# Sound localization in world and head-centered space in ferrets

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## Abstract

The location of sounds can be described in multiple coordinate systems that are defined relative to ourselves, or the world around us. World-centered hearing is critical for stable understanding of sound scenes, yet it is unclear whether this ability is unique to human listeners or generalizes to other species. Here, we establish novel behavioral tests to determine the coordinate systems in which non-human listeners (ferrets) can localize sounds. We found that ferrets could learn to discriminate sounds using either world-centered or head-centered sound location, as evidenced by their ability to discriminate locations in one space across wide variations in sound location in the alternative coordinate system. Using infrequent probe sounds to assess broader generalization of spatial hearing, we demonstrated that in both head and world-centered localization, animals used continuous maps of auditory space to guide behavior. Single trial responses of individual animals were sufficiently informative that we could then model sound localization using speaker position in specific coordinate systems and accurately predict ferrets' actions in held-out data. Our results demonstrate that non-human listeners can thus localize sounds in multiple spaces, including those defined by the world that require abstraction across traditional, head-centered sound localization cues.

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# Introduction

The ability to localize sound sources in our environment is critical for both humans and other animals, across a variety of behaviors ranging from hunting to communication, and in a wide range of ecological settings. In contrast to other senses such as vision or somatosensation, the auditory system lacks a spatially-organized sensory epithelium such as the retina or skin from which to extract spatial information, and therefore sound location must be computed from localization cues provided by signals arriving at the two ears. Extensive research has shown how the brain computes sound location relative to the head using inter-aural cues (Litovsky et al., 2021) and the spectral filtering properties of the head and body (Algazi et al., 2002; Kulkarni and Colburn, 2004), as well as how listeners exploit dynamic cues using head movements to improve spatial hearing (Brimijoin et al., 2013; Perrett and Noble, 1997; Wallach, 1940).

The use of head movements illustrates the importance of studying spatial hearing in freely moving subjects, as these listeners can map sounds into the local environment by constructing abstract representations of sound location across head motion. This abstraction is critical to build a stable understanding of sound scenes that would otherwise change as our movements affect head-centered localization cues. Recent work has identified neural mechanisms through which sound localization cues may be integrated with information about head direction (Wigderson et al., 2016; Wu and Shore, 2018). This integration may offset effects of head movement in spatial hearing, ultimately leading to neurons coding for world-centered space (Town et al., 2017). However, these advances in our understanding of sound localization in the brain leave open key questions regarding the ability of non-human animals to experience sounds in both head and world-centered space, and whether sound localization in these two spaces can be clearly dissociated without language.

Spatial hearing in animals is frequently studied using sound localization tasks in which a subject is presented with a sound and approaches it's source to report the relevant location (Bajo et al., 2019; Keating et al., 2015; Lomber and Malhotra, 2008; Payne, 1971; Wood et al., 2017). However, the coordinate system(s) in which animals report sound location in conventional approach-to-target tasks can be ambiguous because each trial in the task begins with a consistent head pose. This allows animals to 'solve' the task either by reporting a sound's position relative to the head (e.g. "the speaker is in front of me") or relative to the world ("the speaker is at the front of the test chamber"). To resolve this ambiguity, we designed two tasks in which ferrets were trained to discriminate sound location in either world or head-centered space across changes in head rotation that explicitly rendered sound location in the other coordinate system uninformative. This allowed us to demonstrate that, like humans, ferrets can report a continuous sound space centered unambiguously either in the external world, or relative to the listener's head.

# Results

## World-centered discrimination of sound location

In the world centered task, listeners were required to discriminate sound location based on its position in the test arena. Ferrets (n=3: F1701, F1703 and F1811) were presented with sounds (250 ms broadband noise, 60 dB SPL) from either the North or South of a test chamber and trained to report speaker location by visiting response ports with fixed locations in the chamber (East or West respectively, **Fig. 1A**). On each trial, the subject initiated stimulus presentation from a central platform, at which they were required to remain stationary for the full duration of the sound (**Fig. 1B**).

Across sessions, we rotated the center platform at which sounds were presented to subjects in 30° intervals around the full circle (**Fig. 1C** and **Supplementary Fig. 1)**. Sounds from North and South speakers were therefore presented across the full range of angles relative to the head, so that head-centered sound location was not informative about the correct behavioral response. Instead, the task could only be solved on the basis of sound location in the chamber (world). These inferences were confirmed quantitatively using simulations in which behavioral responses were modelled as a function of sound angle in either world or head-centered space (**Fig. 1D**, see Methods and also Fig. 5 for more details). Models based on head-centered sound location could only solve the task at specific platform angles, and subsequently failed as the platform rotated; whereas models based on world-centered sound location performed better than chance at all platform angles. In a later variant of the task, we also trained a fourth ferret with another pair of world-centered locations (F1902: North-West vs. South-East, **Fig. 1E**).

Ferrets successfully learned to discriminate between sounds based on sound source location in the world. **Figure 2A** shows the behavior of each ferret trained in the task, with performance being better than chance at all platform angles (n = 12 angles, 400 trials per angle: range = 66.6 to 85.9% vs. 50% chance; mean performance of each ferret: F1701 = 74.6%, F1703 = 76.3%, F1811 = 80.3%, F1902 = 77.3%). Binomial tests confirmed that the probability of performance arising by chance was significantly low at all platform angles for each subject (Bonferroni corrected, $p < 0.001$). Similar results were obtained when considering the first or last ten trials in each session after platform rotation (**Supplementary Fig. 2**), indicating that accurate performance did not simply result from rapid relearning of the task after every change in platform angle.

To ensure that animals were using speaker location to solve the task, we also swapped the specific speakers used at test locations (e.g. North and South, or North-West and South-East). Swapping speakers did not affect ferrets' ability to discriminate world-centered sound location as performance remained consistent before and after swaps (mean ± s.d. change = 1.906% ± 7.670%, **Supplementary Fig. 3A**). Thus, ferret behavior was driven by sound location rather than the specific speaker from which sounds were presented.

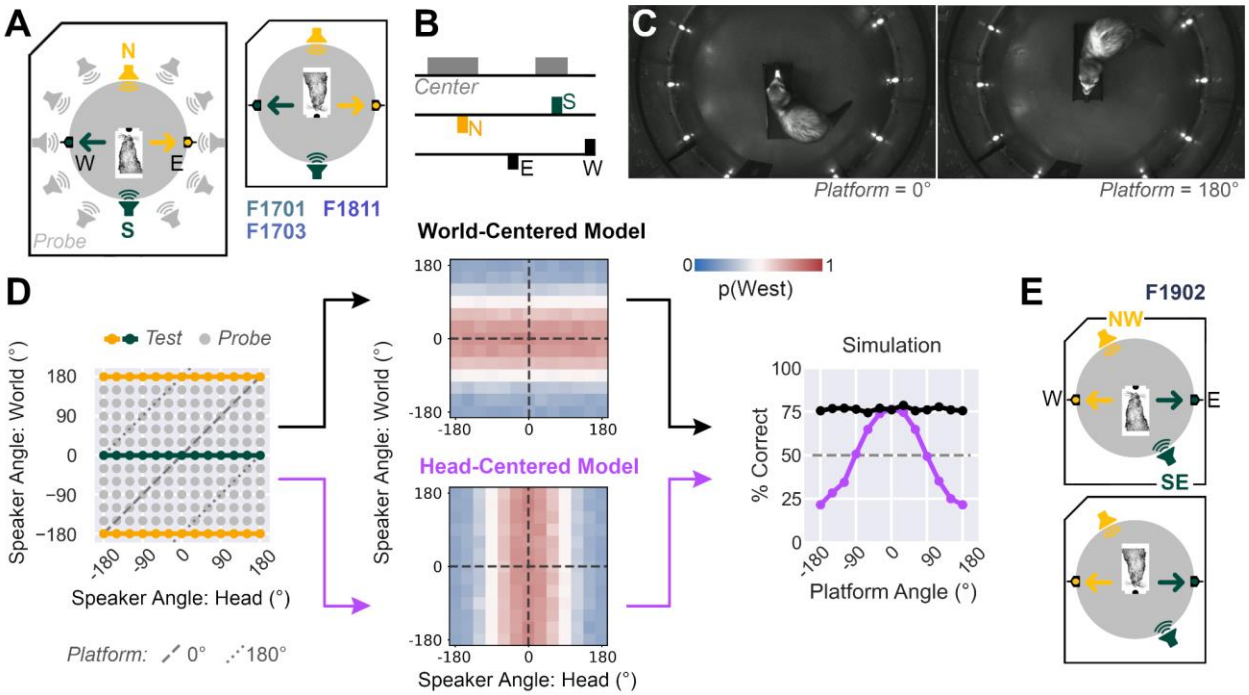



***Figure 1.*** *World-centered sound localization task.* ***A.*** *Experimental design in which ferrets approached the center of a speaker ring to initiate presentation of a 250ms broadband noise burst from a speaker either at the North or South of the arena (yellow/green), or later from probe speakers around the remainder of the arena (grey). Arrows show the position of correct responses, which remained constant as the central platform from which animals initiated sounds was rotated. F-numbers (F1701 etc.) refer to ferrets trained in the North-South discrimination.* ***B.*** *Timeline showing completion of two trials in which animals were required to hold at the center of the chamber during stimulus presentation.* ***C.*** *Screenshots showing a ferret performing the task with two head directions (top: facing north [0°], bottom: facing south [180°]).* ***D.*** *Dissociation of speaker angles in head and world-centered space as platform angle is rotated, with only world-centered sound location being informative about the correct response. Probe sounds (grey) were also presented on a random subset (10%) of trials. Simulations using models that responded based on sound angle in specific coordinate frames demonstrate that this task can be performed accurately at all platform angles when using sound angle in the world (black), but not when using sound angle relative to the head (purple). Simulated performance shows results of assessment with test sounds only. Dashed line shows chance performance; all data are shown wrapped to ±180°.* ***E.*** *Variant of the task for an additional ferret (F1902) in which we altered the world-centered locations to be associated with each response.*

