Exploring the perceptual and neural representation of vowels in ferrets

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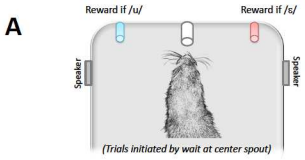
Object identification depends on the exploitation of variation in object properties.

In speech, auditory objects such as vowels can be distinguished on the basis of peaks in the spectral envelope known as formant frequencies.

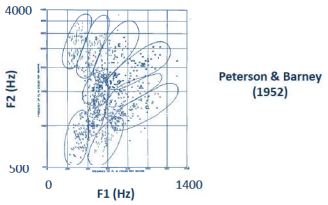
Formants & Perception

To investigate vowel perception, ferrets (n = 2) were trained in a 2-alternative forced choice task in which 250 ms presentations of /u/ or /ɛ/ were associated with a water reward at a left or right spout (**A**).

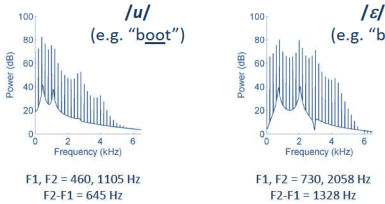


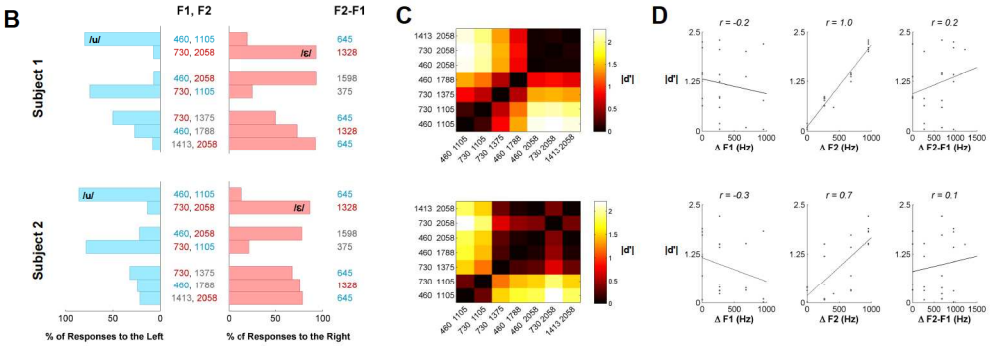
The contributions of F1, F2 and F2-F1 were tested by swapping formants or inter-formant distances to create mismatch vowels. Mismatch vowels put cues into conflict with one another and so the animal's response in such conditions should reveal whether either cue dominates perception. Mismatch vowels were presented amongst learnt vowels as probe trials (20% of trials) and always rewarded.

In particular, the first (F1) and second formants (F2) and the distance between formants (F2-F1) offer potential cues for vowel identification across talkers and voice pitches (Peterson & Barney, 1952; Kewley-Port et al, 1996).



Here, we investigated the contributions of F1, F2 and F2-F1 to vowel perception and neural processing in ferrets using two artificial vowels that differ in both F1 and F2:





Both subjects responded to mismatch vowels more often at the location previously associated with F2 than F1 (**B**).

To quantify the contributions of F1, F2 and F2-F1 to task performance, the discriminability index[1] (d') was calculated between all combinations of vowel pairs.

Discrimination was greatest for vowels that differed most in their F2 values (**C**) and d' was positively correlated with the F2 separation (ΔF2) between vowels (Pearson's *r*) (**D**).

Neither F1 separation (ΔF1) or inter-formant distance separation (Δ[F2-F1]) of vowel pairs was correlated with d'.

Multi-unit Neurophysiology

To investigate the neural processing of vowels, multi-unit recordings of were made in auditory cortex of untrained, ketamine-medotomidine anesthetized ferrets.

Units were selected that responded significantly to vowels (250 ms duration)(t-test, $p < 0.05$) and whose firing rated during stimulation was significantly modulated by vowel identity (ANOVA, $p < 0.05$).

