Gradient boosted decision trees reveal nuances of auditory discrimination behavior

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ABSTRACT

Animal psychophysics can generate rich behavioral datasets, often comprised of many 1000s of trials for an individual subject. Gradient-boosted models are a promising machine learning approach for analyzing such data, partly due to the tools that allow users to gain insight into how the model makes predictions. We trained ferrets to report a target word's presence, timing, and lateralization within a stream of consecutively presented non-target words. To assess the animals' ability to generalize across pitch, we manipulated the fundamental frequency (F0) of the speech stimuli across trials, and to assess the contribution of pitch to streaming, we roved the F0 from word token-to-token. We then implemented gradient-boosted regression and decision trees on the trial outcome and reaction time data to understand the behavioral factors behind the ferrets' decision-making. We visualized model contributions by implementing SHAPs feature importance and partial dependency plots. While ferrets could accurately perform the task across all pitch-shifted conditions, our models reveal subtle effects of shifting F0 on performance, with within-trial pitch shifting elevating false alarms and extending reaction times. Our models identified a subset of non-target words that animals commonly false alarmed to. Follow-up analysis demonstrated that the spectrotemporal similarity of target and non-target words rather than similarity in duration or amplitude waveform was the strongest predictor of the likelihood of false alarming. Finally, we compared the results with those obtained with traditional mixed effects models, revealing equivalent or better performance for the gradient-boosted models over these approaches.

Keywords: Shapley Additive Explanations; auditory scene analysis; pitch; ferret, behavioral data analysis in neuroscience;

AUTHOR SUMMARY

The sorts of listening challenges faced by real-world listeners are rarely captured by most laboratory-based auditory paradigms, particularly those testing animal models. However, many labs are attempting to utilize more realistic experiments, and more complicated behavioral paradigms require more sophisticated approaches to analyzing the resulting data. Here, we used a new behavioral paradigm to test the ability of ferret listeners to identify target speech sounds and assess their ability to generalize across changes in pitch. To make sense of the resulting dataset, we used machine learning algorithms to understand how trained ferrets perform this task. Gradient-boosted regression and decision trees are well-established machine learning methods that do not require users to predetermine interaction effects and are accompanied by visualization methods that allow insights to be gained into how multiple factors ultimately shape behavior. We compare the use of gradient-boosted models to more standard regression approaches and, by applying these methods, we demonstrate key features of ferrets' performance on this task. Our results suggest that this machine learning approach is ideal for analyzing behavioral data in animal models.

INTRODUCTION

Psychophysics paradigms in non-human animals are often designed to yield tractable datasets for relating brain and behavior. Most common laboratory-based paradigms rely on artificial stimuli presented within the confines of simple tasks – such as two-alternative forced choice paradigms in which animals must discriminate a single sound token, or go/no-go tasks in which animals detect a change in a repeating

sequence of sounds. Such paradigms offer tight experimental control, and can be successfully analyzed using standard statistical approaches such as mixed effect models and more sophisticated approaches that allow, for example, the identification of how and when non-sensory factors shape performance (Ashwood et al. 2022 Roy et al. 2021). Yet animals can be trained to perform more complex tasks, generating rich behavioral datasets that potentially can require new approaches for their interpretation. One promising approach for modeling both categorical and continuous data is gradient-boosted decision trees (Grinsztajn, Oyallon, and Varoquaux 2022). Not only are such models powerful, but they are also interpretable through the use of tools that allow visualisation of the contributions of variables and combinations of variables to prediction outcomes.

The general approach of the gradient-boosted decision tree model is a form of ensemble learning in which we use an initial weak decision tree to predict an outcome of a trial and then iteratively build upon the error of the first tree (after calculating the loss) by further splitting the data in a way that improves the model prediction. Once our loss plateaus or we reach the maximum number of training epochs, we stop training the model and calculate our test accuracy, or how well the model could predict our target variable on a held-out test set of data. We chose this method as our data is inherently dense (from long periods of behavioral training and testing) and tabular, which makes gradient-boosted regression and decision trees an excellent candidate for the prediction of binary data (such as was the trial a hit or a miss) and continuous data (such as reaction times) compared to a nonlinear neural-network-based classifier (Grinsztajn, Oyallon, and Varoquaux 2022). Here, we highlight the utility of both the model itself and the visualization tools available to understand what features the model finds informative and compare this approach to more traditional mixed effects models.

We applied gradient-boosted models to animal psychoacoustics data designed to probe the role of pitch in perceptual invariance and auditory scene analysis. Pitch is a fundamental feature of a person's voice, and a hallmark of human voice processing is recognizing a word regardless of voice pitch. Differences in pitch allow us to separate competing voices, while sounds are grouped together over time into 'streams' if they share a common pitch (Darwin 2005). However, it is not clear whether the ability to use pitch continuity to link sounds into streams is uniquely human or whether it can be considered a more general feature of the mammalian auditory system. To address such issues, we trained ferrets to detect the word "instruments" within a stream of other randomly drawn non-target words (Sollini and Bizley, in prep.). Within a trial, all word tokens were drawn from a single female or male voice, and the whole stream could be shifted upwards or downwards in fundamental frequency (F0, which determines pitch). The F0 of each word within a stream could also be randomly shifted to assess whether pitch contributes to streaming. We collected 20487 trials of data from 5 animals. We analyzed these using gradient-boosted models to address two research questions: firstly, can trained ferrets generalize their learned discrimination across variations in pitch, and secondly, whether, like humans, animals use the pitch as a streaming cue to link sounds together over time.

Through the application of gradient-boosted models, we were able to demonstrate that while performance was robust to changes in pitch, shifting the F0 of words within a trial significantly slowed reaction times and elevated the likelihood of a false alarm, providing evidence that ferrets, like humans, use pitch to form perceptual streams. Moreover, this approach allowed us to identify words that ferrets consistently confused with the target word, suggesting that errors were not simply random lapses in attention. Analysis of acoustic features of non-target words identified spectro-temporal similarity but not duration or waveform similarity as a predictor of the likelihood of a false alarm.

74 # RESULTS

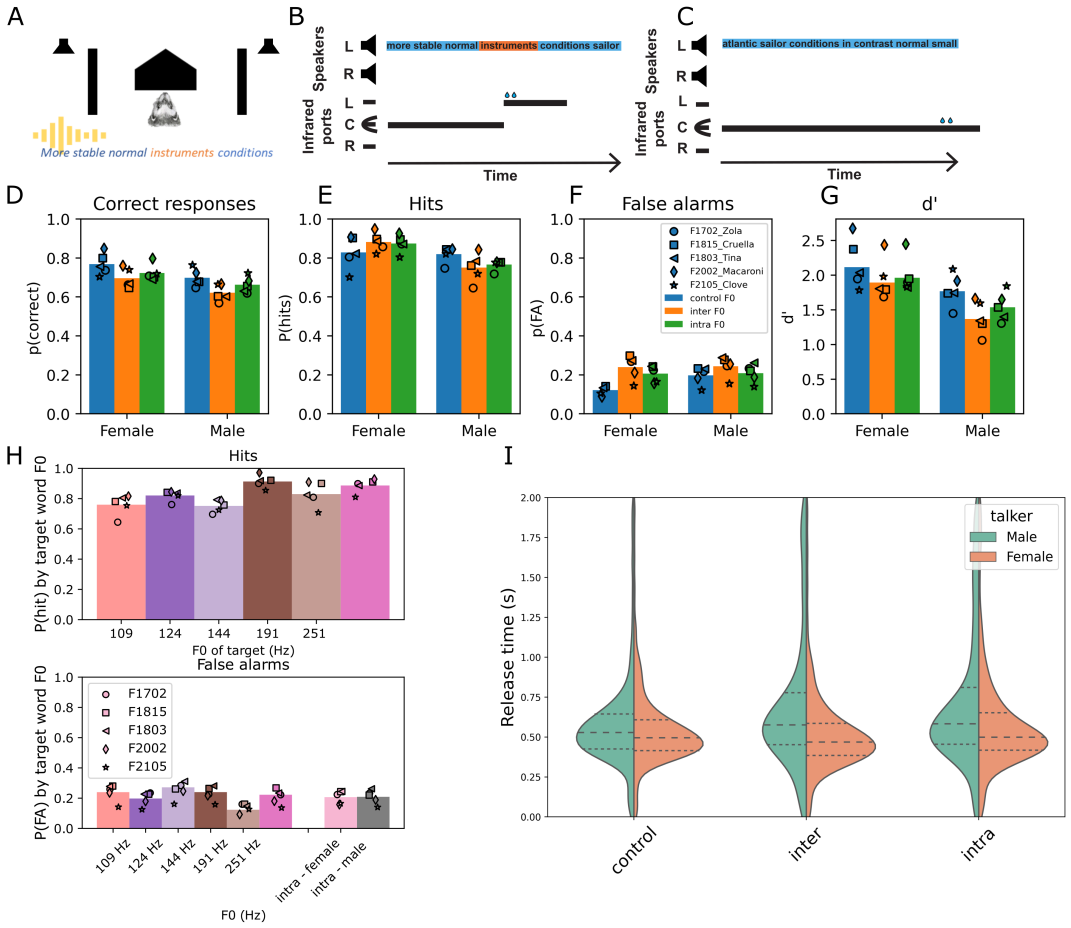
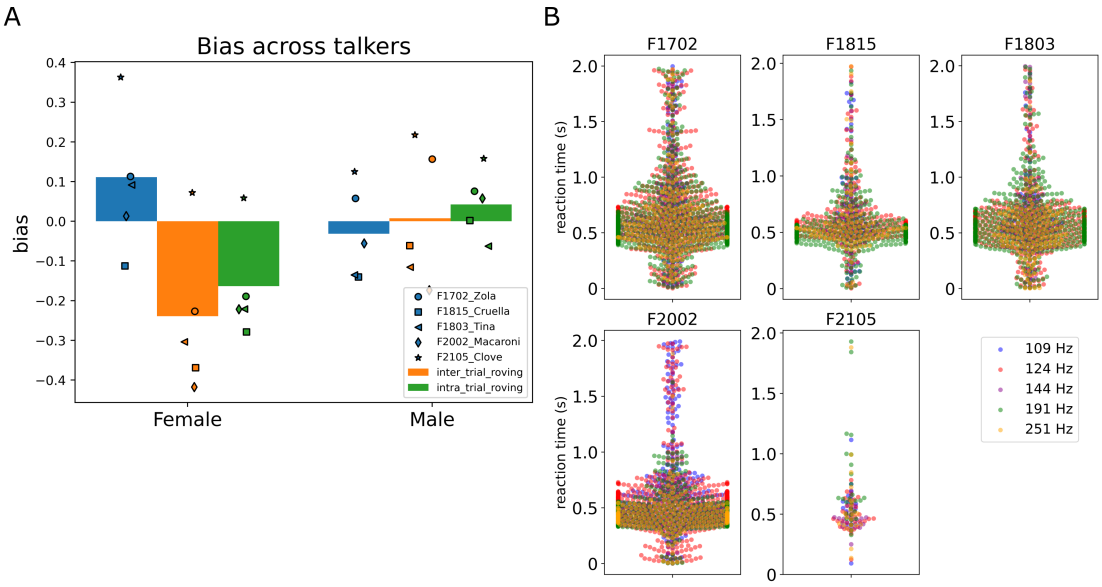


Figure 1. Task design and basic behavioral data. A, Schematic of the experimental booth. To trigger a trial, ferrets had to nose-poke a center port that contained an IR sensor and water port. This triggered the presentation of a stream of words from either the left or right speaker. B, Ferrets were trained to remain at the center until the presentation of the target word ('instruments') and received a water reward at a lateral port if they correctly released within 2s of target presentation and responded to the lateral port whose side matched that of the speech stream. C, Catch trials did not contain the target word, and the ferret was rewarded if she remained at the central port for the duration of the trial. D, Behavioral metrics across animals distributed by talker type. Bars indicate the across-animal average; symbols show the individual animals. Trials are separated according to the identity of the talker and the pitch roving condition (control = no pitch shifting, inter = F0 shifting of the whole trial, intra = F0 shifting of the tokens within a trial). (D) % correct over all trials, E, hits; F, false alarms; G, sensitivity (d'). H, impact of F0 on hit rate (top) and false alarm rate (bottom). False alarm rates are plotted separately for intra-trial pitch roving because the F0 changed from token to token, making it impossible to assign a false alarm to a distractor of a given F0. I, Violin plot of reaction times during correct responses on trials in which the target was correctly identified for all animals, separated by talker type.



Supplementary Figure 1. A, bias across trial conditions and talker types; B, reaction times of each animal for correct responses color-coded by F0 of the target word.

Ferrets can discriminate speech sounds, and their performance is robust to pitch shifting

Ferrets were trained to detect the target word "instruments" within a stream of randomly drawn non-target word tokens. Subjects initiated a trial by nose-poking in a central port that contained an infrared sensor and water delivery spout and were required to remain at the center port until the presentation of the target word. On each trial, all tokens came from the same talker and position in space, and ferrets were rewarded for responding at the lateral port adjacent to the speaker within 2s of the target word (Fig. 1A, B). On catch trials, in which only non-target words were presented, ferrets were rewarded for remaining at the central port (Fig.1C). Ferrets were trained with a single male and single female voice. Once performance was stable, trials were introduced in which the F0 of the whole trial was shifted ('inter-trial roving') or individual word tokens within the trial were shifted ('intra-trial roving'). We will first provide an overview of the data before using Gradient Boosted decision trees to understand and quantify the factors that shape the animals' performance in this task.

Ferrets' were able to learn and perform the task across control and F0-shifted conditions; performance ranged from 57% -85% correct for all animals and conditions, where 33% would be considered chance performance (Fig.1D). Hit rates were generally high (Fig.1E) and false alarms low (Fig. 1F) for both talkers and both types of pitch-shifted trials. Overall, performance was higher for the female voice, with a small decrease in d' evident for pitch-roved trials compared to natural F0 ones (Fig.1G). Nonetheless, all d' values were well above 1, indicating the animals were well able to perform the task.