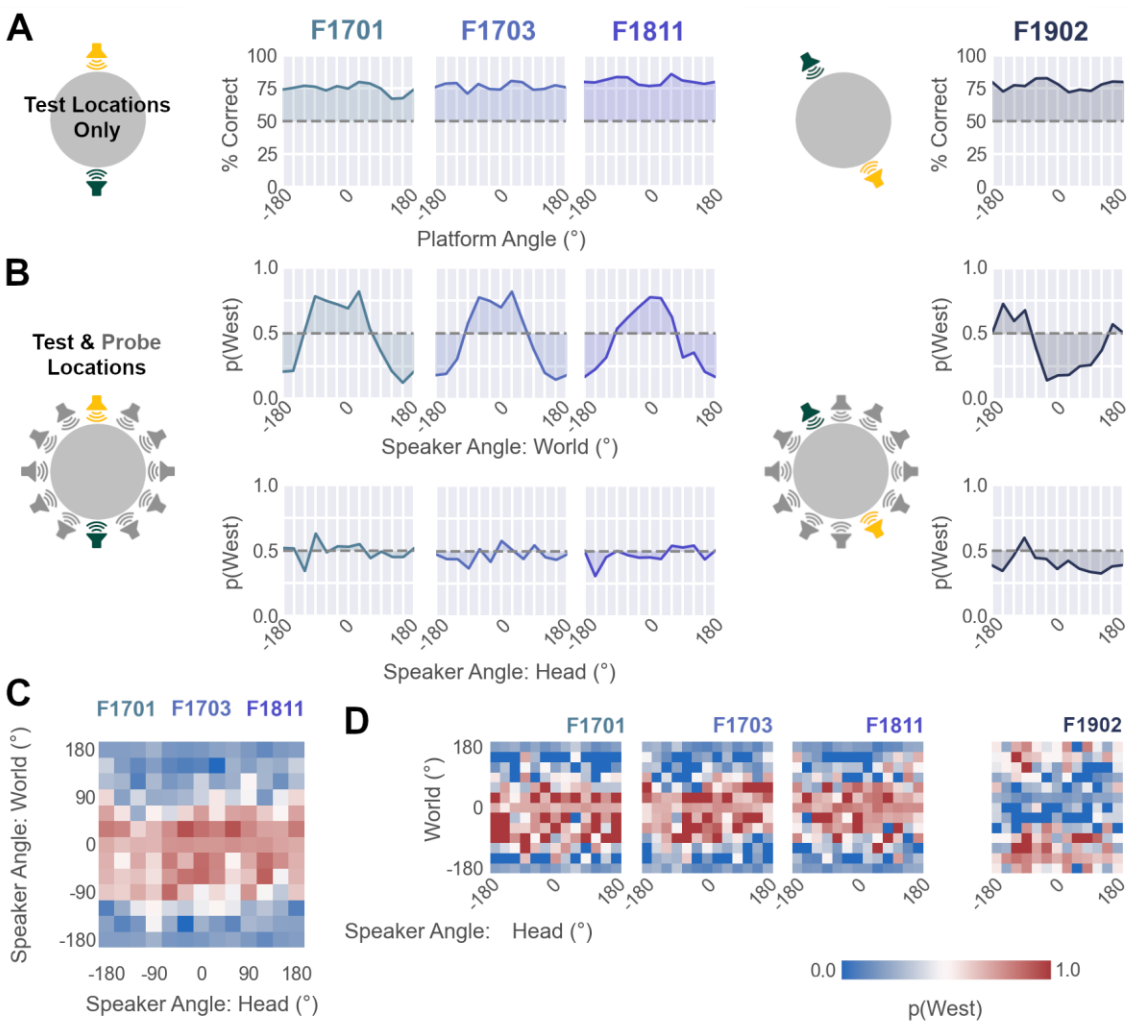
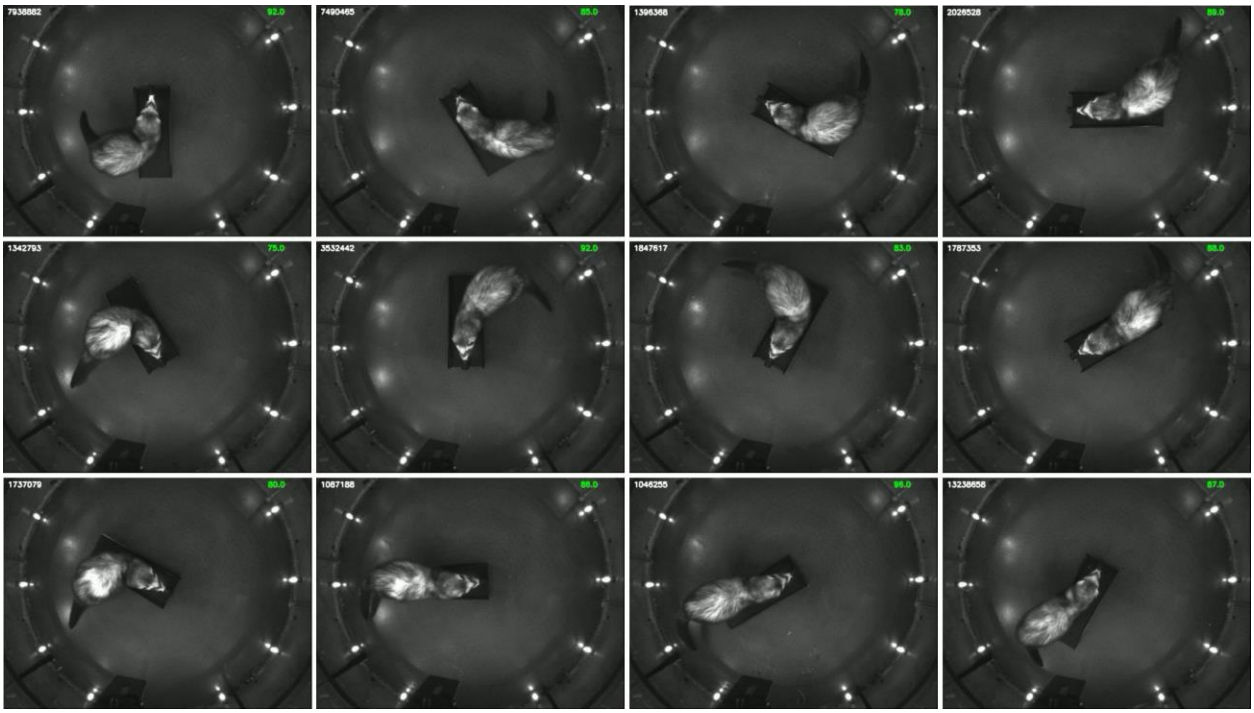
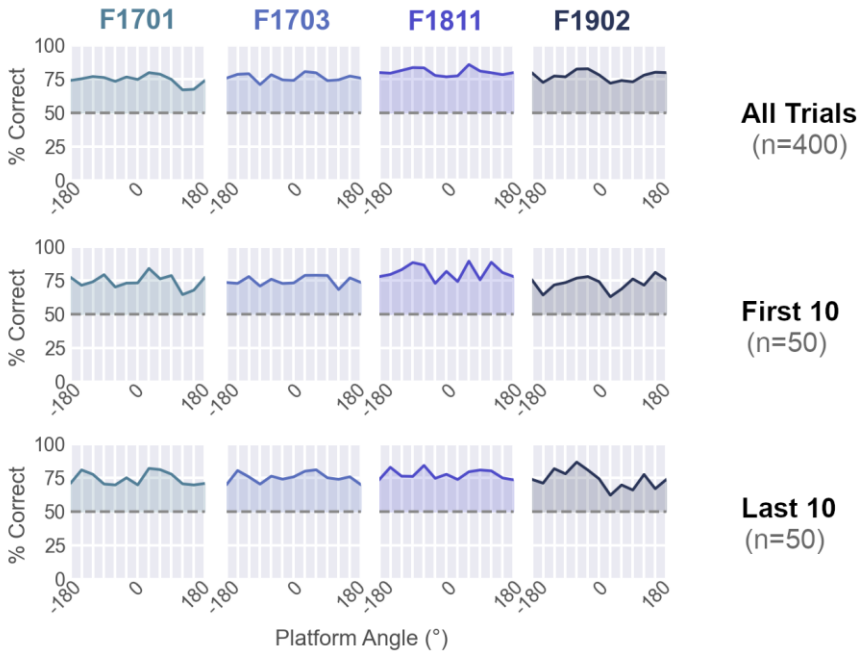



