity while field AAF showed significantly greater timbre*pitch combination sensitivity.

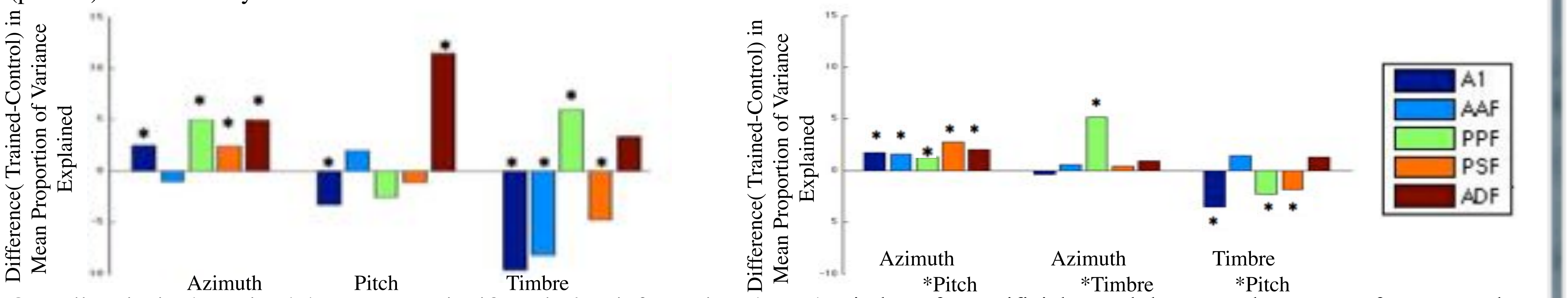
Pitch timbre and location sensitivity was calculated using only the trained vowels (/u/ and /ɛ/).



Parameter sensitivity was broadly similar to that observed with all four vowels: Azimuth sensitivity was increased in the trained animals. Overall timbre sensitivity was *decreased* in trained animals. Primary fields in the control animals were most sensitivite to sound timbre, whereas field PPF was most sensitive to timbre in trained animals.

Summary of differences between control and trained animals

Plots show the difference in the average parameter sensitivity in each cortical field. We ran a 3-way ANOVA with stimulus, cortical fields and training as factors and proportion of variances as the dependent value. Significant pairwise *Post Hoc* comparisons between trained and control data (p<0.05) are marked by *.



Overall, units in the trained dataset were significantly *less* informative about the timbre of an artificial vowel than neural responses from control animals, and significantly more informative about the azimuth.
Tukey–Kramer post hoc comparisons (*p* <0.05) on the responses recorded in each of the cortical fields individually, revealed higher azimuth sensitivity in all fields except for trained animals compared to controls. Timbre sensitivity was lower in the primary fields and in field PSF, but higher in field PPF.
In the control animals, nonlinear interactions were predominantly timbre*pitch, whereas in the trained animals, azimuth*timbre and azimuth*pitch interactions are higher.

SUMMARY

We hypothesized that training animals in a timbre discrimination task might result in: (1) an overall increase in neural sensitivity to sound timbre, (2) changes in the distribution of timbre sensitivity across auditory cortex and/or (3) neural responses becoming more robust to changes in nuisance parameters such as pitch or location.

Recordings made from neurons in the auditory cortex of trained animals show that training causes a general *decrease* in timbre sensitivity. The pattern of timbre sensitivity across cortical fields was significantly different for control and trained animals - timbre sensitivity was significantly lowered in fields A1 and AAF (which showed the highest timbre sensitivity in control animals) but was markedly increased in field PPF.
We saw no evidence for an increase in neural invariance for sound timbre.

Sensitivity to changes in sound azimuth increased across all cortical fields, except field AAF, which remained unchanged. While this might seem counter-intuitive, these animals were required to discriminate sound timbre in the presence of a background noise which was spatially separated from the target vowel sound. Pitch sensitivity remained mostly unchanged after vowel training and pitch sensitive neurons were found to be all across cortical fields.

Analysis exploring the discriminability of different vowel pairs demonstrates that these changes are not specific to only trained vowels.