To understand whether ferrets form a pitch-tolerant representation of the target word, we considered the impact of F0 changes on performance (Fig 1D-F). Two-way repeated measures ANOVAs with factors talker (male/female) and rove type (control / inter / intra) showed that for hit rates, there was a significant effect of talker and significant talker x rove interaction but no significant pairwise comparisons across pitch roved conditions (supplementary tables 1 and 2). For false alarms, there was again a significant effect of talker, rove, and talker x rove interaction, with posthoc comparison showing that for the female talker control, F0s elicited significantly lower false alarm levels than either rove type but that the rove types were not significantly different from each other (supplementary tables 3 and 4). For sensitivity (d') measures, there were again significant effects of talker and rove type, but post hoc comparisons showed no rove conditions to be significantly different from each other (supplementary tables 5 and 6). Therefore, overall, while subjects were better on female talker trials than on male talker trials, the performance on inter and intra-trial roved trials was largely equivalent (Fig.1D-F). When the performance was broken down according to the actual F0 value, we observed there was a modest influence of F0 on hit rates, such that the highest hit rates were observed for the female talker's up-shifted F0 trials (Fig.1H). False alarms, in contrast, were lower for the control F0 values for both the male and female talkers.

Reaction times varied by ferret and according to the talker (Figure S1B). The trend for lower hit rates at lower F0 and for the female voice to elicit faster reaction times may be a consequence of training, as 3/5

subjects were initially trained on only the female talker. However, while the hearing range of ferrets fully encompasses that of humans, their frequency resolution is poorer and most notably so at the lowest audible frequencies (Sumner et al. 2018), and this too may limit performance at the lowest F0s.

These basic behavioral metrics are designed only to show that ferrets can successfully discriminate a target word from non-target words despite variation in F0. We now turn to gradient-boosted models (GBMs) to further consider how acoustic and non-acoustic factors influence individual trial outcomes.

Introduction to gradient boosted models

Gradient boosting is a supervised machine learning algorithm used for classification and regression problems and is particularly advantageous due to the tools available to visualize how a model exploits information to perform the task. The basic principle is that decision trees are built by splitting observations based on feature values, with the algorithm seeking and selecting a split that results in the highest gain in information by comparing predicted outcomes to observed ones. We chose this machine learning approach as our data is abundant in sample size and tabular. While its application to animal behavioral work is to our knowledge novel, this scenario of structured, dense data is ideal for gradient-boosted decision trees, as this type of method has often been used in recommender systems (Luo et al. 2022) as well as economic predictive modeling for human behavior in customer loyalty (Machado, Karray, and Sousa 2019). A machine learning approach is ideal because it can uncover non-linear dependencies in the data without users being required to predetermine interaction effects in their model. Moreover, we can consider multiple stimulus features, such as the talker and pitch of the word, as well as the trial history parameters (was the previous trial correct, was the previous trial a catch trial) and non-stimulus features (such as the timing of the trial within the session, the time of the target word within the trial, and the side that the animal was required to respond) that may influence performance but do not necessarily inform our experimental hypothesis.

We used lightGBM (Ke et al. 2017) to implement a gradient-boosted machine (GBM) approach. We considered two types of models – decision-tree models that performed categorical discriminations, for considering whether responses to targets were misses or hits and whether responses to catch trials were false alarms or correct rejections, and decision-tree regression models to predict continuous reaction time data. In each case, we trained models using 5-fold cross-validation and used held-out data to report both the accuracy and balanced accuracy (which is particularly helpful for data in which observations are unequal in number between categories and where accuracy may, therefore, be overinflated). To assess which variables were utilized by the model, we used two metrics; feature importance and permutation importance. The GBM decision and regression tree method consists of many decision trees, and features will potentially be used many times to split the data; to understand the contribution of a feature, the gain provided must be aggregated across trees. Therefore, the feature importance metric assesses how a given feature improves the model's accuracy by summing the gain provided by that feature across all of the times that it's used in the model. A higher gain implies that the feature is more important for generating predictions. In lightGBM, the loss functions (from which gain is computed) are the mean squared error (MSE) for regression tasks and the log loss for classification tasks. Its units are the same as the target variable, seconds, and its upper and lower bounds are minus to positive infinity. Permutation importance provides a complementary measure of the importance that any given feature provides to the model. The permutation feature importance is the decrease in a model score when a single feature is randomly permuted. The higher the permutation importance, the larger the contribution a variable makes to the model; a score of 0.1 for a model with 70% accuracy reflects a drop to 60% accuracy for a classification problem. One caveat with the permutation importance is that it assumes that all variables are independent, so it can underestimate the contribution of a given variable in some circumstances (Molnar 2023).

To visualise the way in which variables impacted model predictions, and how variables interact with one another we used SHapely Additive exPlanations (SHAPs) which are a common way of understanding machine learning models based on Shapely values. Shapely values were derived from cooperative game theory and represent the average contribution of each feature to all possible combinations of features (Lundberg and Lee 2017). SHAPs extend this to machine learning models; for every feature and every observation in the training set, we obtain a SHAP value, and therefore, there are as many SHAP values as there are observations. For a classification task the SHAP values are expressed as the log(odds) so can be directly interpreted as the impact of a given feature on the probability e.g. of making a miss. For our regression models, the SHAP scores are the impact on reaction times, expressed in seconds. Here we use SHAP summary plots to provide intuitive and interpretable visualizations of the effects of all variables in a model and partial dependency plots to visualize combinations of features of interest. The

partial dependency plots are particularly helpful for understanding how, for example, behavior varies across individual subjects and for examining the potentially non-linear interactions between features that the model has learned to exploit.

Talker identity drives miss responses

We used lightGBM (Ke et al. 2017) to model the likelihood of a miss vs hit response using only trials in which the target sound was presented(i.e., excluding false alarms and catch trials). The variables provided to the model were: the talker (male/female), the side (left/right) of the audio presentation, the trial number (in the session), the subject identity (ID), target presentation time (within the trial), the target F0, whether the previous trial was a catch trial, whether the previous response was correct, and whether the F0 of the non-target word preceding the target matched that of the target (non-target F0=target F0, this selects intra-trial roved trials eliminating those trials where by chance the word before the target matched the target F0).

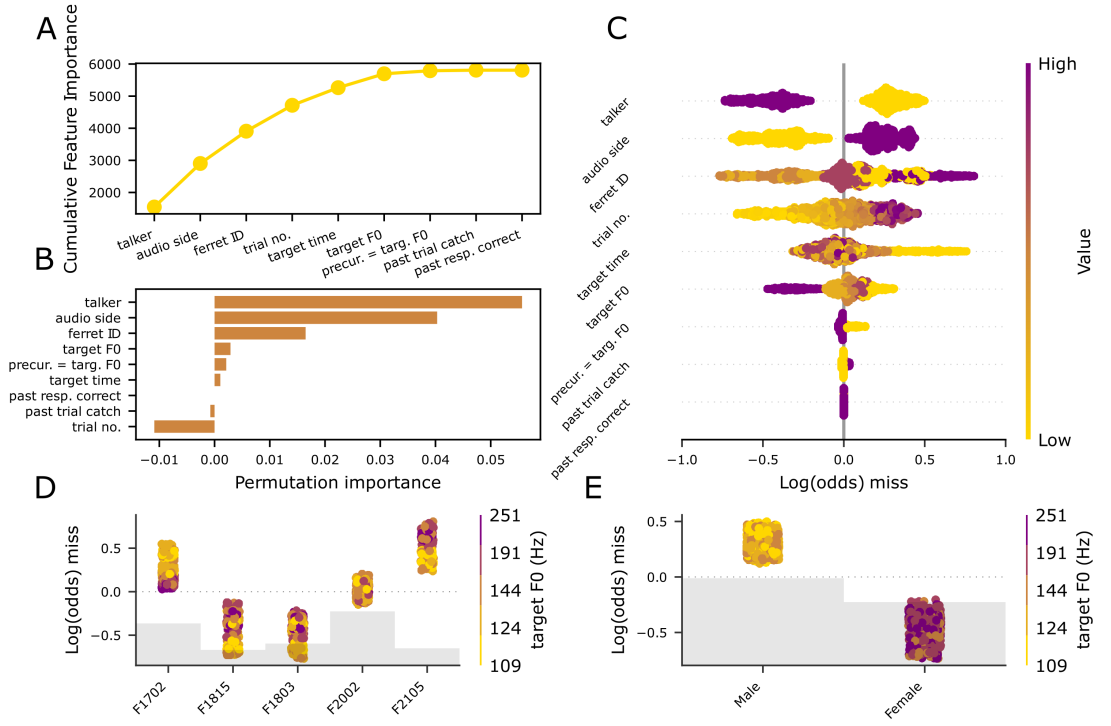
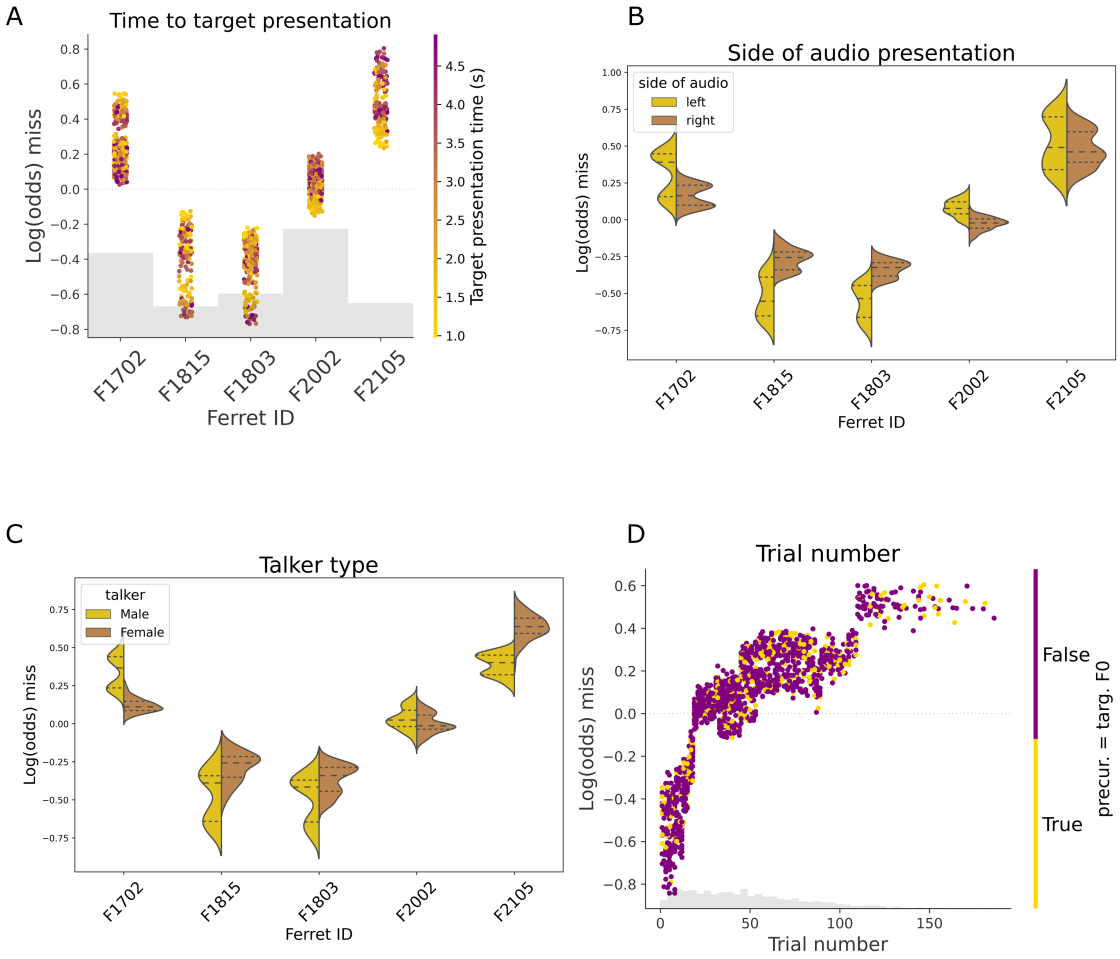


Figure 2. Factors that drive the miss/hit model; A, the elbow plot of cumulative feature importance over trial features; B, permutation importance bar plot of the features in the correct hit/miss model; C SHAP feature importances of the miss/hit model; D, SHAP partial dependency plot depicting the SHAP impact over each ferret ID color-coded by target F0. E, SHAP partial dependency plot showing the SHAP impact over each talker type color-coded by target F0. Gray bars indicate the distribution of the number of observations across variables



Supplementary Figure 2. Partial dependency plots for the correct hit response/miss response model. A; SHAP values over the ferret ID color-coded by target presentation time; B, SHAP values over ferret ID color-coded by the side of audio presentation; C, same as B but color-coded by talker type; D, SHAP values over trial number color-coded by whether the trial had the precursor word F0 equal to the target F0.

The performance of the miss/hit model was reasonable despite the sparsity of miss responses in the behavioral data, with an average balanced accuracy on our a training set of 62.17% and an average test balanced accuracy of 62.09%. We eliminated factors that either did not significantly increase the cumulative feature importance plot (Fig.2A) or if a permutation test that randomized the variable in question did not impact model fit (Fig.2B). Thus, trial history factors (the past trial was correct or a catch trial) and the prior non-target F0=target F0 parameter were eliminated. For the remaining features, the feature importance metrics, permutation tests, and SHAP feature values were all in concordance with each other, with only minor differences in the ranking of features. The top three features were the talker (the male talker increased the probability of a miss, Fig.2C), the side of the audio presentation (which was idiosyncratic across animals, likely reflecting their own individual biases, see Fig.S2B). The trial number (with trials earlier in the session reducing the likelihood of a miss, and later trials being associated with higher miss rates). While significant, the target presentation time within the trial (Fig.S2A) did not show a strong relationship across all animals, as shown by the lack of consistent stratification in the SHAPs plot examining the target presentation time for each ferret. The F0 of the target sound also had a small but significant effect, which varied by ferret (Fig. 2E). Only 3/5 animals had stratified miss probabilities which suggested higher F0s were more likely to elicit false alarms. In contrast, one animal (F1702) showed the opposite pattern the final animal (F2002) showed no consistent pattern. Whether the non-target word that preceded the target word was matched in F0 did not significantly influence the likelihood of missing. We conclude that the talker's identity was the single biggest stimulus factor that altered the likelihood of missing, with the F0 of the target word having a modest effect in some animals. Changing the F0 from word token to word token did not change the likelihood of correctly detecting the target.