***Figure 2.*** *World-centered sound localization behavior.* ***A.*** *Performance discriminating sounds at trained locations for each ferret as a function of platform angle (n=400 trials per angle). Data shown as mean percent correct across bootstrap resampling (n=100 iterations). Dashed lines show chance performance (50%). Cartoons show the training configurations (either North vs. South [F1701, F1703, F1811], or South-East vs. North-West [F1902]).* ***B.*** *Probability of making 'West' responses to test and probe sounds as a function of sound angle in the world, or relative to the head (n=36 trials per angle).* ***C-D.*** *Response probability as a joint function of head and world-centered sound angle, shown for individual ferrets (**C**, n =432 trials over 144 locations) and when grouping across the three animals with the same training (**D**, n = 1296 trials).*

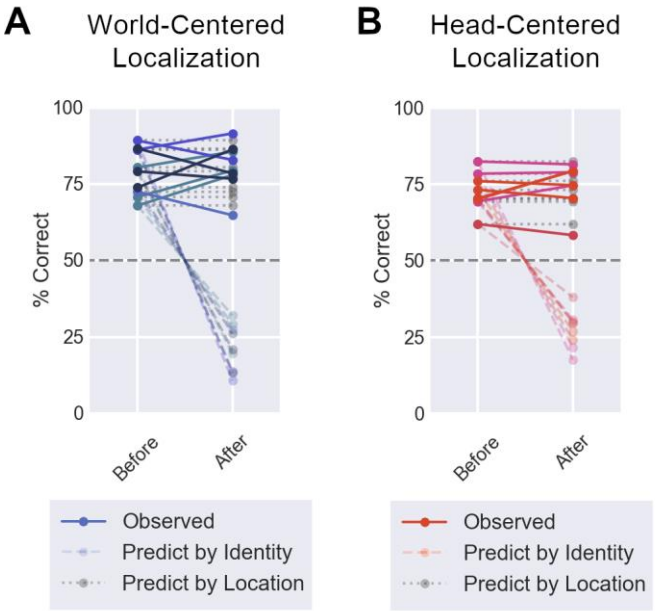


***Supplementary Figure 1:*** *Images of one animal (F1701) performing the task at each platform rotation.*




***Supplementary Figure 2:*** *Performance discriminating sounds at trained locations for each ferret as a function of platform angle. Data shown as mean percent correct across bootstrap resampling (100 iterations) when trials were subsampled from either all trials in a test session,*

*or the first or last 10 trials of each session after platform rotation. Dashed line shows chance performance (50%). Sample sizes (n) refer to the number of trials used to calculate performance at each platform angle, and was constrained by the number of sessions on which platform angle was changed.*




***Supplementary Figure 3:*** *Performance on sessions immediately before and after swapping the speakers at test locations during world-centered (**A**) and head-centered (**B**) localization. Observed data (full lines) is compared to predictions made if animals were responding based on speaker identity (dashed lines) or sound location (dotted grey lines). Predictions based on speaker identity were made by subtracting performance before swap from 100%. Predictions based on sound location were simply the same performance before and after swap.*

## Generalization of world-centered space

Discrimination of sounds based on world-centered sound location suggests that ferrets have the ability to map sounds into their environment. To determine if our animals experienced a continuous world-centered sound space, rather than learning arbitrary associations, we also measured ferrets' responses to probe sounds presented on a random subset (10%) of trials from speakers at untrained angles (n=10) around the test arena (**Fig. 1A** and **1D**). Probe testing allowed us to assess how animals generalized sound location without training, and to contrast the association between behavioral responses and sound location in head and world-centered spaces.

Probe testing revealed that the probability of each ferret making a specific response (e.g. to visit the West response port) was a continuous function of sound angle in the world, while changes in sound angle relative to the head had no consistent effect on behavior (**Fig. 2B**). This graded pattern of responses was observed regardless of whether we trained animals to visit the West port to indicate sounds from the South (F1701, F1703 and F1811) or from the North West (F1902). We also contrasted the relative influence of head- and world-centered sound location using the joint distribution of responses (**Fig. 2C-D**). Here, the many combinations of sound angles in head and world-centered spaces (n=144), coupled with the low probability of probe sounds, meant that sample sizes for each bin were relatively small (minimum 3 trials), and so we also combined data from animals with the same task training (F1701, F1703 and F1811). The same coordinate frame-specific modulation of behavior was apparent in the joint distribution of responses, where, at both the group level (**Fig. 2C**), and for each ferret (**Fig. 2D**), behavior was more strongly influenced by the position of sounds in the world than relative to the head.

We quantified modulation in each coordinate frame by calculating the variance in response probability across sound angles in head or world-centered space; higher variance indicates greater modulation of behavior by sound angle in the respective coordinate frame. For each animal, we found larger variance associated with sound angle in world-centered than head-centered space (Variance: World vs. Head; F1701: 0.067 vs. 0.005, F1703: 0.066 vs. 0.004, F1811: 0.052 vs. 0.004, F1902: 0.043 vs. 0.007). Likewise, across animals the variance in response probability associated with sound angle in the world was again larger than variance associated with sound angle relative to the head (World = 0.056 vs. Head = 0.001). Together these results thus confirm that not only could ferrets discriminate world-centered sound locations, but that they were able to generalize the location of novel sound sources into a continuous world-centered space.

## Head-centered sound localization

To establish that ferrets could also localize sounds in head-centered space, we developed a second task that required discrimination of sound location relative to the head, irrespective of the sound's position in the world (**Fig. 3A**). The basic structure of the task was similar to the world-centered design described above, in that animals had to approach the center of a speaker ring to initiate presentation of a sound from one of two sources (**Fig. 3B**). However, here speaker location was described relative to the head (e.g. Front and Back) and response ports

were positioned on the rotating platform from which animals initiated trials (**Fig. 3C**). This meant that when the platform rotated, the ports rotated with the animal, such that the subject was always responding left or right relative to themselves, rather than at east or west locations defined by the test chamber.

As the platform rotated, we maintained the position of test sounds relative to the head by presenting stimuli from different speakers around the ring. We therefore maintained fixed sound angles relative to the head, while varying sound locations in the world (**Fig. 3D**). Our simulations confirmed that, in this design, world-centered sound location was thus uninformative about the task; whereas head-centered sound location could be used to consistently perform above chance. For two animals (F1901 and F1905; **Fig. 3A**), we trained subjects to respond to sounds from directly in front (180°) by going right, and sounds directly behind the head (0°) by going left. We also trained an additional animal (F1810; **Fig. 3E**) to respond left for sounds to the left (-90°) and right for sounds on the right (+90°) of the head.

Ferrets learned to discriminate head-centered sound location accurately across platform rotations (**Fig. 4A**). Each animal performed above chance at all platform angles (range = 69.7 to 86.5% vs. 50% chance, mean performance of each ferret: F1810 = 73.4%, F1901 = 74.6%, F1905 = 82.7%). Binomial tests comparing observed performance to chance confirmed significant differences at all platform angles in each subject (Bonferroni corrected, $p < 0.001$). Swapping speakers to assess the influence of speaker identity on behavior did not disrupt task performance (**Supplementary Fig. 3B**) and only resulted in minor changes (mean ± s.d = +1.915 ± 4.868%) that were indistinguishable from those observed when swapping speakers in the world-centered task.

Testing with probe sounds demonstrated that ferrets' behavior was strongly modulated by sound angle relative to the head, and that animals reported the location of probe stimuli using a continuous head-centered function (**Fig. 4B** and **4D**). In contrast, sound location in the world had no comparable effect on response probability. Quantifying modulation by sound angle in each coordinate system confirmed that sound angle relative to the head was the major influence on animal behavior; Variation in response probability of each animal was between 10 and 70 times larger when considering head-centered than world-centered sound location (Variance: World vs. Head; F1810: 0.003 vs. 0.043, F1901: 0.002 vs. 0.102, F1905: 0.001 vs. 0.140).

The importance of head-centered localization was also evident when considering the joint distribution of responses across animals (**Fig. 4C**). As with individual behavior, variation in responses of all animals combined was larger when considering head-centered than world-centered sound location (World = 0.000 vs. Head = 0.091). Thus, ferrets in this task reported the location of sounds as a continuous function of sound angle relative to the head, regardless of sound location in the world.