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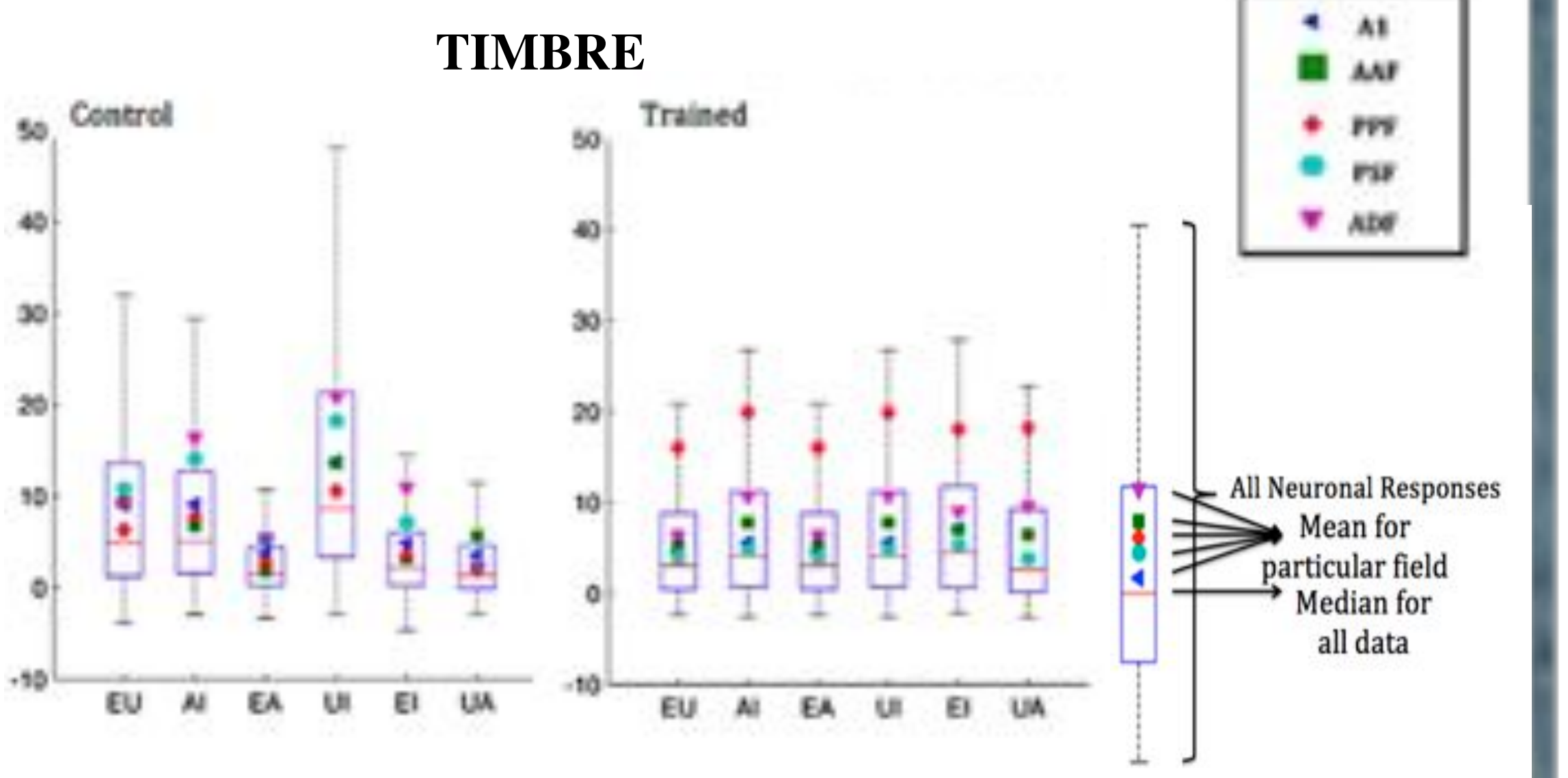
Exploring neural timbre discrimination

We re-computed the variance decomposition analysis for all possible pairs of vowels to give a measure of how well auditory cortical neurons could discriminate different vowel pairs. The distribution of all values (across all fields) is shown by the boxplots with the individual field means overlaid.



Timbre sensitivity for each vowel pair (which we can use to estimate how well neurons can differentiate those two vowels) showed that three vowel pairs were more discriminable in the control data (/u/-/i/, /a/-/i/, and /ɛ/-/u/, Tukey–Kramer post hoc comparisons, p <0.05). In the trained data however, all vowel pairs showed a similar discriminability. Note the elevated timbre sensitivity in PPF.

Pitch and azimuth sensitivity did not vary according to the particular vowel combinations in either the control or trained data.