False alarms are influenced by talker identity and F0

Next, we modeled whether a subject would false alarm based on all trial types, using the following features: the talker, the pitch (F0) of the trial or for intra-trial roved trials the F0 of the last non-target word in the trial, the side of audio presentation, the trial duration, the time elapsed since the start of the trial, the trial number within the experimental session, the ferret ID, whether the past response was correct, whether the past trial was a catch trial, and whether there was intra-trial F0 roving. The false alarm model had above-chance accuracy (mean test accuracy of 61.54% over 5-fold cross-validation; balanced accuracy 61.46%) and returned the following as the most significant contributors: the time elapsed since the trial started, the trial number, the ferret ID, the non-target F0, the audio side, and whether the trial was intra-trial F0 roved (Fig. 3A, B, D).

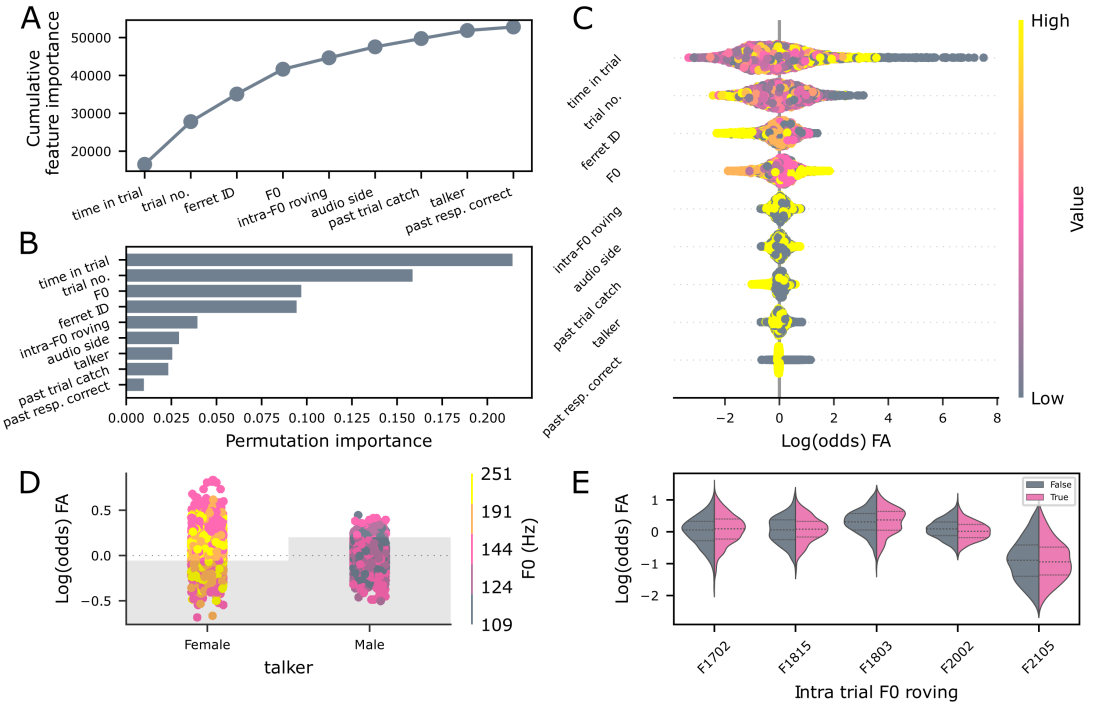
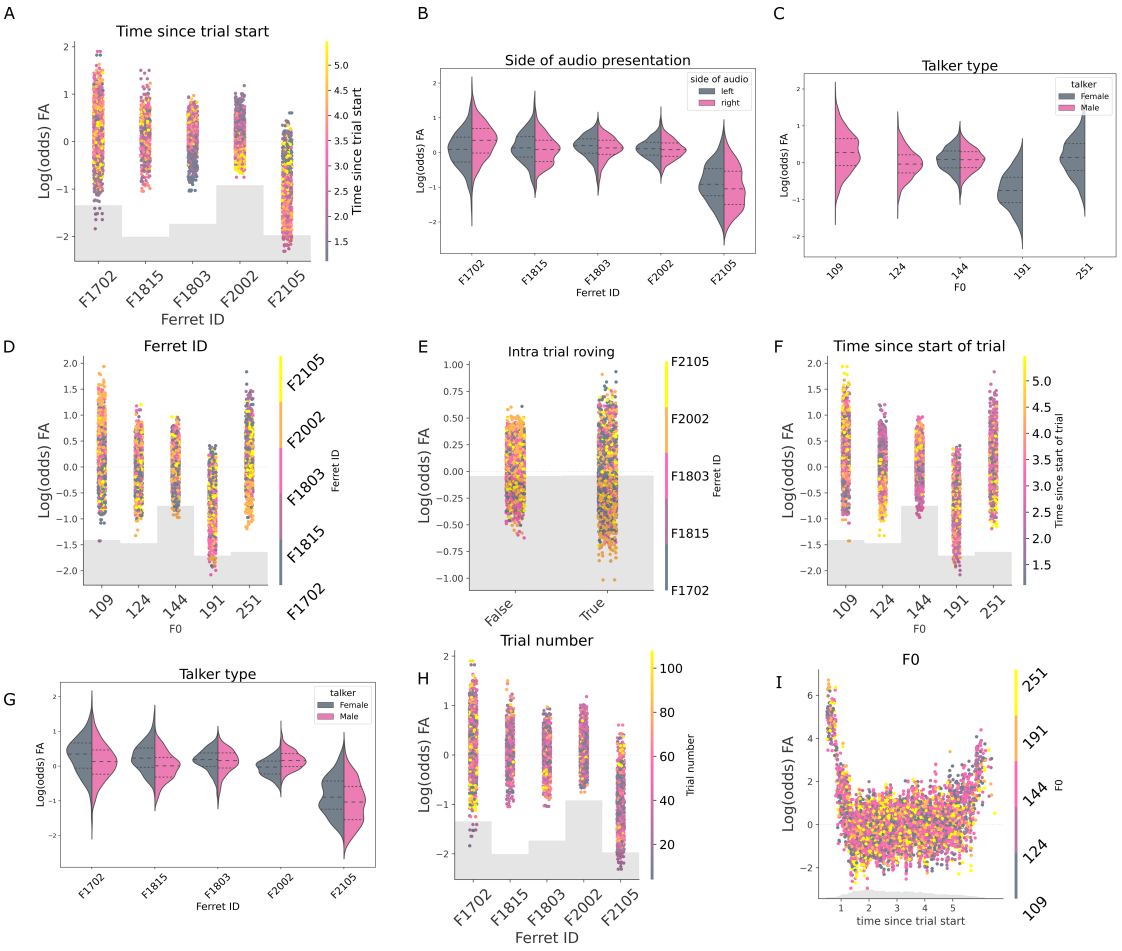


Figure 3. Precursor F0 determines the probability of a false alarm A, elbow plot depicting the cumulative feature importance of each factor used in the false alarm decision tree model; B, Permutation importance plot. C, SHAP feature importance values; D, partial dependency plot depicting the SHAP value over whether the trial was intra-trial roved color-coded by F0. E, partial dependency plot showing the SHAP value (representing the impact on the probability the trial would be predicted as a false alarm) over ferret ID color-coded by whether the trial was intra-trial roved; Gray bars illustrate the relative proportion of trials across categories.



Supplementary Figure 3. Partial dependency plots for the correct reject/false alarm model. A, partial dependency plot depicting the mean SHAP impact over the ferret ID color-coded by time within the trial; B, violin plot of the SHAP value over the ferret ID color-coded by the side of audio presentation; C, violin plot of the SHAP values over the F0 of the trial color-coded by talker type; D; SHAP partial dependency plots of false alarm likelihood by F0, color-coded by ferret ID; E, SHAP values over the F0 of the stream color-coded by trial number; F, same as E but color-coded by time since the start of the trial; Note that while the 191Hz F0 is associated with a higher false alarm rate, this should be interpreted in the context of the much lower FA rate associated with the female talker. G, violin plot of the SHAP value over ferret ID color-coded by talker type; H, SHAP value over ferret ID color-coded by trial number; I, SHAP value over trial duration color-coded by F0.

In contrast to the miss model, the strongest determinants of whether an animal was likely to false alarm were timing parameters (time in the trial and trial number within the session) and the individual ferrets. Partial dependency plots (Fig S3) showed that two ferrets were more likely to false alarm early in the trial, one late in the trial, and two animals showed unstratified responses, implying they were not systematically influenced by this parameter (FigS3A). Trial number, although significant, did also not show clear stratification when considered by animal (FigS3H).

The speech sound F0 and talker both impacted the likelihood of FA, with the partial dependency plot showing that low F0 words spoken by the female talker were most likely to elicit a FA. In contrast, the control F0 for the female talker was least likely to elicit a FA (Fig.3D, Fig S3C). The audio side and intra-trial roving also contributed to the model: the audio side was again idiosyncratic across animals (Fig.S3B). Whether or not word tokens within a trial varied in F0 (i.e., intra-trial roving) contributed a significant effect in the predicted direction (i.e., intra, intra-trial roving was more likely to elicit an FA), but only 3 / 5 ferrets showed this, and overall, it was a small effect(Fig.3E).

In summary, the FA model suggests that non-acoustic factors are the key drivers in whether animals false alarm with only a small contribution of acoustic factors. Pitch-shifting generally and particularly

229 within trials, both had small but measurable effects on false alarm rate.

230 **Gradient boosted regression of reaction time data reveals the impact of pitch on target**
231 **detection and streaming**

232 Given our performance measures were generally quite high with, in particular, a very limited number of
233 miss trials with which to explore whether F0 changes impacted performance, we focused next on reaction
234 time (RT) measures. To explore whether RTs provided a more sensitive measure of how acoustic and
235 task parameters influenced performance, we used gradient-boosted regression (Ke et al. 2017). In our
236 RT model, derived from responses from correct non-catch trials, we considered the following factors:
237 ferret ID, talker (male or female), time to target presentation (within a trial), the trial number (within a
238 session), the side of audio presentation, the target F0, whether the F0 changed from the preceding non-target
239 word to the target word (preceding F0 = target word F0), whether the past trial was a catch trial, and
240 whether the past trial was correct. Our test-set mean squared error (mse) using 5-fold cross-validation was
241 0.102s compared to a noise floor (calculated by randomizing the relationship between trials and reaction
242 times) test mse of 0.133s (train mean-squared error = 0.092s, compared to a noise floor train mse of 0.105s).
243

244 From our permutation test, the ferret ID, the talker, the side of the audio presentation, the time to target
245 presentation, the target F0, and trial number were significant factors (Fig. 4B), whereas SHAP values
246 additionally considered whether the F0 of the previous word equaled the target word as a significant factor
247 in this reaction time model (Fig. 4A). This difference in traditional permutation importance versus SHAP
248 feature importance is not necessarily surprising, as target F0 is highly correlated with the precursor = target
249 F0 feature (i.e., if the target F0 is not a control F0, the likelihood of precursor not equalling target F0
250 increases), something which the permutation importance method struggles to account for (Molnar 2023).
251 Interestingly, a traditional mixed effects model (see below and Fig. 7C) also returned whether the percursor
252 was the same F0 as the target word as a significant variable, with trials in which both shared the same F0
253 having faster reaction times than those that did not. Similar to the miss/hit and false alarm/correct reject
254 performance models, the model heavily weighted both ferret ID and talker ID; reaction times were longer
255 for the male talker (in 4/5 ferrets, see Supplemental S4D, female faster in F2105) and varied systematically
256 across ferrets (Fig.4C). Overall, later targets had faster responses, Figure 4B, 3/5 ferrets showed this effect,
257 1/5 had faster reaction times for earlier targets, and 1 showed no difference, Fig.S4A).