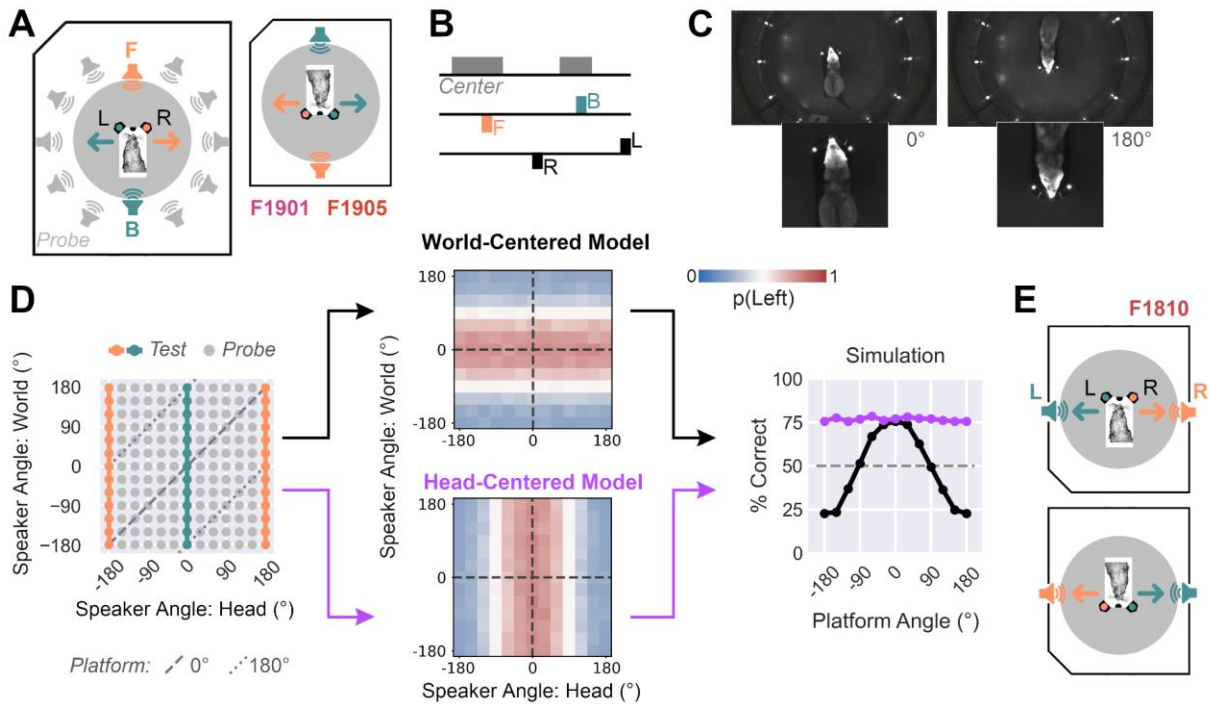



***Figure 3.*** *Head-centered sound localization task.* ***A.*** *Experimental design in which ferrets discriminate 250ms broadband noise bursts from a speaker either at the Front ("F") or Back ("B") of the head, by visiting response ports either to the left ("L") or right ("R") of the head. Arrows show the direction for correct responses; F-numbers (e.g. F1901 etc.) refer to animals trained in the Front-Back discrimination.* ***B.*** *Timeline showing completion of two trials in which animals were required to hold at the center of the chamber during stimulus presentation.* ***C.*** *Screenshots showing a ferret performing the task with two head directions (facing north [0°] or south [180°]).* ***D.*** *Dissociation of speaker angles in head and world-centered space as platform angle was rotated, with only head-centered sound location being informative about the correct response. Probe sounds (grey) were also presented on a random subset (10%) of trials. Simulations using models that responded based on sound angle relative to the head (purple) performed this task accurately at all platform angles, but not when using models based on sound angle in the world (black). Simulated performance shows results of assessment with test sounds only. Dashed line shows chance performance; all data are shown wrapped to ±180°.* ***E.*** *Variant of the task in which we altered the head-centered locations associated with each response.*

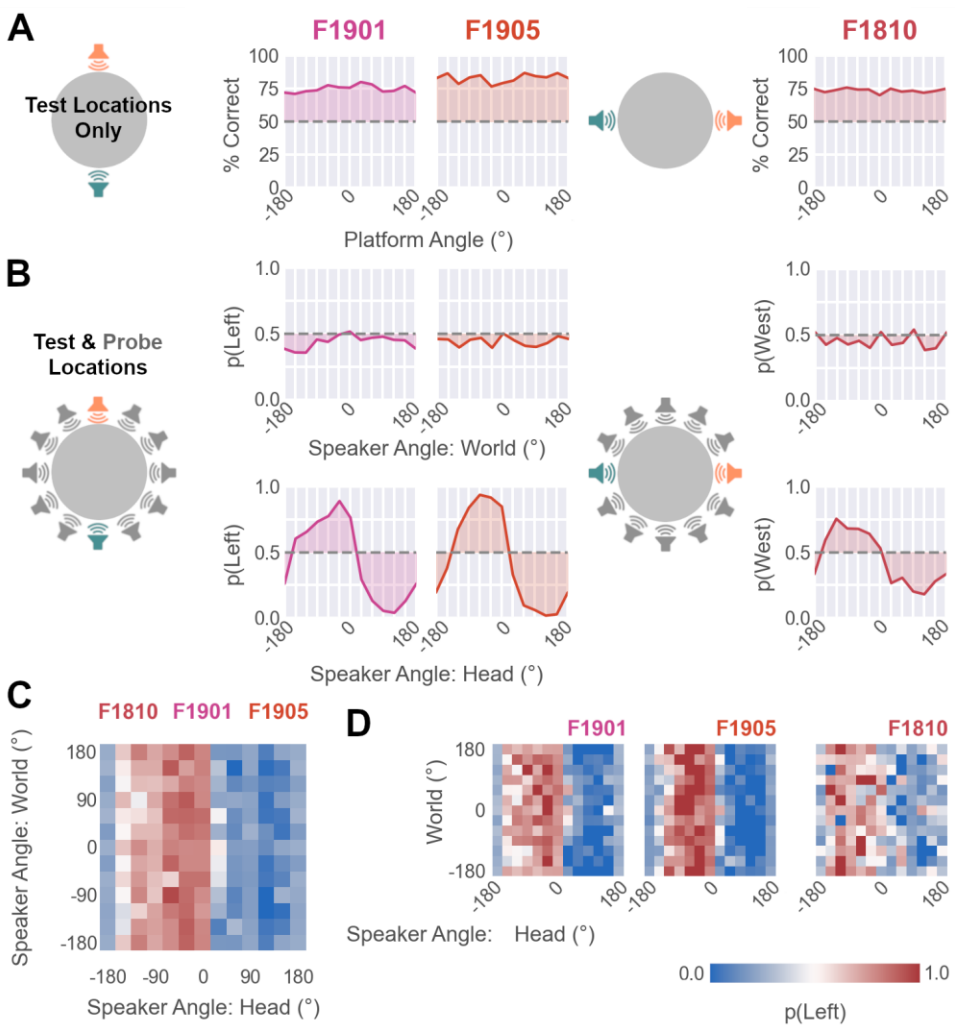



***Figure 4.*** *Head-centered sound localization behavior.* ***A.*** *Performance discriminating sounds at trained locations for each ferret as a function of platform angle (n = 400 trials per angle). Data shown as mean percent correct across bootstrap resampling (n=100 iterations). Dashed lines show chance performance (50%). Cartoons show the training configurations (either Front vs. Back [F1901 etc.], or Left vs. Right [F1811]).* ***B.*** *Probability of making 'Left' responses to test and probe sounds as a function of sound angle in the world, or relative to the head (n=36 trials per angle).* ***C-D.*** *Response probability as a joint function of head and world-centered sound angle, shown for individual animals (****C,*** *n=432 trials over 144 locations) and when grouping across animals (****D****, n=1296 trials).*

## Modelling behavior

To formally capture ferrets' sound localization performance in world or head-centered space, we fitted sinusoidal models to animal behavior. These models were of the same definition as those used in simulations of head and world-centered systems (**Fig. 1D** and **3D**), in which an activation value ($z$) that may determine the probability of a particular response (i.e. to go to the Left or West port) was based on sound angle ($\theta$) in a specific coordinate system:

Head-centered model: $$z = \beta_0 + \beta_1 \cos(\theta_{\text{HEAD}} - \beta_2)$$

World-centered model: $$z = \beta_0 + \beta_1 \cos(\theta_{\text{WORLD}} - \beta_2)$$

In abstract terms, the model parameters affected the vertical offset ($\beta_0$), amplitude ($\beta_1$) and horizontal offset ($\beta_2$) of the activation function (**Fig 5A**), but these parameters may also have biological interpretations: Vertical offset may reflect a listeners' bias to make a particular response, amplitude captures how strongly behavior varies with sound location in the relevant coordinate frame, and horizontal offset indicates the sound location at which a response is most likely. As there were only two responses in the tasks, we defined the activation value for the alternate response ($z'$)(i.e. to go Right or East) as:

$$z' = 1 - z$$

We used the softmax function to convert activation values for each response into probabilities, with the inverse temperature parameter ($\beta_{\text{inv. temperature}}$) reflecting the extent to which the decision making of the model or animal was deterministic ($\beta \rightarrow \infty$) or random ($\beta \rightarrow 0$).

For each ferret, we fitted head and world-centered models to single trial behavioral responses. Data was initially split into train and test sets for cross-validation (k = 20 folds), with fitting then performed on a fixed number of trials (n=1440) drawn with replacement from the training dataset, with equal numbers of trials for each combination of sound angle in head and world-centered space. Fitting was performed by minimizing the negative log likelihood between the responses of animal and model, with 20 repeats of the fitting procedure, and subsequent examination of the convergence of model parameters (**Fig. 5B**).