Neural discrimination was quantified by comparing the spike distance[2] between responses to pairs of vowels binned in PSTHs (0 to 400 ms; bin width: 20 ms, averaged over ≥ 20 repeats)(**E** & **H**).

3 Anesthetized ferrets

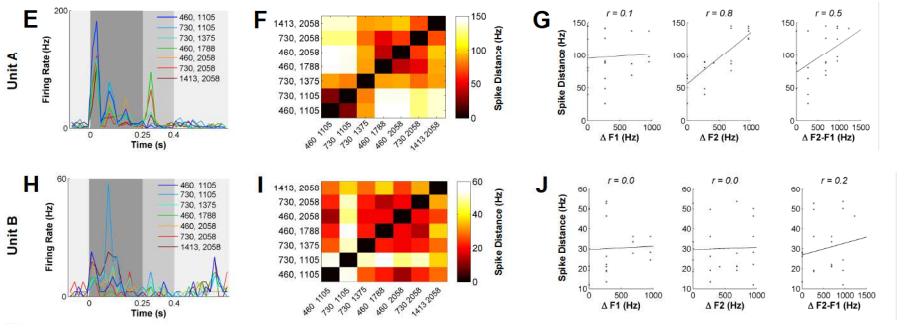
727 Units responsive to vowels (t-test)

84 (11.6%) Responsive units also vowel sensitive

Individual units (e.g. Unit A, **E-G**) were found in which spike distance was well correlated with ΔF2 separation.

However other units (e.g. Unit B, **H-J**) showed weak correlations with formant separation. The example unit in this case responded strongly to only one vowel, making that stimulus notably discriminable from the rest.

The variation in response of such units is poorly described by a linear correlation with cue separation. Indeed, most vowel sensitive units (55/84; 65%) showed weak correlations between spike distance and F1, F2 or F2-F1 separation (**K**).



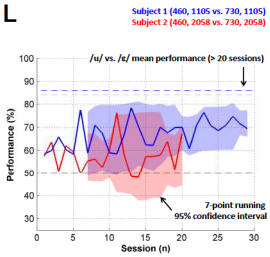
F1 Discrimination

Finally, to determine if ferrets can discriminate between F1 values, subjects are learning to discriminate vowels differing in F1 but not F2 position.

Task performance fell sharply when variation in F2 was removed (**L**), supporting its suggested importance in discrimination.

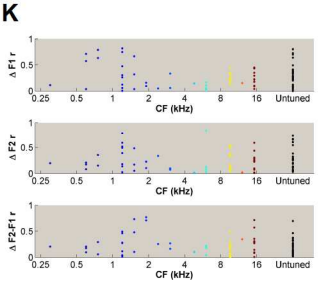
Performance of subject 1 subsequently improved across training sessions, indicating that F1 based discrimination may be possible in ferrets.

However, performance for both subjects remains below their mean performance when discriminating /u/ and /ɛ/. It remains to be seen whether variation in F1 alone can consistently support such performance levels.



Summary

- Ferret's perception of vowels is strongly influenced by F2 position
- With training, ferrets may be able to discriminate vowels using F1 position
- In naïve animals, neural discrimination of vowels by some multi-unit clusters is linearly related to F1, F2 or F2-F1 separation between vowels
- However, the vowel sensitive population contains many units whose responses do not correlate linearly with cue separation
- Future work will focus further on the cortical location and behavioral contributions of different response types



Appendix

[1]d' was calculated as the normalized probability of responding left given vowel *X* (i.e. hit rate) minus the normalized probability of responding left given vowel *Y* (i.e. false alarm rate):

$$d' = Z_{P(Left\ Response\ |\ Vowel\ X)} - Z_{P(Left\ Response\ |\ Vowel\ Y)}$$

[2]Spike distance between responses to vowels *X* and *Y* was calculated as the root of the sum of squared differences across PSTH bins:

$$Dist = \sqrt{\sum_{bin=1}^{20} (X_{bin} - Y_{bin})^2}$$

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References

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Kewley-Port D, Li X, Zheng Y, Neel AT (1996) Fundamental frequency effects on thresholds for vowel formant discrimination. *J Acoust Soc Am.* 100: 2462-70.