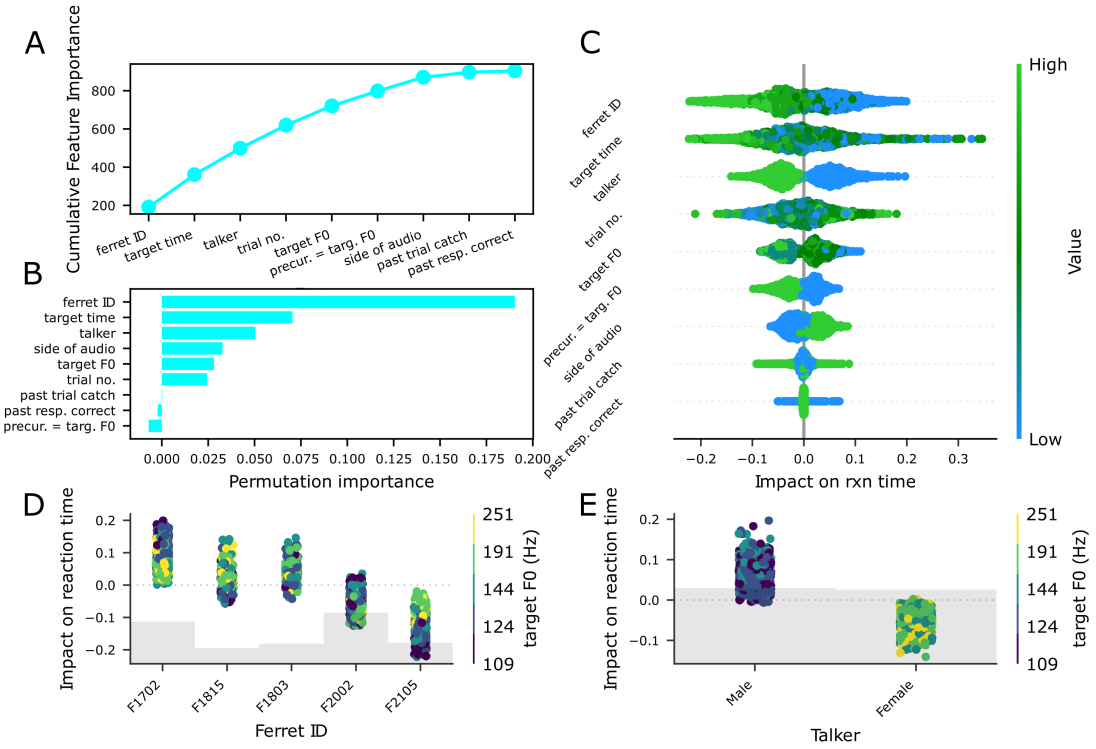
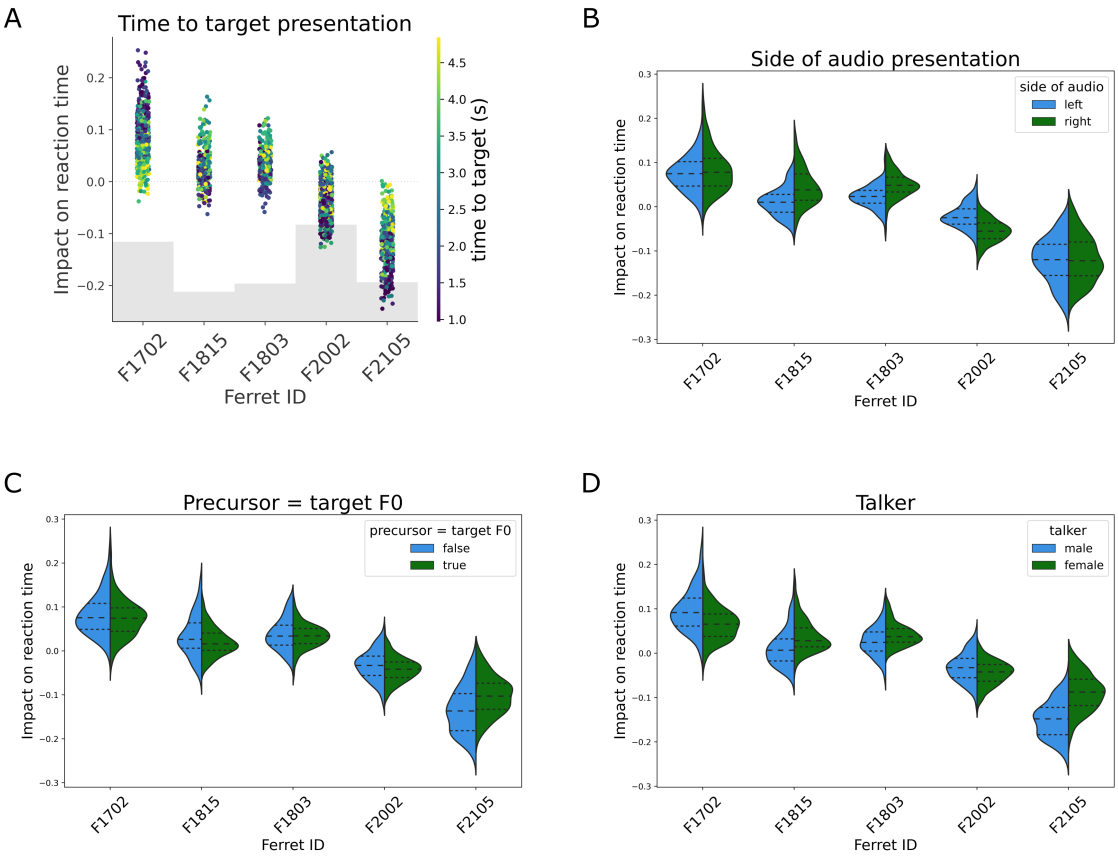


Figure 4. Reaction time models establish a contribution of F0 to target detection. A, feature importances of the hit model; B, permutation feature importance of each factor in the model; C, SHAP summary plot of ranked feature SHAP values of each factor in the reaction time model; D, partial dependency plot of SHAP impact versus ferret ID color-coded by target F0; E, partial dependency plot of SHAP impact over talker identity color-coded by the target F0.



Supplementary Figure 4. Correct hit response reaction time model partial dependency plots. A, SHAP values over the ferret ID color-coded by the time to target presentation; B, violin plot of the SHAP value over ferret ID color-coded by the side of audio presentation; C, same as B but color-coded by whether the precursor word's F0 was the same as the target word's F0; D, same as C but color-coded by the talker type for the trial.

Other factors that significantly predicted reaction times were the side of the audio (left responses were slightly faster than right responses in 2/5 ferrets, right faster than left in 2/5 ferrets, 1/5 did not differ, FigS4B. The model dissociated the effects of talker and F0, with the effect of F0 being somewhat variable across ferrets, with three ferrets showing slower reaction times for the lowest male talker F0, one showing slower reaction times for the pitch-shifted F0 values, and one not showing any F0 effects (Fig 4C). Reaction times were faster when the preceding non-target word had the same F0 as the target in 4/5 animals (Fig. S4C). Factors that did not influence reaction times - as assessed by the permutation test and feature importance values were the trial number and trial history factors (the previous trial was a catch trial / correct). Therefore, despite equivalent performance in inter and intra-trial roving trials by applying gradient-boosted regression to the reaction time data, we observe that ferrets' reaction times are faster when pitch provides a consistent streaming cue (Fig.4B, E).

Gradient boosted decision tree models reveal systematic false alarms to some non-target words

Our false alarm model implied that false alarms were potentially lapses in concentration related more to timing than acoustic parameters. However, an alternative possibility is that particular words drive false alarms independently of the characteristics of the talker. To investigate this, we used gradient-boosted regression to ask whether subjects consistently false alarmed to particular non-target words by modeling the animals' response time within a trial based on the word token. We modeled data from the female talker and the male talker separately using only the timing of each word token in a trial, relative to the onset of the trial, to predict the animals' eventual response time (again relative to the onset of the trial rather than the onset of the target word as in the previous reaction time analysis). The prediction accuracy of this model was excellent for both talker types, with a test mse of 0.0193s for the female talker compared to a noise-floor test mse of 1.804s (see methods) and a train mse of 0.0189s compared to a noise-floor train mse of 1.792s. The test mse for the male talker was 0.0499s compared to a noise-floor test mse of 1.959s, with a train mse of 0.0493s compared to a noise-floor mse of 1.949s (5-fold cross-validation for both train and test metrics).

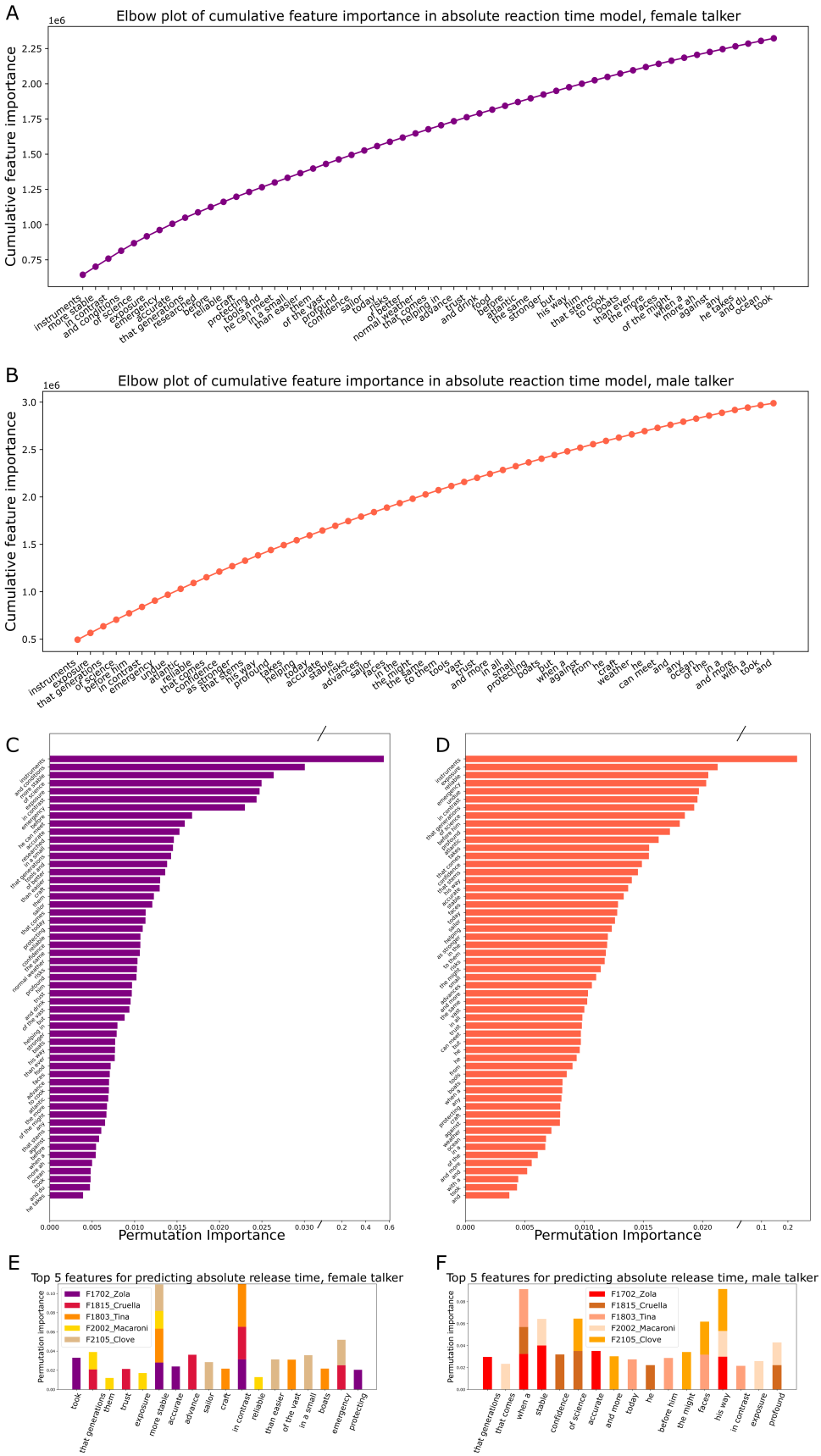


Figure 5. Gradient boosted models identify words that animals consistently false alarm to A, elbow plot of cumulative feature importance in the female talker model; B, same as A but for the male talker; C permutation importance of features included in the female talker model; D, same as C but for the male talker; E, top 5 permutation importances for each individual animal model for the female talker model; F, same as E but for the male talker.