For those parameters that gave lowest negative log likelihood for each fold, we evaluated models by generating responses to stimuli in the held-out test set and measuring the accuracy with which we could predict animal behavior on each trial (**Fig. 5C**). For each ferret trained in world-centered localization, models using sound angle in the world better predicted held-out behavior (performance range: 59.4 to 70.4% correct) than models using head-centered sound angle (range: 46.5 to 55.0% correct). Conversely, for each ferret trained in head-centered localization, models using sound angle relative to the head performed better (range: 58.0 to 72.7% correct) than models using world-centered sound angle (range: 47.5 to 53.6% correct). Thus, for each task, we found that the best predictive model of animal behavior was the model based on sound angle in the task-relevant coordinate system.

We also visualized behavior of models using simulations of response to sound at all locations that could be directly compared with animal behavior (**Fig. 5D**). Simulations illustrated that our models captured the same clear modulation of responses by sound location in the task relevant dimension that was shown by ferrets. Moreover, changes in model parameters successfully replicated the variations in behavior that arose, for example, by changing the location of test sounds in world-centered localization between subjects (e.g. F1701 vs. F1902). It was also clear that models based on sound location in the irrelevant coordinate system corresponded poorly to animal behavior, even though trained and tested on matched data. This poor correspondence between model and behavior could be linked to the broad distribution of inverse temperature coefficients observed (**Fig. 5B**) that ultimately resulted in low coefficient values being selected for softmax decision making in the examples shown in Fig. 5D (See **Supplementary Table 1** for parameter values). These parameter observations may reflect a difficulty for the model in converging on an activation function in which responses could be confidently made, and thus indirectly reflect the way in which ferrets abstracted across sound locations in the task-irrelevant space.

## Coordinate frames of action

We designed our sound localization tasks such that animals made behavioral responses in the same reference frame as they were required to judge sound location. In world-centered localization, animals responded at East and West ports that had fixed locations in the world across rotations of the central platform. Likewise, in head-centered localization, animals responded at Left and Right ports that rotated with the platform and remained at the same position relative to the head during sound presentation (**Supplementary Fig. 4A**). However, when comparing sound localization behaviors, the coordinate frame of *response* may be as important as that of the sound. Specifically, we found that matching of stimulus and response coordinate frames was critical for learning tasks, as when we attempted to train ferrets to report sound location in one reference frame using response ports in the other coordinate system, animals made systematic mistakes in favor of the response space.

We measured the ability of two ferrets to report sound location in an alternative response space as platform angle varied: One ferret (F1806) was asked to discriminate Front and Back speakers at East and West ports. The other ferret (F1811) was asked to discriminate between North and South speakers using Left and Right response ports. In both cases, animals learned the initial discrimination at the platform angle used during training (0° for F1806 and 90° for F1811) and performed well with small (±60°) variations in platform angle (**Supplementary Fig. 4B**). However, performance of both animals collapsed when the platform was rotated by more than 90°, indicating that animals could not generalize the discrimination across all conditions.

Examining the association between behavioral response and sound angle in head and world-centered spaces (**Supplementary Fig. 4C**), each ferret showed clear modulation of behavior in the coordinate system of response. That is, the subject trained to use East/West ports (F1806) responded to sounds as a continuous function of sound angle in the world, even though the aim was to train discrimination of Front vs. Back locations in head-centered space. Conversely, the animal trained to use Right/Left ports (F1811) responded to sounds as a function of head-

centered sound angle, even though the aim was to train discrimination of North/South sound locations in the world. Here, we did not use probe sounds to fully capture sound localization behavior; however the results nonetheless indicate that the coordinate system in which action is organized is a key part of sound localization, and emphasize the importance of sensorimotor transformations in spatial hearing.

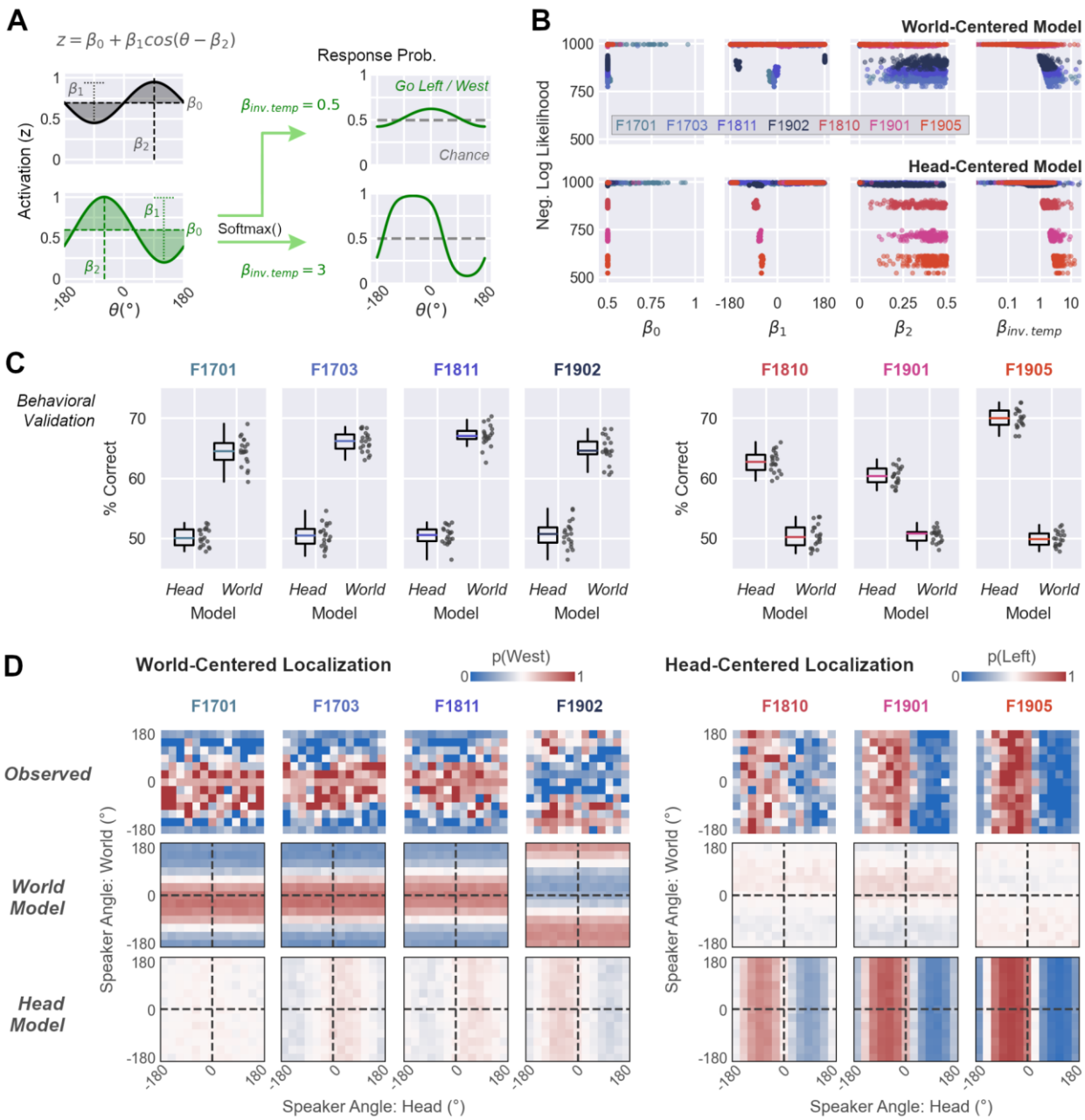


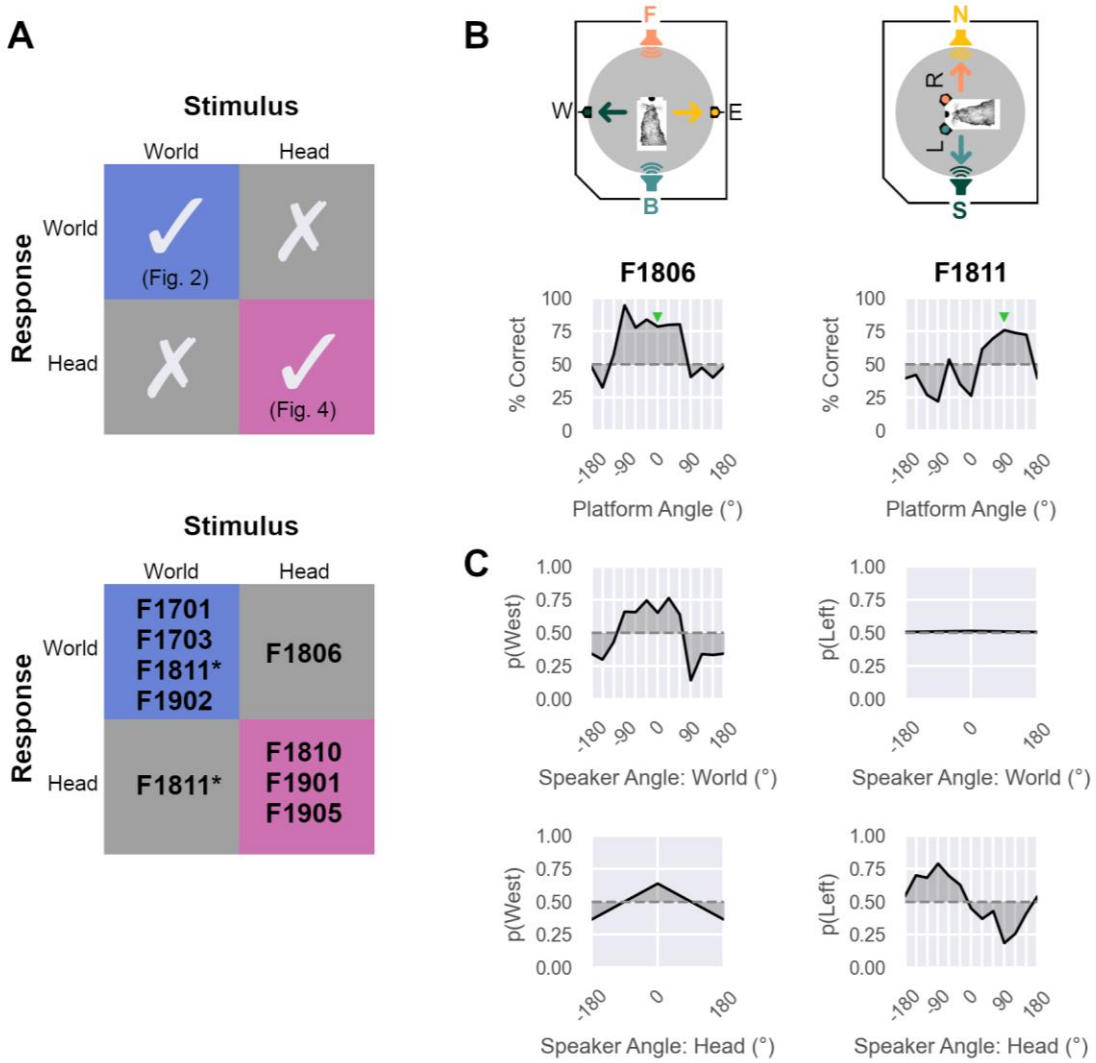

***Figure 5.*** *Modelling ferret behavior.* ***A.*** *Model design in which activation values (z) associated with a behavioral response (e.g. to go Left) was computed as a cosine function of sound angle in head or world-centered space (θ), with free parameters affecting the amplitude ($\beta_1$), vertical*

($\beta_0$) *and horizontal position* ($\beta_2$) *of the activation function. The activation for the alternative action (e.g. to go Right) was calculated as* $1\text{-}z$ *and probabilities for the two responses computed using the softmax function, with inverse temperature as a free parameter.* ***B.*** *Parameter estimates fitted to individual ferret behavior for models using sound angle relative to the head or in the world, as a function of negative log likelihood.* ***C.*** *Model validation performance predicting single trial behavior of each ferret from held-out data (20-fold cross-validation). Box plots show median and interquartile range (IQR); individual data points show validation performance for each fold.* ***D.*** *Comparison of animal behavior with simulated performance of head and world-centered models that were fit with lowest negative log likelihoods. Parameter values for each model are given in Supplementary Table 1.*

***Supplementary Table 1.*** *Parameter values for models shown in Fig. 5D.*

| ***Ferret*** | ***Model*** ($\theta$) *(sound angle w.r.t.)* | **Vertical offset** ($\beta_0$) | **Amplitude** ($\beta_1$) | **Horizontal offset** ($\beta_2$) | ***Inverse Temperature*** |
|---|---|---|---|---|---|
| *1701* | *World* | *0.502* | *0.276* | *-27.1* | *2.983* |
| | *Head* | *0.500* | *0.106* | *-12.8* | *0.366* |
| *1703* | *World* | *0.500* | *0.216* | *-12.4* | *4.115* |
| | *Head* | *0.500* | *0.293* | *37.3* | *0.535* |
| *1811* | *World* | *0.500* | *0.364* | *-1.40* | *2.014* |
| | *Head* | *0.500* | *0.337* | *73.9* | *0.386* |
| *1902* | *World* | *0.500* | *0.350* | *-147.7* | *1.844* |
| | *Head* | *0.500* | *0.165* | *-59.1* | *1.308* |
| *1810* | *World* | *0.500* | *0.112* | *62.2* | *0.846* |
| | *Head* | *0.500* | *0.364* | *-82.7* | *1.788* |
| *1901* | *World* | *0.500* | *0.314* | *42.8* | *0.550* |
| | *Head* | *0.500* | *0.419* | *-70.4* | *2.677* |
| *1905* | *World* | *0.500* | *0.336* | *-125.7* | *0.187* |
| | *Head* | *0.500* | *0.395* | *-60.9* | *4.091* |

***Supplementary Figure 4:*** *Interactions between stimulus and response coordinate frames.* ***A.*** *Two-way space in which the coordinate systems in which sounds and behavioral responses are independent. Fig 2 (main text) shows that animals can report the location of sounds in world-centered space by responding at ports with fixed locations in the world. Fig. 4 (main text) shows that animals can report the location of sounds in head-centered space by responding at head-centered response ports. However, it is also possible to mismatch the coordinate systems of stimulus and response, which we tested in two animals (F1806 and F1811*). Note that the ability of F1811* to discriminate world-centered sound location was tested when using both world-centered and head-centered tasks.* ***B-C.*** *Performance of one ferret (F1806) asked to discriminate sounds in head-centered space (Front vs. Back) by responding at world-centered (West and East) response ports, and one ferret (F1811) tested with sounds in world-centered space (North vs. South) via head-centered response (Left and Right) ports. Green triangles (top row) indicate platform orientation during the initial training phase, before animals were subsequently tested at different platform rotations. These animals were not presented with sounds from probe locations.*



# Discussion

Here, we have demonstrated for the first time that non-human listeners (ferrets) can report the location of sounds in multiple coordinate systems centered either on the listener's head or the external world. In both tasks, we successfully dissociated the influence of sound location in the two coordinate systems, demonstrating unambiguously that animals discriminating sound locations in the world were not guided by sound location relative to the head, and vice versa. Using ferrets' responses to probe sounds at untrained locations, we extended our results from discrimination of two points in space, to reveal general functions with which animals localized sounds. Together these results confirm that, like humans, ferrets can access continuous representations of sound location in both head and world-centered space.

Our data show that ferrets can be trained to report sound location in head and world-centered space, but so far do not indicate whether the observed behavior is simply learnt, or reflects the subject's natural sound perception. Clearer insight on this issue could be gained by observing task performance when the opportunity for learning is absent. Such conditions arise on the first trial after rotating the platform by 180°, where the animal has yet to receive feedback about which coordinate system is task relevant. Our data are limited as we did not conduct these switch tests cleanly; instead we introduced small platform rotations at first to gauge their impact on animal behavior, which turned out to be minimal. However, this gradual introduction also gave animals the opportunity to learn about the task and thus prevented a clear test of the animals' naive response. Future tests of world and head-centered sound localization should therefore build on the current results by conducting one-shot tests of spatial generalization to gain a clearer picture into the coordinate frames animals inherently use without behavioral training.

A notable feature of head-centered localization was the strong lateralization in response probabilities of animals trained to discriminate front vs. back sounds (F1901 and F1905). That is to say, the curves showing the association between head-centered sound angle and response probability in **Fig. 4B** are shifted leftwards, so that the animal is most likely to respond to sounds on the left by turning left (and vice versa on the right), even when trained to report sound in front at the left port. This behavior may have arisen because these animals slightly offset their head angle relative to the platform when initiating sounds: Post-hoc video tracking revealed that this offset was small but statistically greater than zero (**Supplementary Fig. 5**: median = 2.22°, n = 87 trials, Wilcoxon rank sum test, $p < 0.001$) and aligned so that the rear speaker (to which animals responded by going left) tended to fall more often on the left side of the midline. Likewise, the front speaker (to which animals responded by going right) tended to fall more often on the right side. Across thousands of trials with test sounds, this small bias may have reinforced ferrets' natural inclination to orient towards speakers.

Access to multiple sound spaces raises the question of how flexible spatial representations are: Can ferrets switch rapidly between coordinate systems, as humans do when shifting between egocentric and allocentric descriptions of object location, or does switching require many trials for longer-term learning to take place? Cueing animals to locate sounds in specific spaces on

each trial (Stoet and Snyder, 2003) offers one approach to address these questions in future work.