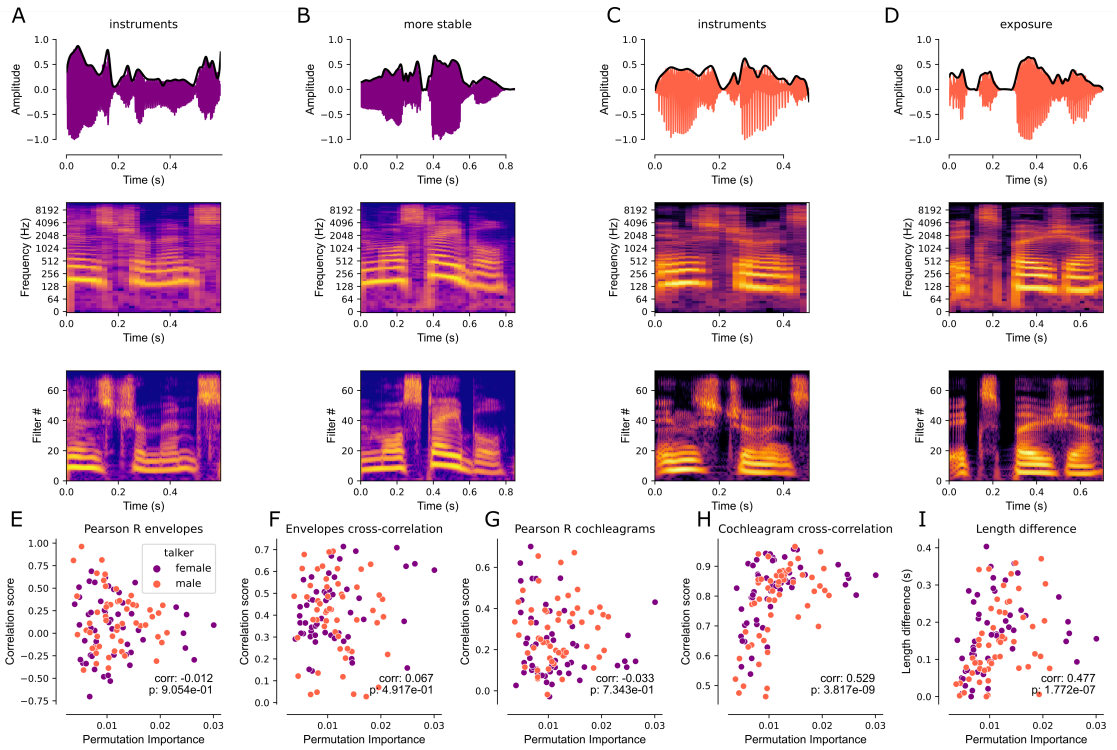


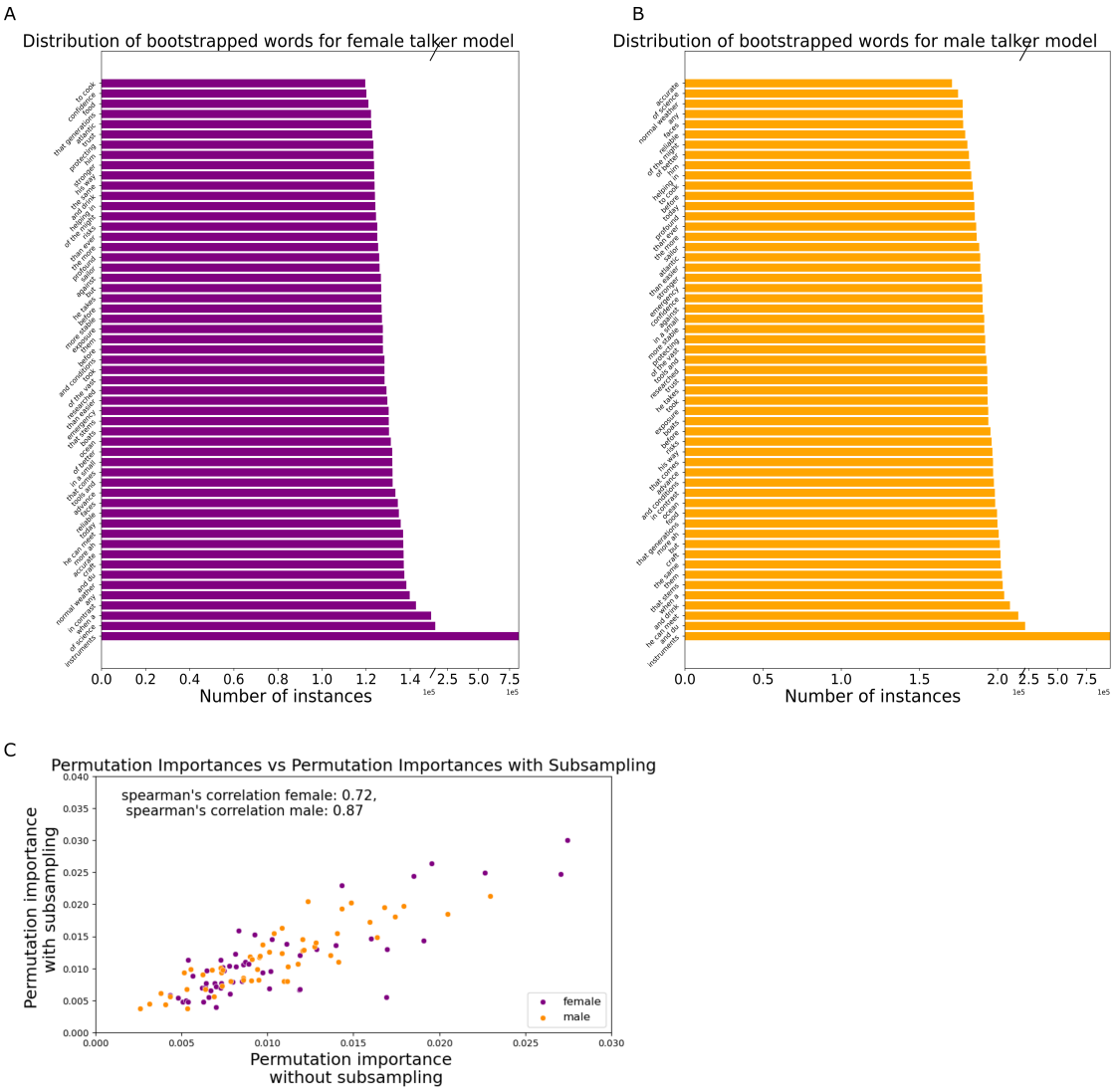
Figure 6. Spectrotemporal similarity predicts false alarm likelihood A, top to bottom: waveform, spectrogram, and cochleagram of instruments for the female talker stimulus. The black line in the waveform plot indicates the extracted envelope. B, top to bottom: waveform, spectrogram, and cochleagram of 'more stable', one of the words associated with a high chance of response in our absolute reaction time model for the female talker. C, same as A but for the male talker stimulus. D, same as B but for the word 'exposure', which was associated with a high rate of response in our male talker absolute reaction time model. E, the Pearson's correlation between the envelopes of the non-target words relative to the target over each non-target word's respective permutation importance. F, the maximum cross-correlation coefficient between each non-target word and the target word over each non-target word's respective permutation importance. G, same as E but using the cochleagram representations of the target and non-target words rather than the envelopes. H, same as F but for the cochleagram of each non-target word relative to the target word rather than the envelope. I, the absolute difference in duration (length) between each non-target and target word over its respective permutation importance.

Reassuringly, in both male and female talker models, the presence and timing of the target word had the strongest predictive power about when animals would release from the center port (Fig.5A-D). Nonetheless, some words consistently elicited behavioral responses as shown by both feature importance and permutation importance metrics, suggesting that false alarms are not simply temporary lapses in attention but rather that some words are perceived as more similar to the target. Running models on each animal separately (Fig. 5E, F) confirmed that these were repeatable errors across ferrets and talkers. To better understand the model output, we asked whether any particular acoustic features predicted the errors the animals made.

Words tokens that elicit false alarms share spectrotemporal similarity with the target

To explore the acoustic features that might underlie the animals' false alarm pattern, we considered three types of measures; first, we used a cochleagram model to estimate the representation of each token at the auditory periphery (Fig.6A-D), with the caveat that this is a human model, and therefore likely overestimates the frequency resolution available to the ferrets) (*mcdermottLab/pycochleagram* 2023). Second, we extracted the envelope of the amplitude waveform in order to explore the role of the temporal envelope. Third, we considered the difference in the duration of each word token and the target word. For the first and second measures, we compared the target and each word token (for all tokens from the same talker) using firstly a point-by-point Pearson's correlation, aligning the tokens at their onset. We also calculated the maximum of the cross-correlation to acknowledge that we don't a priori know which elements of a given token animals might confuse (e.g. we might imagine the "idence" of "confidence" might be more

303 readily confused with “instr” of ”instruments” than ”con” might be).
304
305 To relate acoustic and behavioral measures, we calculated Spearman’s correlation coefficient between
306 the permutation importance derived from the GBMs and each measure of acoustic similarity. The maximum
307 cross-correlation between the cochleagram provided the strongest relationship (Fig.6G spearman’s r =
308 0.529), explaining 28% of the variance in the animals’ behavior. Differences in word duration also had a
309 significant relationship with permutation importance (r = 0.424). Still, this relationship is in the opposite
310 direction of that that would be predicted (greater duration differences predict a greater likelihood of
311 false alarms). Words with the highest permutation importance can be seen to span a range of duration
312 differences, further confirming the observation that, in all likelihood, similar duration is not a cue that
313 the ferrets are relying upon to solve the task. Neither of the amplitude waveform measures produced
314 statistically significant relationships. From this, we therefore conclude that animals rely most heavily on
315 spectrotemporal features of the world to perform the task.



Supplementary Figure 5. A, distribution of the probability of occurrence in the resampled dataset used for the response time model in Figure 5; B, same as A but for the male talker absolute reaction time model; C, scatter plot of the permutation importance of each word with subsampling to equalize the frequency to the distribution plotted in A and B, versus the corresponding permutation importance scores obtained from a model with the uncorrected word distributions.

Comparison to traditional linear mixed-effects models

To compare the average performance of our gradient-boosted tree models with traditional linear-mixed effects models, we ran linear mixed-effects models on the variables used in our corresponding gradient-boosted regression tree models with ferret as a random (group) effect using the statsmodels package in Python. Like our gradient-boosted trees, we implemented five-fold cross-validation for a fair comparison. In most cases, our gradient-boosted decision and regression tree models were better or comparable to the linear mixed effects models. Reassuringly, many of the same statistical main effects were found with both approaches. However, there were some specific instances in which the GBM approach was superior (described below), and the available tools for the visualization of partial dependencies offered the advantage that the non-linear interactions between features could be meaningfully explored and quantified using SHAP values.

A mixed effects GLM (binomial, logit link) predicting hit vs. misses had an accuracy of 62.47% for the train split, 62.12% for the test split (this was comparable to the gradient-boosted regression trees, where the model had an average train balanced accuracy of 62.17% and an average test balanced accuracy of 62.09%). Mirroring the GBM, significant coefficients were returned for a talker, audio side, and target pitch (for 191 Hz vs reference of 109 Hz, Fig.7A). Neither the ferret ID, trial number nor target time parameters returned by the GBM were returned as significant by the mixed effects model (Tables S7, S8).

A mixed effects model predicting false alarms during catch trials had lower accuracy than the corresponding GMB model (balanced accuracy was 54.90% on the train data set vs. 61.5% and 54.70% on the test dataset compared to 61.46%). The mixed effects GLM returned significant coefficients for F0 (all values vs reference 109Hz), the previous response being correct, and the trial number (Fig.7B, Tables S9, S10). The GBM additionally assigned feature importance to the time within the trial, ferret ID, and whether the trial was intra-trial roving (Fig.3).

A mixed effects model predicting the reaction time for correct hit responses from behavioural variables had a mse of 0.091s for the train dataset, 0.092s for the test dataset, which was comparable to the mse of the gradient-boosted regression tree model (train mse = 0.092s, train mse =0.102s). Given the restriction that reaction times are between 0-2 s (meaning there are few outliers and a relatively normal distribution), this is perhaps not surprising. The model recapitulated the effects of the GBM, returning significant coefficients for talker (faster to female voice), F0 (124 Hz faster than 109 Hz), trials in which the precursor and target had the same F0 were faster than those in which they differed, reaction times were faster for targets later in the trial and for later trials in the session (Fig.7C, Supplemental Tables S11 S12). While the key results were the same across analysis approaches, the ability to visualize SHAP scores for all observations from each animal across multiple variables still provides additional clarity, which could be advantageous when trying to relate brain and behavior. For example, Figure 4D shows how target F0 impacts reaction time for each individual ferret, showing opposite patterns in F1702 and F2105, something that would not be apparent with the mixed effects model coefficients.

Where the linear model failed was in predicting the absolute release time solely based on which words were in a trial. To match the GBM approach, we used ordinary least squares, which, like the GBM, did not consider ferret as a factor, and again separated male talker and female talker trials to generate two models. The mse for the OLS model was nearly an order of magnitude larger than the GBM model, 0.15 and 0.19s, respectively for the male and female talker models, compared to errors of 0.0193s and 0.049s for the female and male talker for the GBM (Fig.S5C, Supplemental Tables S13, S13). Critically, the size of the coefficient for 'instruments' was barely greater than for the first-ranked non-target word in either model. Although there was some similarity in the ranking of non-target words between the linear regression and the GBM, the low overall model accuracy would make it hard to confidently make conclusions about false alarm behavior based on the linear regression alone. This analysis highlights that the GMB model has an advantage when predicting outlier behavior; false alarms to individual non-target word tokens are inherently rare in trained animals, and there is not a fixed response latency (as shown in the reaction time analysis) even if we can assume that animals trigger responses to the onset of word tokens (which the strong relationship between false alarms and cochleagram cross-correlation but not between correlation coefficients suggests is not the case). When performing the response time analysis with the GBM, we subsampled data to ensure that word frequency could not erroneously bias the resulting models; however we repeated the modeling with the original (non-uniform) distribution of word frequencies and the resulting permutation importance scores for non-target words were highly correlated (Fig.5C, Spearman's R = 0.72 and 0.87 for female and male talker models respectively) suggesting that this subsampling was unnecessary.

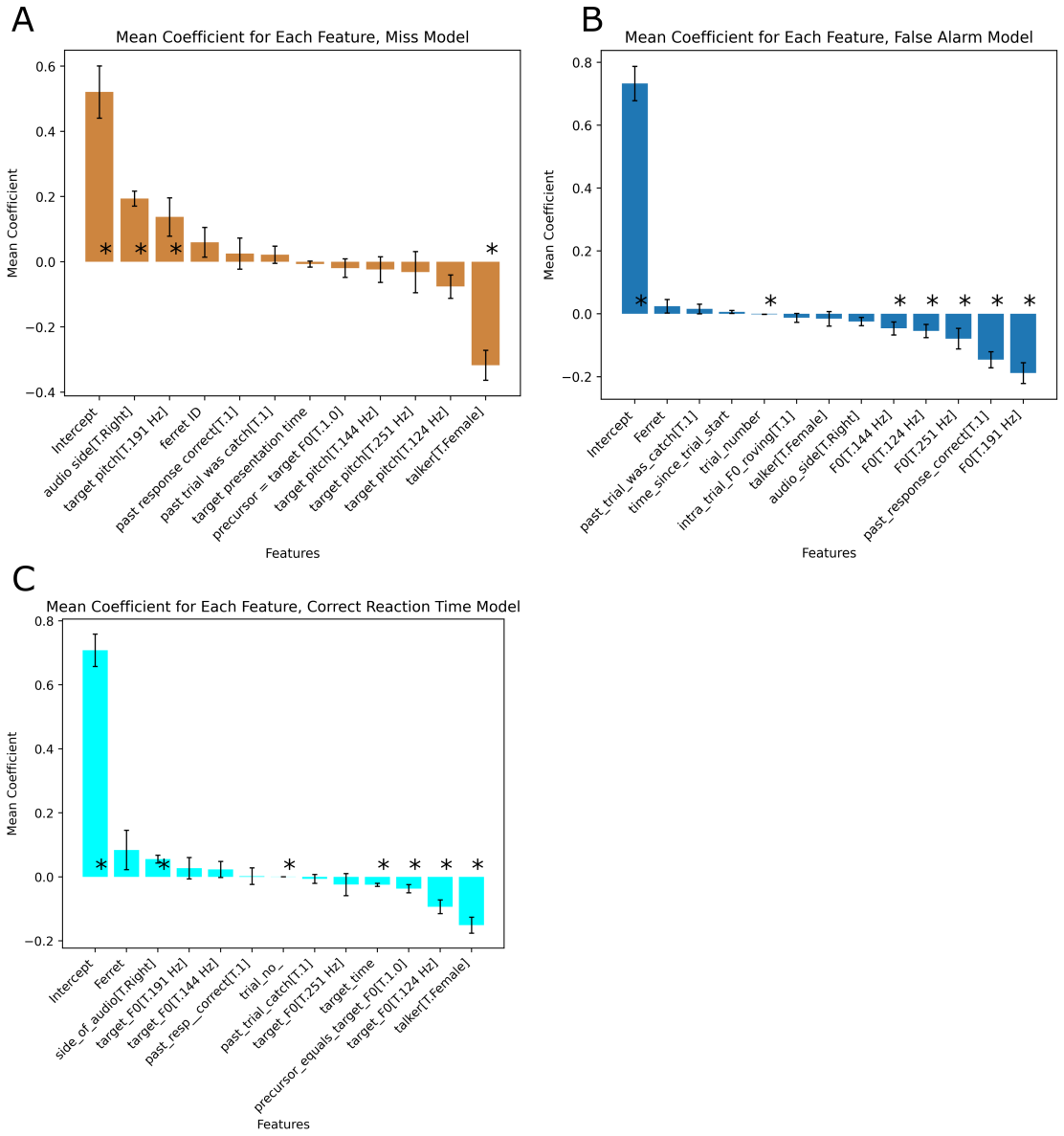


Figure 7. Mixed effects models show equivalent or worse performance Average coefficient values for the mixed effects model predicting A, a miss response for a target trial, B, a false alarm for a catch trial, and C, the reaction time during a correct target trial. Reference talker: male talker, reference F0: 109 Hz, reference side of audio: left side. Asterisks represent mean p-values < 0.05. Error bars represent the mean standard deviation.

DISCUSSION

We describe a novel behavioral task in which animals are trained to recognize a target word embedded in a series of non-target words and employed gradient-boosted models to analyze the subsequent behavior. The results of these models allowed us to understand that, like humans, ferrets are able to form F0-tolerant representations of auditory objects and use F0 to link sounds together into auditory streams. (Aulanko et al. 1993, Haykin and Chen 2005). The ability to identify and discriminate sounds across pitch is likely to be a fundamental property of mammalian audition, as the pitch of a vocal call conveys information about an individual's size, age, and emotional state (Hauser 1993, Charlton, Zhihe, and Snyder 2009).

We used gradient-boosted models to analyze the rich behavioral dataset we acquired comprising many 1000s of trials from 5 individual animals. We visualized the features that the models used to make predictions using SHAPs feature importance measures and partial dependency plots. This allowed us to understand not only what independent contributions specific variables made to behavior but also how combinations of variables interacted. We compared the output of the GBM models with traditional mixed

effects models, which, in most cases, were similar or slightly worse in overall model accuracy and returned very similar main effects. The GBM approach offered two advantages; firstly, the visualization tools are beneficial for understanding how different animals differentially weigh variables when performing the task (which in turn will be helpful for later relating brain and behavior). In a mixed-effects design, this is possible by fitting random slopes in addition to random intercepts. However, understanding and interpreting interaction effects - particularly between multiple categorical variables - quickly becomes intractable. Secondly, for some datasets, where the underlying relationships are inherently non-linear, and the samples are unbalanced, the GBM approach was much more effective, with eventual mean square error substantially lower than corresponding linear regression models. This, in turn, allowed us to relate false alarm behavior to acoustic features, revealing that spectrotemporal similarity was the strongest predictor of an increased likelihood of a false alarm.

The data presented here, in which pitch made only a minor contribution to overall performance, supports previous behavioral work in animals, showing that non-human listeners can generalize across variations in F0 for relatively simple sounds. For example, ferrets trained to discriminate artificial vowel sounds with an F0 of 200 Hz maintain their performance at F0s from 150 to 500Hz (Bizley et al. 2013, Town et al. 2015). Both rats (Engineer et al. 2013) and zebra finches (Ohms et al. 2010) trained to discriminate human speech sounds can generalize across different talkers who naturally vary in their voice pitch, and marmosets can discriminate pitch-shifted vocalizations ((Osmanski and Wang 2023)). However, not all species show pitch constancy; guinea pigs trained to categorize calls (e.g., chut vs. purr) in a Go/No-Go task struggled to perform the task with F0 shifts of +/- half an octave (Kar et al. 2022). In our models, F0 had only a very small effect on the ability of animals to correctly identify a target word (Fig.2) or on their likelihood of making a false alarm (Fig.3) and only modest differences in their reaction times (Fig.4). Together, these results suggest that performance is robust across variations in pitch. Our reaction time models suggest that variation in F0 impacts individual animals differently. One benefit of the models developed in this study is that such individual differences can be explored and potentially taken into account when interpreting and analyzing brain signals.

Our analysis of response time data on false alarm trials identified words that animals consistently false alarmed to. Analysis of the underlying acoustic cues highlighted spectrotemporal similarity as the strongest predictor of the likelihood of a word eliciting a false alarm. Previous work in songbirds has found that songbirds do not require spectral cues to distinguish between ascending or descending tones and only need the temporal features of the sound to identify the tones (Bregman, Patel, and Gentner 2016). Other work in mice has shown that mice could discriminate ultrasonic vocalizations but that vocalizations that were similar to one another were correlated with poorer performance, suggesting that mice also use spectrotemporal properties to categorize vocalizations (Neilans et al. 2014). Recent behavioral work by Osanki and Wang found that marmosets could also categorize intra-species vocalizations through a similar Go/No-Go task paradigm, in which marmosets had to recognize a target vocalization in the presence of an alternate reference vocalization by licking a metal feeding tube, and could successfully discriminate the same calls when the mean fundamental frequency was shifted upwards from the original F0 (Osmanski and Wang 2023); the authors concluded that the marmosets were using multiple acoustic properties to make their categorization choices.

While speech recognition is robust to variation in voice pitch for non-tonal languages, humans use the pitch of complex sounds to separate simultaneous competing sounds and to link sounds together over time to form auditory ‘streams.’ Auditory streaming has been studied in many species, including frogs (Bee and Riemersma 2008), starlings (Bee and Klump 2004, Hulse, MacDougall-Shackleton, and Wisniewski 1997) and gerbils (Dolležal et al. 2020). Evidence from birds suggests that avians use similar strategies to humans, with differences in intensity and spatial location used to segregate sounds into streams but a greater tolerance to changes in frequency or timing (Dent et al. 2016). Ferrets can also detect the presence of ‘mistuning’ when a single component of a harmonic complex is shifted in frequency, suggesting that, like humans, harmonicity is a strong grouping in animals (Homma et al. 2016). However, to our knowledge, no one has assessed whether non-human listeners use the pitch of a complex sound in the formation of auditory streams. The impact of pitch roving in increasing the likelihood of false alarms and slowing reaction times is consistent with ferrets using common pitch to link together sounds over time, offering an advantage for subsequent word recognition. Nonetheless, in the absence of a competing stream of information, we cannot be sure that it is streaming per se or simply that greater changes from word token to token make it a more difficult task. One feature of streaming is that it builds up over time (Moore and Gockel 2012), and consistent with streaming occurring, the likelihood of missing a target was higher, and

reaction times were significantly longer for trials in which the target was early in the stream compared to those in which it was in the middle or late in the stream. We predict that the impact of removing pitch constancy might be more strongly evident in tasks that require separating competing streams.

Here, we demonstrate that gradient-boosted decision trees have high predictive power even when incorporating highly correlated or very sparsely sampled variables and are ideally suited for unpicking multiple contributing factors to behavior. Moreover, this gradient-boosted regression tree method allows us to be agnostic to how factors in our metadata are related to each other and thus presents an excellent way to conduct both hypothesis-driven and exploratory data analysis to uncover otherwise hidden trends in behavioral data and drive analysis. Overall, these findings from these sensitive and powerful models could inform later behavioral and neural data studies by giving us an idea of which behavioral factors impact decision-making in individual animals.

MATERIALS AND METHODS

Animals

Subjects were five pigmented ferrets (*Mustela putorius*, female) who started training from 6 months of age and were tested between 18 months and 4 years of age. Animals were maintained in groups of 2 or more ferrets in enriched housing conditions, with regular otoscopic examinations to ensure the cleanliness and health of ears. All animals were trained in the behavioral task, using water as a reward. During testing periods, animals were water-regulated. Animals were tested twice daily from Monday to Friday, with free access to water from Friday afternoon to Sunday afternoon. Each ferret received a minimum of 60 ml/kg of water per day through a combination of task performance and supplementation with a wet mash made from water and ground high-protein pellets. Each ferret's weight and water consumption were logged daily throughout the experiment. All experimental procedures were approved by local ethical review committees (Animal Welfare and Ethical Review Board, at University College London and the Royal Veterinary College, University of London, and performed under license from the UK Home Office (Project Licenses PP1253968, 70/7267)

Equipment

We controlled the task and stimulus presentation through an RZ6 controller (Tucker Davis Technology, Florida, USA) using OpenEx with custom-written "GoFerret" software (Town et al. 2015) on a Windows PC. The right and left-hand speakers were calibrated to match the sound levels using a Bruel & Kjaer measuring amplifier (Type 2610). We presented each trial at a mean sound level of 65 dB SPL; stimuli were scaled to be constant in sound level across trials and talker types.

Stimuli

Stimuli were composed of a sequence (or 'stream') of consecutively presented words, all of which came from the same talker. Continuous speech from two talkers (1 male, 1 female) reading the same passage from the SCRIBE database was manually segmented into words and linked together with a minimum gap of 0.08s between words. The audio files were recorded at 20000 Hz but upsampled to 24,414 Hz for presentation.

Task

In a sound discrimination task, we trained five ferrets to recognize the target stimulus (the word 'instruments') against 54 other non-target stimuli (which were also English words) in a stream. Each stream (or string of words) consisted of a series of non-target words and one occurrence of the target word, which could occur anytime from 500 ms to 6.5 s after the onset of the trial (with the target timing drawn from a uniform distribution). As well as being preceded by non-target words, the target was followed by a sequence of non-target words that exceeded the duration of the response time (2s, see below). Streams were constructed de novo at the start of each trial with non-target words drawn randomly (with replacement) from the pool of 54. Non-target words were chosen at random (from a set of 54 words per talker).

The whole trial was comprised of word tokens from the same talker and presented from either the left or right speaker. Once trained, animals were required to initiate a trial by nose-poking at a center port that contained an infrared sensory and water delivery system. They were required to maintain contact until the target was presented. Once the target sound was presented, they were required to move to the response port on the same side as the stimulus presentation. A correct response required the animal to release the center port within 2s of the target word onset and correctly lateralize the sound stream (although, in practice,

animals rarely made localization errors). Catch trials (25% of all trials) contained only non-target words and were constructed to be equal in duration to the non-catch trials. On catch trials, the animal was required to remain at the center port and received a water reward from the central port at the end of the trial if they did so.

Training

Initially, ferrets were trained to move between the 3 lick ports (left, center, and right side) by alternating water reward at each port. Once this was accomplished (usually within 1 to 2 sessions), they were trained to lateralize the target sounds ('instruments'). This was achieved by rewarding the initiation of a trial (a response at the center port) and presenting several repetitions of the target sound from one of the lateral locations (either left or right). The ferret would receive a second reward only if they responded at the corresponding location. Once ferrets could perform this target lateralization task at a high rate of performance (>90% correct) over =>2 sessions, the delay between initiating the trial and presenting the target word was systematically increased (from 0 to 5 seconds) between sessions (but only if performance remained above 80% correct for the last two sessions). Once the ferret was capable of waiting 5 seconds at the center port for target presentation and accurately lateralizing the stimulus, we reduced the target presentation to a single-word token. We then gradually introduced non-target words before and after the target. Non-target words were initially presented with a 60 dB attenuation cue that was gradually reduced until animals were performing with the target and non-target at an equivalent sound level. 3/5 animals were trained first on the female and then the male, whereas F2105 and F2002 were trained with both from the beginning of training. All word tokens within a trial were drawn from the same talker, but the talker identity was randomly drawn across trials. Even once trained, we included a proportion of trials (25-50 %) that included a 10 -20 dB attenuation cue. These trials were excluded from the analysis but helped maintain the animals' motivation to perform the task. 25% of trials were catch trials in which the target word was not presented (the same port where ferrets initiated each trial). Baseline training varied in duration from 3 months to 8 months.

Pitch Roving

Animals were considered fully trained once they consistently performed above 70% correct on trials without an attenuation cue (chance performance is approximately 33% given the 6s trial duration and a 2s response window, i.e., 2s / 6s = 1/3). Once trained on the natural ('Control') F0 trials, we introduced F0 (pitch) roving. For each talker, we used STRAIGHT (which separates source and resonator information, therefore allowing manipulation of F0) (Kawahara 2006) to shift the F0 up or down by 0.4 octaves. This resulted in F0 values of 109 and 144 for the male voice, where the natural F0 was 124 Hz, and 144 and 251 Hz for the female voice, where the natural F0 was 191 Hz.

In inter-trial roving, the pitch of the entire trial shifted up or down, whereas, in intra-trial roving, the F0 value of each word was randomized. As in training, all word tokens within a trial came from the same talker.

Data Analysis

Any trial has four possible outcomes: hit, correct response, miss, and false alarm. A hit was defined as moving away from the center port ('release') and responding at the target location within 2s of the target word presentation. A correct rejection was defined as remaining at the central port for the entire duration of the trial (on a catch trial), a miss as failing to leave the central port within 2s of the target word presentation, and a false alarm as releasing from the center port before target word presentation or the end of a catch trial. False alarms immediately terminated the sound presentation and elicited a time-out (signaled by a modulated noise burst). Time outs lasted 2 seconds, during which the ferret could not reinitiate a trial.