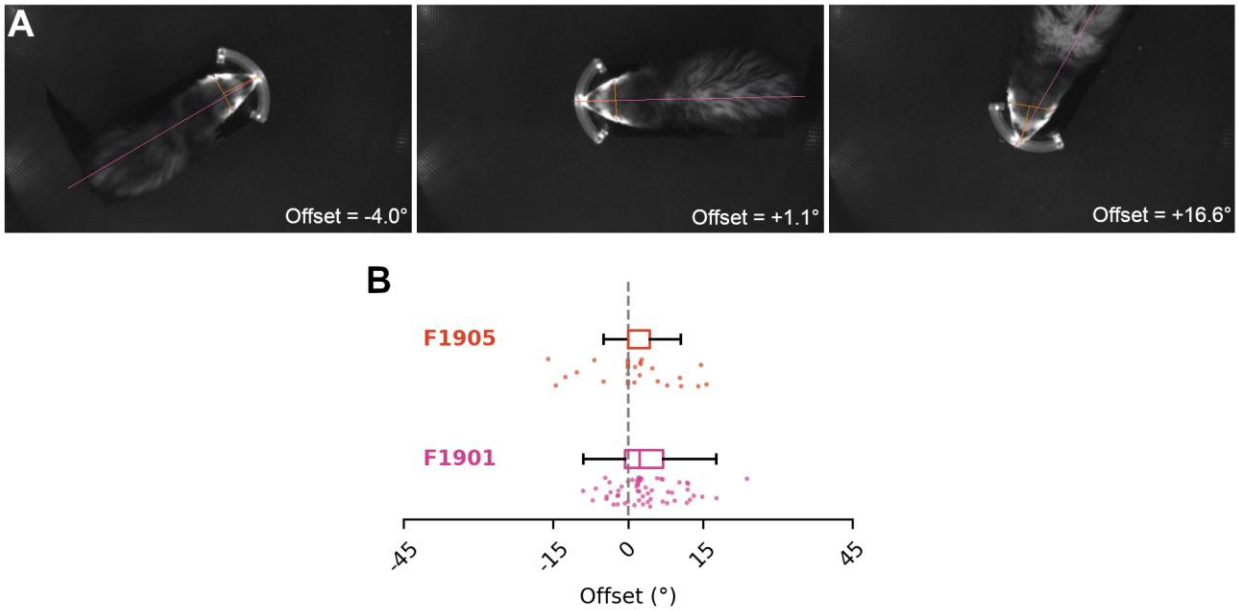
Although we have shown that ferrets can report the location of sounds in the world across changes in head pose, it is unclear what cues animals use to construct representations of the world itself. Key candidates for mapping include the visual and somatosensory landmarks involved in navigation, and integration of head direction into sensory processing in the hippocampus, entorhinal and retrosplenial cortex (Alexander and Nitz, 2015; Fyhn et al., 2007), and similar features may also be critical for mapping sounds into the environment. Although we did not manipulate salient visual landmarks to study remapping, ferrets clearly knew the position of key features of the environment; most obviously the entrance to the arena, at which they would wait at the end of each session. By systematically varying environments (for example by having a moveable door or rotating arena), it may be possible to induce predictable shifts in world-centered sound localization that reveal the key anchors that ferrets use.

An emerging question in the study of spatial hearing is how far sound location can be dissociated in egocentric and allocentric (world-centered) spaces. Egocentric coordinate frames defined by the head and eye are typically dependent; the eye cannot rotate fully within the head, nor can the head move freely without indirectly moving the eye. In contrast, egocentric and allocentric spaces can be independent; a listener can rotate their head without affecting the position of a sound source in the environment. Here we demonstrate this independence at the behavioral level; ferrets can utilise sound angle in one coordinate frame while generalizing across the other. This dissociation mirrors that observed at the neural level, where tuning preferences of neurons (sampled across uniform distributions of head directions) in world and head-centered spaces can be distinguished (Town et al., 2017).

Our results tally with a series of observations in other species; cats can update spatial judgements of sound location with proprioceptive and motor information during ongoing head and pinna movements (Ruhland et al., 2015) and gerbils can identify a sound source based on it’s position in the world (Amaro et al., 2021; Ferreiro et al., 2020). Our results extend these findings by fully dissociating sound localization in head and world-centered space to reveal that ferrets can access continuous representations of sound location in the world. More broadly, and consistent with the egocentric coordinate frame transformations observed across the primate brain (Caruso et al., 2021; Werner-Reiss et al., 2003), our data contribute to a growing view that reconfiguration of sound space is a fundamental function of the auditory system that has clear and observable relevance for behavior.

***Supplementary Figure 5:*** *Measurement of head alignment during stimulus presentation.*

***A.*** *Three example images in which we estimated the offset between platform angle and head direction. For each sample image, we marked the position of the left and right ears, as well as the tip of the snout. From these landmarks, we estimated the center position and midline of the head, and then measured the offset between head direction and the orientation of the platform. Positive offset values indicate the head was offset by counter-clockwise angles relative to the platform (such that a speaker directly in front of the platform would move to the right of the animal's midline). We repeated the estimation procedure for images taken on randomly selected trials with varying platform angles.* ***B.*** *Distribution of offset values across trials (n=87) for animals trained to discriminate front and back sounds in head-centered space (F1901 [n=57] and F1905 [n=30]). In both cases, median offsets were significantly greater than zero (Wilcoxon rank sum, $p < 0.001$). Data shown as box plots indicating median and interquartile range, with individual trials shown as separate markers.*



# Methods

## Animals

Subjects were eight pigmented female ferrets (0.5 to 3 years old, weighing 600-1100g) maintained in groups of two or more ferrets in enriched housing conditions. Ferrets were trained either to report sound location in head or world-centered coordinates in return for water rewards. Water received during the task was part of a daily minimum (60 ml/kg body weight) as part of a water regulation schedule in which animals also received supplementary wet mash made from water and ground high-protein pellets. Animals were water-regulated on a maximum of 50% of days, and were trained / tested in series of morning and afternoon sessions on consecutive weekdays, with rest weeks without testing at frequent intervals. The weight and water consumption of all animals was measured throughout the experiment. Regular otoscopic examinations were made to ensure the cleanliness and health of ferrets' ears.

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 License 70/7267) and in accordance with the Animals (Scientific Procedures) Act 1986.

## Experimental Apparatus

Testing was conducted in a double-walled sound proof acoustic chamber (IAC Acoustics: 1.6m wide, 1.6m long and 1.1 m height) dimly illuminated using white LED striplights. Within the chamber, ferrets performed psychoacoustic tasks inside a custom-built, circular behavioral arena (0.5m radius) covered by plastic mesh to prevent animals escaping. The arena was surrounded by a ring of twelve speakers (Visaton FRS8) positioned at 30° intervals, 55 cm from the arena center. Below each speaker were also positioned lick ports that could detect the presence of animals via infra-red reflectance sensors (Optek OPB710), and deliver water via solenoid control (Flo-Control, N-series, Valeader, Cambridge, UK). Lick ports were also equipped with white LEDs that could present visual stimuli to guide animals to rewards during the early stages of training. Animals were monitored using an infra-red camera (Intel Realsense D435) suspended above the test chamber (Fig. 1C).

At the center of the arena was a 3D printed platform from which animals initiated trials. The platform consisted of a 30-cm long section on which ferrets could align themselves, and an array of three lick ports (center, left and right) that detected nose-pokes and channeled water delivery. The platform was offset such that the center of the ferret's head was at the center of the test arena (and thus surrounding speaker ring) when visiting the center port on the platform. The platform itself could be rotated at 30° intervals about the arena center, allowing us to orient animals throughout 360° within the test arena. Platform rotation had to be performed manually (by screwing/unscrewing mounts in the arena floor) between test sessions.

Visual landmarks within the test environment were limited. Each wall of the sound-proof chamber was lined with convoluted acoustic foam that provided a relatively homogenous visual

background. Other landmarks included the amorphous speaker wiring and two black transceivers for recording neural activity in other projects. However, the doors to the test arena and chamber provided salient cues that animals used to orient themselves with respect to the environment; (e.g. ferrets would wait at the arena door to exit at the end of testing).

## Task Design

Animals in both tasks were trained in a two-choice design to discriminate between a pair of sound sources from the speaker ring (e.g. North and South, or Front and Back). On each trial, the animal would initiate presentation of a single 250 ms broadband noise bursts (60 dB SPL, generated afresh on each trial - i.e. not frozen; for F1902 sound level was increased to 63 dB SPL) to which she could then respond.

Sound presentation required that the ferret approach the central lick port on the platform and hold her head at the center of the arena in order for a sound to be presented. To successfully initiate the trial, the subject was required to hold at the port for a variable delay (from 200 to 700 ms), as well as the full duration of the sound. This hold period ensured that animals had a stationary head position during sound presentation (Dunn et al., 2021) and thus could not exploit dynamic head-centered localization cues during the world-centered task. To encourage subjects to hold at the center port, rewards were delivered at this location on randomly allocated trials with a variable probability (typically 1 to 10% of trials). If an animal failed to wait for the full hold time, the trial was not initiated and the animal was required to release and re-engage the center port to try again.

Following stimulus presentation, animals could respond by visiting a lick port to the left/right of the head (head-centered localization) or the east/west of the test arena (world-centered localization). Correct responses were determined by the task rules (see below) and were rewarded with water; errors were signaled by presentation of a brief tone (500 Hz, 100 ms) and led to a short timeout (between 1 and 5 seconds) in which animals could not initiate further trials. Incorrect responses also led to correction trials, on which the same stimulus was presented. On a small proportion of trials (~10%), probe sounds were presented from untrained locations; responses to probe sounds were always rewarded. Animals were required to respond within a set time window (5 minutes) however animals rarely failed to respond, except when the ferret lost interest in performing the task, at which point the session was ended.