We define $p(hit) = n\ hits/(n\ hits + n\ misses)$, and the proportion of false alarms (FA) as $p(FA) = n\ false\ alarms/[n\ hits + n\ misses + n\ correct\ rejections + n\ FA]$. We consider correct responses (C.R.) as either a hit or a correct reject, where $p(correct) = [n\ hits + n\ correct\ rejections]/[n\ hits + n\ misses + correct\ rejections + n\ FA]$. We also calculated a sensitivity metric (d') (Green and Swets 1966), where $d' = z(p(hits)) - z(p(FA))$, where z represents the normal distribution function. We define reaction time as the central port release time rather than the lateral response time relative to the timing of the target word. To analyze whether word tokens systematically elicited behavioral responses, we defined the response time as the exit time from the central port relative to trial onset. All data analysis, from behavioral metrics to computational models, was programmed using Python 3.9.

Computational Models

The general approach of the gradient-boosted decision tree model is a form of ensemble learning in which we use an initial weak decision tree of a depth larger than 1 to predict an outcome of a trial based on our behavioral data and then iteratively build upon the error of the first tree (after calculating the loss) by constructing the next tree based on the residuals of the previous tree. Once our loss plateaus or we reach the maximum number of training epochs, we stop training the model and calculate our test accuracy, or how well the model could predict our target variable on a held-out test set of data. We chose this method as our data is inherently dense (from long periods of behavioral training and testing) and tabular, which makes gradient-boosted regression and decision trees an excellent candidate for the prediction of categorical and continuous data compared to a nonlinear neural-network-based classifier (Grinsztajn, Oyallon, and Varoquaux 2022).

Linear mixed effect and generalized linear models are commonly used alternatives that allow trial-based analysis of categorical or continuous behavioral data. While powerful, such models can fail to capture non-linear or non-monotonic relationships that might be present in behavioral data. Machine learning approaches offer an alternative model-free approach to uncovering statistical structure in rich behavioral data sets such as those typical of animal behavioral work. Models were generated using LightGBM (Ke et al. 2017). Gradient-boosted regression trees were used to model reaction time data. Gradient-boosted decision trees were used to make classification models for binary trial outcomes (hit vs. miss and false alarm vs. correct rejection). To optimize hyperparameters for this model, we implemented a grid search using optuna (Akiba et al. 2019).

We generated 5 models to address our research questions. Two classification models were developed; one considered determining whether a ferret missed a target word (miss vs. hit model), and the second considered the factors that influenced the likelihood of a false alarm/correct rejection of a non-target word (false alarm/correct reject model). Our reaction time model used gradient-boosted regression to determine the parameters influencing the animals' reaction time to the target word. Our response time models (one each for male and female talker trials) predicted the release time within a trial based on the timing of the words. They were used to assess whether animals made systematic false alarms with particular words.

We determined which features were significant using cumulative feature importance, which sums the contributions of each variable across all of the trees in which it is utilized, and permutation testing, which shuffles a feature of our data (e.g., the target F0) and then selects the drop in performance the model has due to that feature being shuffled. We generated permutation importance plots from the sci-kit learn (sklearn) package to quantify the extent to which shuffling any given feature decreased teh quality fo the model, thereby establishing which features contributed significantly to model performance. The classification models were tuned using binary log loss with an evaluation metric of binary log loss across 10,000 epochs and implemented early stopping of 100 epochs. The regression models implemented the l2 loss function over 1000 epochs with an early stopping of 100 epochs. For the classification models, all hyperparameter optimization minimized binary log loss, whereas, for the regression (reaction time) model, hyperparameter optimization minimized the mean-squared error (l2 loss function).

The regression models' test and train mean-squared error was calculated using 5-fold cross-validation. The train and test accuracy and balanced accuracy were calculated using 5-fold cross-validation for the classification models. Noise floors were calculated for the regression models by calculating model performance when utilizing trials in which the relationship between reaction / response times was randomly shuffled. and the trial variables 1000 times while keeping the hyperparameters constant. We then used Shapley Additive values to assess parameter influence on the trial outcome. For the classification models, this was the likelihood of a miss/hit or false alarm; for the regression models, this was the reaction time. To visualise the contributions of model features (i.e., feature importance and cumulative feature importance), we used the SHAP package (Lundberg and Lee 2017), an implementation of Shapely Additive Importance features to elucidate explainability from the typically 'black-box' regression and classification tree models. The SHAP package allowed us to plot partial dependency plots to see how the impact of the model would vary as inter-related features changed (such as talker gender and trial number). For the categorization models, we applied subsampling of the data to equalize trial counts; to force the model to weight trial types with equal importance, we sub-sampled control F0 trials to match intra and inter-F0 roved trials. To weigh the trial outcomes with equal importance, we sub-sampled hit responses to match the number of miss responses for the miss/hit classification model and sub-sampled non-false alarm responses to match the number of false alarm responses in the false alarm model.

For the regression model that calculated the absolute response time within the trial (rather than relative to the target), we used sub-sampling to create a uniform distribution of words. This sub-sampling, or bootstrapping, was done so our gradient-boosted regression tree model wouldn't associate higher-frequency words with a higher likelihood of a false alarm or response just because of its higher frequency. However, this is mathematically impossible to do precisely, as the words were not presented independently. In other words, each trial consisted of multiple word tokens analogous to a sentence, pooling each word from a word bank sampled with replacement. Moreover, in F1702, some of the words were programmed to occur 80% more frequently than other words for neural recordings. Thus, to achieve something close computationally to a mathematically perfect bootstrapping procedure, we created a loop for each of the 54 non-target words, found the trials that contained that non-target word, and placed them into a data frame. We then sub-sampled this resulting data frame to 700 samples (the minimum number of counts across all words in the original data frame) unless the non-target was a naturally high-frequency occurring word, where it was sub-sampled to 50 samples or skipped entirely. After all 54 words were iterated through in order, the resulting sub-sampled data frame was appended to an array. Next, we repeated the same process but went through the non-target words in reverse order to ensure some words wouldn't be over-sampled in the resulting distribution. This whole process of iterating through all the non-target words and flipping the order of iteration was repeated 18 more times (Supplementary Figure 5A,B, the results obtained implementing this subsampling were very similar to those obtained using the natural distribution of word occurrences). The results reported (Figure 5) are from this subsampled data frame. However, we repeated the analysis using the natural (biased) frequencies of word occurrences and obtained very similar results (Supplemental Figure 5C), illustrating that the GBM does not require balanced data to yield sensible results.

AUTHOR CONTRIBUTIONS

CG, JS, and JKB conceived of the original study and the mechanisms of the perceptual constancy task. CG generated the data analysis and code required to produce this paper's gradient-boosted regression and classification models. JL wrote helper functions to extract MATLAB metadata into a standardized Python format and performed the acoustic similarity analysis. CG and JL were responsible for the data collection. CG and JB wrote the manuscript. All authors have read and agreed to the published version.

DATA AVAILABILITY

Behavioral data is available [link to UCL data repository to be added on publication].

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CODE AVAILABILITY

Code used to reproduce the models is available on Github: https://github.com/carlacodes/boostmodels.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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SUPPLEMENTARY MATERIAL

Repeated-Measures ANOVA with posthoc testing

Within-group factor	SS	Degrees of freedom (numerator)	Degrees of freedom (denominator)	MS	F-value	Uncorrected p-value	GG corrected p-value	Generalized eta-squared	GG epsilon factor
roving_type	0.0002851	2	8	0.00014255	0.1673	0.8488	0.8339	0.0037	0.9247
talker	0.050970082	1	4	0.050970082	12.0173	0.0257	0.0257	0.3979	1
roving_type * talker	0.0215	2	8	0.0108	16.3772	0.0015	0.0099	0.2181	0.5936

Supplementary Table S1. Repeated-measures ANOVA for the hit statistic with roving type and talker as factors.

A	B	mean(A)	mean(B)	diff	se	T	p-tukey	hedges	talker
control	inter	0.8280	0.8823	-0.0542	0.0390	-1.3916	0.3756	-0.7149	Female
control	intra	0.8280	0.8738	-0.0458	0.0390	-1.1752	0.4893	-0.6126	Female
inter	intra	0.8823	0.8738	0.0084	0.0390	0.2164	0.9746	0.1648	Female
control	inter	0.8201	0.7508	0.0693	0.0324	2.1367	0.1239	1.0451	Male
control	intra	0.8201	0.7659	0.0542	0.0324	1.6725	0.2551	1.3949	Male
inter	intra	0.7508	0.7659	-0.0151	0.0324	-0.4642	0.8891	-0.2455	Male

Supplementary Table S2. Pairwise Tukey HSD posthoc test statistics for the hit statistic comparing the roving types for each talker type.

Within-group factor	SS	Degrees of freedom (numerator)	Degrees of freedom (denominator)	MS	F-value	Uncorrected p-value	GG corrected p-value	Generalized eta-squared	GG epsilon factor
roving_type	0.0347	2	8	0.0174	32.541	0.0001436	0.0011539	0.3932	0.6985
talker	0.0057	1	4	0.0057	7.7165	0.04993	0.04993	0.0961	1
roving_type * talker	0.0087	2	8	0.0043	16.3283	0.0014991	0.0082412	0.1391	0.6338

Supplementary Table S3. Repeated-measures ANOVA for the false alarm statistic with roving type and talker as factors

A	B	mean(A)	mean(B)	diff	se	T	p-tukey	hedges	talker
control	inter	0.1213	0.2395	-0.1181	0.0288	-4.0986	0.0039	-2.2667	Female
control	intra	0.1213	0.2069	-0.0855	0.0288	-2.9677	0.0294	-2.2529	Female
inter	intra	0.2395	0.2069	0.0326	0.0288	1.1310	0.5143	0.5526	Female
control	inter	0.1969	0.2445	-0.0476	0.0309	-1.5418	0.3072	-0.8621	Male
control	intra	0.1969	0.2089	-0.0120	0.0309	-0.3884	0.9207	-0.2324	Male
inter	intra	0.2445	0.2089	0.0356	0.0309	1.1533	0.5016	0.6446	Male

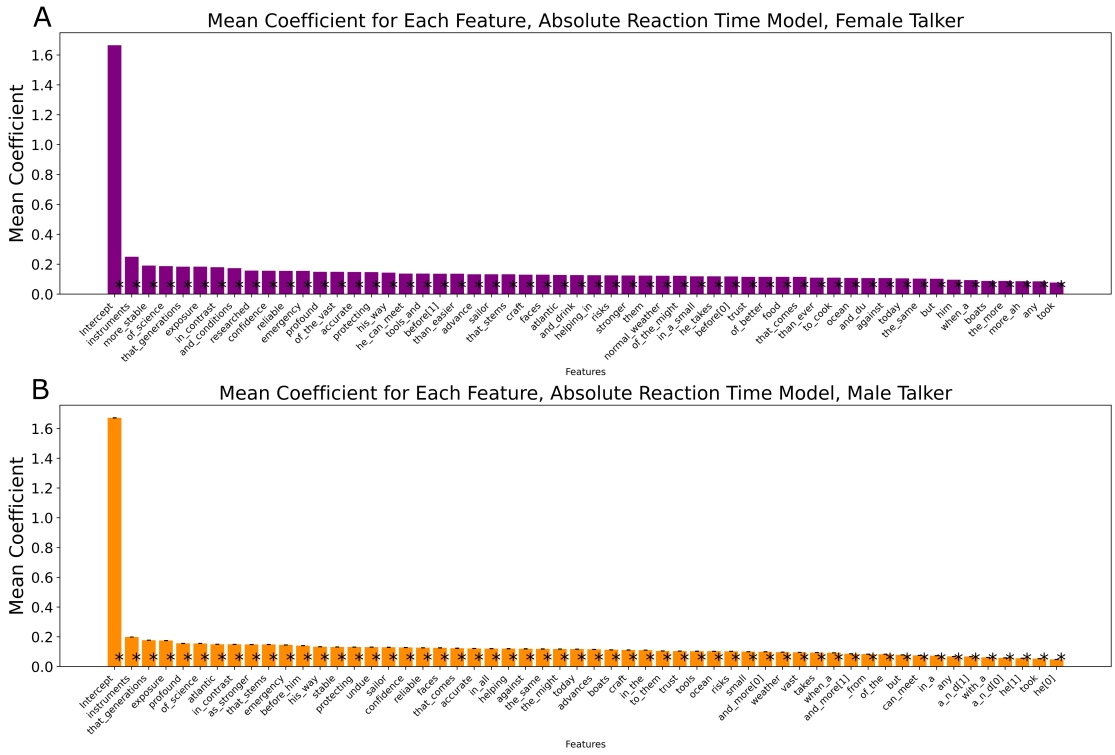
Supplementary Table S4. Pairwise Tukey HSD posthoc test statistics for the false alarm statistic comparing the roving types for each talker type.

Within-group factor	SS	Degrees of freedom (numerator)	Degrees of freedom (denominator)	MS	F-value	Uncorrected p-value	GG corrected p-value	Generalized eta-squared	GG epsilon factor
roving_type	0.4941	2	8	0.2470	19.0512	0.0009067	0.0016395	0.2171	0.8836
talker	1.5566	1	4	1.5566	13.3321	0.0217	0.0217	0.4662	1
roving_type * talker	0.0379	2	8	0.0190	1.4193	0.2968	0.3006	0.0208	0.5931

Supplementary Table S5. Repeated-measures ANOVA for the d' statistic with roving type and talker as factors

A	B	mean(A)	mean(B)	diff	se	T	p-tukey	hedges
control	inter	1.9759	1.6675	0.3084	0.1582	1.9500	0.1443	0.8036
control	intra	1.9759	1.7690	0.2070	0.1582	1.3086	0.4028	0.5891
inter	intra	1.6675	1.7690	-0.1014	0.1582	-0.6414	0.7987	-0.2727

Supplementary Table S6. Pairwise Tukey HSD posthoc test statistics for the d' statistic comparing the roving type.



Supplementary Figure 6. Average coefficients for the mixed effects model predicting the absolute reaction time of A, the female talker and B, the male talker. Asterisks represent mean p-values < 0.05. Error bars represent standard deviation.