Although testing was performed in a sound-proof chamber, we also presented a low level of background noise (45 dB SPL) from all 12 speakers continuously throughout each session to mask any variations in room noise.

## Training

We initially trained animals using a typical approach-to-target sound localization task. Animals were first acclimatized to the test arena and then trained to associate lick ports with water. Training took place with the platform facing the same direction (North), with the exceptions

F1810 (head-centered task trained facing West) and F1811 (when testing discrimination of world-centered sounds using head-centered response spouts, Supplementary Fig. 4).

### World-Centered Task

We then presented subjects with repeating colocalised audiovisual stimuli (the noise burst, accompanied by a white LED with an inter-stimulus interval of between 100 and 250 ms) from the east / west response port locations surrounding the edge of the arena. Ferrets typically learn quickly to approach such stimuli in return for water rewards; initially responses at either port were rewarded, however error trials were introduced once animals had established a reliable pattern of initiating stimuli at the center platform and visiting response ports. The timeout duration following error trials was initially set to zero, and increased gradually as animals performed more trials with training. Through training, we also gradually increased the time animals were required to hold at the center platform before stimulus presentation.

Once the animal was accurately performing the baseline audiovisual localization, we progressively shifted the speaker presenting sounds away from the (e.g. East or West) response port to the final trained location (North or South) over a series of weeks. Over the same period, we also (i) lowered the LED intensity at the response port until it was completely absent and no visual stimulus was presented and (ii) reduced the number of stimulus repetitions to one. By the end of this stage, the animal was responding accurately to a single auditory stimulus (250 ms broadband noise). We considered animals to be fully trained and ready for testing if they could maintain good performance (typically ≥ 70%) under these conditions, over multiple days.

### Head-Centered Task

Training to discriminate sounds based on head-centered location proceeded using the same general strategy as described above for the world-centered task. However, rather than responding at east / west response ports around the edge of the arena, subjects responded at left / right response ports placed on the central platform.

## Testing

Once animals had successfully learned to discriminate the training pair of locations, we began rotating the central platform at which trials were initiated. Platform rotations were initially made at small angles (e.g. 30°) to ensure that animals could continue to initiate trials successfully, and then broadened to larger angles until the full 180° rotation was achieved. Animals were then tested at all platform angles (30° intervals, 360° range) in a pseudorandom order that aimed to ensure all directions were tested on similar numbers of sessions (with the exception of the initial training orientation). Note that here, the platform was manually rotated between behavioral test sessions, when the subject was not in the test chamber, and thus on each session, a subject completed many trials (typically 30 - 100 in world-centered localization, or 50 to 300 in head-centered localization) with the same platform rotation.

### Probe Testing

To determine how animals thought about sound space beyond the locations of the two test sound sources, we also presented probe sounds from the remaining ten speakers in the ring that surrounded the arena. To avoid familiarizing animals to the location of probe sounds, or eroding the subject's discrimination of test sounds, we only presented probe sounds on a maximum of 10% of trials in any session. Occurrence of probe trials and speaker location on each probe was pseudorandom, but always excluded the first 10 ten trials of each session that were reserved for test sound locations. Either response to a probe sound was rewarded.

### Speaker Swaps

To exclude the possibility that world-centered discrimination of sound location was driven by any unknown acoustic properties of sound sources (e.g. notches in spectral output that we could not detect) speaker swaps were performed. This involved physical disconnection of two speakers from the stimulus generation hardware, with each speaker being reconnected in the location and to the input connections of the other.

## Data Analysis

### Simulations

We modelled spatial modulation of a listener's responses to sounds in a specific coordinate frame using a sinusoidal function with three parameters that mirrored subject's response bias (vertical shift: $\beta_0$), modulation depth (amplitude: $\beta_1$) and preferred location (horizontal shift: $\beta_2$) as a function of sound angle in head or world-centered space ($\theta$):

Head-centered model: $$z = \beta_0 + \beta_1 \cos(\theta_{\text{HEAD}} - \beta_2)$$

World-centered model: $$z = \beta_0 + \beta_1 \cos(\theta_{\text{WORLD}} - \beta_2)$$

Here, the response variable ($z$) reflects an activation value associated with making a response at the West or Left response port in world or head-centered tasks respectively. Activation values for the alternative response (East/Right) were defined as: $1 - z$. For the simulations shown in **Fig. 1D** and **3D**, we used the same parameter values: $\beta_0 = 0.5$, $\beta_1 = 0.3$ and $\beta_2 = 0$ to obtain activation values for both head-centered and world-centered models.

To obtain performance metrics (percent correct), we simulated presentation of stimuli from all test locations that were used in experiments with ferrets. For each stimulus condition, we converted activation values into response probabilities using the softmax function (inverse temperature = 2). Response probabilities were then used to define a multinomial distribution (NumPy)(Harris et al., 2020) from which we drew $10^3$ values, each of which represented single trial responses in simulations. We then summed the number of responses that would be correct under the rules of world-centered (**Fig. 1A**) or head-centered tasks (**Fig. 3A**). Separate simulations were run for both head and world-centered models in world and head-centered localization tasks.

### Ferret Behavior

All correction trials were excluded from the analysis.

To report overall performance as percent correct (**Fig. 2A** and **4A**), we combined data across multiple test sessions. As we had unequal sample sizes, with an oversampling of trials with the platform in its initial training orientation, and because there was individual variability in the number of trials performed by each ferret, we randomly subsampled performance on 400 trials without replacement for each animal and each platform direction. (This number was selected based on the smallest sample size in the project dataset). To ensure reliable measurements, we repeated (bootstrapped) resampling 100 times and reported the mean performance. Responses to probe sounds were not included in this analysis.

For each ferret and platform angle, we also assessed the probability of observing task performance by chance using the binomial test, where the probability of success under the null hypothesis was 0.5. Task performance for these tests was defined as the mean number of correct trials performed across bootstrap iterations, rounded to the nearest integer. The total number of trials was fixed (n=400) for all comparisons.

To report response probability as a function of sound angle in head and/or world-centered space (**Fig. 2B-D** and **4B-D**), we included responses to both test and probe sounds. As the number of combinations of possible sound locations and platform angles was large (n = 144) and the probability of a probe sound being presented was low (10%), we had potentially few trials for some data points. To ensure equal sample sizes, we again subsampled our data to measure the probability of making a particular response (to go West or Left) using bootstrap resampling, in this case with replacement (3 trials per combination of head and world-centered sound angles; 432 trials in total across all combinations).

The variance in response probability associated with sound angle in a specific coordinate system was calculated as the sum of squared differences between response probability at each sound angle ($x_\theta$) and mean response probability across sound angles ($\underline{x}$), normalized by the number of sound angles ($n-1$):

$$var = \frac{\sum (x_\theta - \bar{x})^2}{(n-1)}$$

### Behavioral Models

Models fitted to ferret behavior followed the same form as described for simulations; however each parameter ($\beta_0$, $\beta_1$, $\beta_2$ and $\beta_{\text{inv. temperature}}$ ) was treated as a free parameter that could be varied to match single trial responses. To fit models to each ferret's behavior, we used 20-fold cross validation, in which the data for a single animal was split into train and test sets on which we performed model fitting and evaluation respectively. Prior to fitting, we flattened the distribution of sound angles in head and world coordinates in the training dataset by randomly

selecting a fixed number of trials (n=10) for each unique speaker location in head and world-centered space (n=144). Across varying parameters, we minimized the negative log likelihood between training data and model output using the *fmincon* solver (Matlab, R2018b, MathWorks Inc.)(Wilson and Collins, 2019). Initial values were selected randomly within the bounds defined for each parameter (Table 1). Initialization and minimization were repeated 20 times for each fold to avoid local minima and identify the parameters that resulted in the lowest negative log likelihood.

For models using either head or world-centered sound angle, we evaluated the parameters that gave lowest negative log likelihood values on each fold. Evaluation used the sound angle in the modelled coordinate system, together with these parameters, to predict behavioral responses (i.e. whether the subject would go East/West or Left/Right) on single trials in held-out test data. Evaluation performance (**Fig. 5C**) was measured as the percentage of trials on which we correctly predicted responses.

For the simulations shown in **Fig. 5D**, we used the parameters that gave the lowest negative log likelihood across folds. We then simulated experiments in which models were presented with every combination of sound angle in head and world-centered space (n = 1000 trials per combination). We then plotted the proportion of trials on which animals made a specific response, using the same scheme that was applied to animal behavior in **Fig. 2C-D** and **4C-D**.

Table 1: Parameter boundaries for model fitting

| | **Bound** | | **Initial Distribution** |
|---|---|---|---|
| **Parameter** | **Lower** | **Upper** | |
| $\beta_0$ (vertical offset) | 0.5 | 1.0 | Uniform |
| $\beta_1$ (amplitude) | 0 | 0.5 | Uniform |
| $\beta_2$ (horizontal offset) | -180 | 180 | Uniform |
| $\beta_{\text{inv. temperature}}$ | $10^{-4}$ | 20 | Exponential |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## Data Availability

All code and data associated with the project is available at: [github.com/stephentown42/coordinate_specific_sound_localization](github.com/stephentown42/coordinate_specific_sound_localization)

## Competing Interests

No competing interests declared.

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