Mean Coefficients for Correct Response/Miss Mixed Effects Model

	Coefficients	p-values	Std Error	Reference Var.
Intercept	0.520854461	1.52×10^{-10}	0.080041795	NA
talker[T.Female]	-0.317642927	1.51×10^{-10}	0.045732239	Male
side[T.Right]	0.193710621	9.11×10^{-16}	0.022978412	Left
precur_and_targ_same[T.1.0]	-0.019565026	0.553336664	0.028361248	0
pastcorrectresp[T.1]	0.025192459	0.650363275	0.047565918	0
pastcatchtrial[T.1]	0.021765334	0.442912553	0.026426389	109 Hz
pitchoftarg[T.124 Hz]	-0.076117184	0.067420509	0.036043322	109 Hz
pitchoftarg[T.144 Hz]	-0.023891631	0.502165928	0.039155263	109 Hz
pitchoftarg[T.191 Hz]	0.137419137	0.027073213	0.058698022	109 Hz
pitchoftarg[T.251 Hz]	-0.031619663	0.530787218	0.063248187	NA
targTimes	-0.007073769	0.437703962	0.009010698	NA
Group Var	0.059673346	0.191171661	0.045549129	NA

Supplementary Table S7. Average coefficients of the main fixed effects of the miss/correct response model.

Variable	Value
F1702	0.083706212
F1815	-0.103531798
F1803	-0.106645577
F2002	-0.010695264
F2105	0.137166427

Supplementary Table S8. Average coefficients of the random effects for the miss/correct response model.

775 ***Mean Coefficients for False Alarm during Catch Trials Mixed Effects Model***

	Coefficients	p-values	Std Error	Reference Var.
Intercept	0.732556885	3.38×10^{-40}	0.054497305	NA
talker[T.Female]	-0.015609053	0.579346879	0.023068625	Male
audio_side[T.Right]	-0.024267944	0.087824018	0.013355741	Left
intra_trial_F0_roving[T.1]	-0.012606819	0.413351419	0.013948378	0
past_response_correct[T.1]	-0.145910528	2.59×10^{-8}	0.025252469	0
past_trial_was_catch[T.1]	0.015704358	0.34159084	0.015312778	0
F0[T.124 Hz]	-0.054385786	0.015409873	0.021301452	109 Hz
F0[T.144 Hz]	-0.046151527	0.033597362	0.020785748	109 Hz
F0[T.191 Hz]	-0.188231442	9.74×10^{-8}	0.033246797	109 Hz
F0[T.251 Hz]	-0.078706493	0.023296467	0.032719323	109 Hz
time_since_trial_start	0.006276126	0.235041603	0.004998005	NA
trial_number	-0.001258391	2.45×10^{-6}	0.000240217	NA
Group Var	0.0242515	0.256106446	0.021387303	NA

Supplementary Table S9. Average fixed effect coefficients for the false alarm linear mixed effects model. 1 indicates yes, 0 indicates no.

Variable	Value
F1702	-0.021814873
F1815	0.034607429
F1803	0.06438864
F2002	0.025084628
F2105	-0.102265824

Supplementary Table S10. Average random effect coefficients for the false alarm linear mixed effects model.

776 ***Mean Coefficients for Correct Reaction Time Mixed Effects Model***

	coefficients	p_values	std_dev.	reference var.
Intercept	0.7082	1.43E-41	0.0507	NA
target_F0[T.124 Hz]	-0.0936	4.40E-05	0.0214	109 Hz
target_F0[T.144 Hz]	0.0231	0.3965	0.0251	109 Hz
target_F0[T.191 Hz]	0.0271	0.4630	0.0333	109 Hz
target_F0[T.251 Hz]	-0.0241	0.4955	0.0345	109 Hz
past_trial_catch[T.1]	-0.0061	0.6117	0.0140	0
talker[T.Female]	-0.1509	5.63E-08	0.0250	Male
side_of_audio[T.Right]	0.0555	1.13E-05	0.0120	Left
precursor_equals_target_F0[T.1.0]	-0.0369	0.0063	0.0129	0
past_resp__correct[T.1]	0.0024	0.7772	0.0260	0
trial_no_	0.0004	0.0385	0.0002	NA
target_time	-0.0248	6.39E-07	0.0049	NA
Group Var	0.0841	0.1713	0.0615	NA

Supplementary Table S11. Average fixed effect coefficients for the reaction time linear mixed effects model for correct hit responses. 1 indicates yes, 0 indicates no.

F1702	0.0803
F1815	0.0319
F1803	0.0536
F2002	-0.0414
F2105	-0.1244

Supplementary Table S12. Average random effect coefficients mixed effects model predicting reaction time for correct target trial responses.

777 ***Mean Coefficients for OLS Absolute Reaction Time Model, Female Talker***

	coefficients	p_values	std_dev
Intercept	1.6652	0	0.0008
instruments	0.2501	0	0.0003
when_a	0.0933	0	0.0006
sailor	0.1327	0	0.0006
in_a_small	0.1194	0	0.0006
craft	0.1299	0	0.0006
faces	0.1296	0	0.0006
of_the_might	0.1227	0	0.0006
of_the_vast	0.1487	0	0.0006
atlantic	0.1278	0	0.0006
ocean	0.1085	0	0.0006
today	0.1052	0	0.0006
he_takes	0.1193	0	0.0006
the_same	0.1033	0	0.0006
risks	0.1250	0	0.0006
that_generations	0.1839	0	0.0006
took	0.0777	0	0.0006
before[0]	0.1184	0	0.0006
before[1]	0.1364	0	0.0005
him	0.0964	0	0.0006
but	0.1025	0	0.0006
in_contrast	0.1799	0	0.0006
them	0.1236	0	0.0006
he_can_meet	0.1377	0	0.0006
any	0.0855	0	0.0005
emergency	0.1552	0	0.0006
that_comes	0.1152	0	0.0006
his_way	0.1441	0	0.0006
confidence	0.1563	0	0.0006
that_stems	0.1326	0	0.0006
profound	0.1490	0	0.0006
trust	0.1159	0	0.0006
advance	0.1330	0	0.0006
of_science	0.1869	0	0.0006
boats	0.0887	0	0.0006
stronger	0.1242	0	0.0006
more_stable	0.1907	0	0.0006
protecting	0.1472	0	0.0006
against	0.1069	0	0.0006
and_du	0.1076	0	0.0006
exposure	0.1836	0	0.0006
tools_and	0.1371	0	0.0006
more_ah	0.0867	0	0.0006
accurate	0.1480	0	0.0006
the_more	0.0883	0	0.0005
reliable	0.1556	0	0.0006
helping_in	0.1260	0	0.0006
normal_weather	0.1227	0	0.0006
and_conditions	0.1737	0	0.0005
food	0.1154	0	0.0006
and_drink	0.1274	0	0.0006
of_better	0.1157	0	0.0006
researched	0.1577	0	0.0006
than_easier	0.1363	0	0.0006
to_cook	0.1101	0	0.0006
than_ever	0.1103	0	0.0006

Supplementary Table S13. Coefficients for the ordinary least squares (OLS) model predicting absolute reaction time based on word identity in a trial, female talker model.

778 ***Mean Coefficients for OLS Absolute Reaction Time Model, Male Talker***

	coefficients	p_values	std_dev.
Intercept	1.6723	0	0.0008
instruments	0.1992	0	0.0003
when_a	0.0930	0	0.0005
sailor	0.1298	0	0.0005
in_a	0.0734	0	0.0005
small	0.1004	0	0.0005
craft	0.1115	0	0.0005
faces	0.1260	0	0.0005
the_might	0.1180	0	0.0005
of_the	0.0833	0	0.0005
vast	0.0957	0	0.0005
atlantic	0.1501	0	0.0005
ocean	0.1030	0	0.0005
today	0.1174	0	0.0005
he[0]	0.0484	0	0.0005
he[1]	0.0562	0	0.0005
takes	0.0942	0	0.0005
the_same	0.1188	0	0.0005
risks	0.1026	0	0.0005
that_generations	0.1774	0	0.0005
took	0.0531	0	0.0005
before_him	0.1408	0	0.0005
but	0.0788	0	0.0005
in_contrast	0.1495	0	0.0005
to_them	0.1053	0	0.0005
can_meet	0.0754	0	0.0005
any	0.0685	0	0.0005
emergency	0.1460	0	0.0005
that_comes	0.1233	0	0.0005
his_way	0.1336	0	0.0005
with_a	0.0620	0	0.0005
confidence	0.1287	0	0.0005
that_stems	0.1485	0	0.0005
_from	0.0839	0	0.0005
profound	0.1561	0	0.0005
trust	0.1045	0	0.0005
in_the	0.1107	0	0.0005
advances	0.1157	0	0.0005
of_science	0.1557	0	0.0005
boats	0.1129	0	0.0005
as_stronger	0.1488	0	0.0005
and_more[0]	0.1000	0	0.0005
and_more[1]	0.0863	0	0.0005
stable	0.1317	0	0.0005
protecting	0.1312	0	0.0005
against	0.1197	0	0.0005
undue	0.1309	0	0.0005
exposure	0.1753	0	0.0005
tools	0.1033	0	0.0005
accurate	0.1218	0	0.0005
reliable	0.1269	0	0.0005
helping	0.1206	0	0.0005
in_all	0.1209	0	0.0005
weather	0.0971	0	0.0005
a_n_d[0]	0.0586	0	0.0005
a_n_d[1]	0.0676	0	0.0005

Supplementary Table S14. Coefficients for the ordinary least squares (OLS) model predicting absolute reaction time based on word identity in a trial, male talker model.

Trial information

Ferret ID	F1702		F1815		F1803		F2002		F2105	
Talker	M	F	M	F	M	F	M	F	M	F
All trials	2834	2773	1758	1684	3060	3001	6381	3611	2026	2055
Catch trials	717	694	454	439	781	756	1583	918	504	519

Supplementary Table S15. Table of trial type numbers distributed by ferret ID and talker type (M = male talker, F= female talker)

Model Parameters

False alarm categorical model

Parameter	Value
colsample_bytree	0.19088470325102014
subsample	0.9304141034109051
learning_rate	0.477510574908984
num_leaves	115
max_depth	18
min_child_samples	53
reg_alpha	0.2609865674187428
reg_lambda	1.3303484138905937
min_split_gain	0.0007545705453046434
bagging_freq	17
feature_fraction	0.8423132245598192
scale_pos_weight	1.113987259898614
min_child_weight	7.651492399061174
max_bin	786
min_data_in_leaf	52
min_sum_hessian_in_leaf	2.9989911144951256

Supplementary Table S16. Hyperparameter values for the false alarm categorical model

Miss/hit model

Parameter	**Value**
colsample_bytree	0.5826037749242697
subsample	0.9632104755468021
learning_rate	0.22727575447213846
num_leaves	45
max_depth	15
min_child_samples	61
reg_alpha	4.265341824464033
reg_lambda	2.3404053166956853
min_split_gain	0.004157693187481298
bagging_freq	6
feature_fraction	0.9019287831358274
scale_pos_weight	1.0694853574196075
min_child_weight	6.892115531076795
max_bin	224
min_data_in_leaf	79
min_sum_hessian_in_leaf	11.443671701974884

Supplementary Table S17. Hyperparameters for the miss/hit gradient-boosted decision tree model

783 ***Reaction time model***

Parameter	Value
colsample_bytree	0.46168728494506456
alpha	8.758272905706946
n_estimators	82
learning_rate	0.2165288044507529
max_depth	18
bagging_fraction	0.7000000000000001
bagging_freq	0

Supplementary Table S18. Hyperparameters for the reaction time gradient-boosted regression tree model predicting the reaction time from the onset of the target word from the subset of correct hit responses.

784 ***Absolute reaction time model - female talker***

Hyperparameter	Value
colsample_bytree	0.998 448 361 791 188 9
alpha	10.545 892 165 925 359
n_estimators	120
learning_rate	0.258 529 884 871 212 1
max_depth	20
bagging_fraction	1.0
bagging_freq	23
lambda	0.195 381 053 380 844 05
subsample	0.895 804 443 430 478 9
min_child_samples	20
min_child_weight	9.474 782 393 947 127
gamma	0.157 117 421 509 215 9
subsample_for_bin	6200

Supplementary Table S19. Hyperparameters for the absolute reaction time gradient-boosted regression tree model that predicts the reaction time relative to the female talker type trial start time.

785 ***Absolute reaction time model - male talker***

Parameter	Value
colsample_bytree	0.5870762820095368
alpha	10.840482953967314
n_estimators	70
learning_rate	0.18038495501541654
max_depth	20
bagging_fraction	0.9
bagging_freq	30

Supplementary Table S20. Hyperparameters for the absolute reaction time gradient-boosted regression tree model that predicts the reaction time relative to the male talker type trial start time.

Absolute reaction time models - ferret ID specific

Ferret ID	Talker Type	Alpha	Bagging Fraction	Bagging Freq	Colsample bytree	Learning Rate	Max Depth	N Estimators
F1702	Female	14.223322406	0.9	15	0.4376317124943425	0.29507288515060002	17	72
F1702	Male	13.683546599	0.9	27	0.27488570170 4623	0.29969397257415414	8	92
F1815	Female	7.971900722	0.8	3	0.34004453771820 91	0.27676813001474104	18	94
F1815	Male	8.423806867	0.9	17	0.20729967592658163	0.15619521411 2881	18	70
F1803	Female	12.715761382	0.9	3	0.39004198516961 71	0.29997430400741 89	17	86
F1803	Male	9.372039068	0.9	26	0.33678897601201463	0.23050055406320 21	10	94
F2002	Female	14.643599551	0.8	7	0.50032665552942 05	0.24935282553721447	12	96
F2002	Male	7.975250677	0.9	1	0.42291109612903 57	0.26178747945088 51	20	70
F2105	Female	13.306184442	0.9	16	0.24494884931507196	0.29526660334827737	15	100
F2105	Male	5.599860028	0.1	0	0.12944171709698 43	0.24111783056503241	20	42

Supplementary Table S21. Hyperparameters for the absolute reaction time models for each ferret ID broken down by Female/Male talker type.