A general theoretical framework unifying the adaptive, transient and sustained properties of ON and OFF auditory neural responses

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Sounds are temporal stimuli decomposed into numerous elementary components by the auditory nervous system. For instance, a temporal to spectro-temporal transformation modelling the frequency decomposition performed by the cochlea is a widely adopted first processing step in today's computational models of auditory neural responses. Similarly, increments and decrements in sound intensity (i.e., of the raw waveform itself or of its spectral bands) constitute critical features of the neural code, with high behavioural significance. However, despite the growing attention of the scientific community on auditory OFF responses, their relationship with transient ON, sustained responses and adaptation remains unclear. In this context, we propose a new general model, based on a pair of linear filters, named *AdapTrans*, that captures both sustained and transient ON and OFF responses into a unifying and easy to expand framework. We demonstrate that filtering audio cochleagrams with AdapTrans permits to accurately render known properties of neural responses measured in different mammal species such as the dependence of OFF responses on the stimulus fall time and on the preceding sound duration. Furthermore, by integrating our framework into gold standard and state-of-the-art machine learning models that predict neural responses from audio stimuli, following a supervised training on a large compilation of electrophysiology datasets (ready-to-deploy PyTorch models and pre-processed datasets shared publicly), we show that AdapTrans systematically improves the prediction accuracy of estimated responses within different cortical areas of the rat and ferret auditory brain. Together, these results motivate the use of our framework for computational and systems neuroscientists willing to increase the plausibility and performances of their models of audition.

Audition | neural response modelling | deep learning | systems neuroscience

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Introduction

In signal processing, increments and decrements in the intensity of a stimulus constitute, as much as the stimulus intensity itself, valuable features to encode for further analyses. The sensory systems of numerous animal and notably mammal species exploit these intensity changes to encode sparse representations of their inputs and thereby improve their efficiency (Gjorgjieva et al., 2014). While the parallel processing of light intensity increments ('ON' signals) and decrements ('OFF' signals) along the visual pathway is now well documented (Westheimer, 2007) (Jin et al., 2008)) and actually led to the development of a new type of bio-inspired sensors (event-based cameras, see Gallego et al. (2022)), less is known about how sound intensity increments and decrements are processed by the mammal brain. Originally observed in the brainstem of bats (Suga, 1964), auditory OFF responses have since been measured along the auditory pathway in a wide variety of animal species: in the cochlea and auditory nerve (Rhode and Smith, 1985), brainstem (Henry, 1985a)(Henry, 1985b), midbrain (Kasai et al., 2012)(Akimov et al., 2017), thalamus (He, 2002), and cortex (Solyga and Barkat, 2021)(Qin et al., 2007)(Tian et al., 2013). Although less prevalent than ON responses (Li et al., 2021)(He, 2001)(Xu et al., 2014), their ubiquitous occurrence is considered to be due to both bottom-up inheritance (Kasai et al., 2012)(Kopp-Scheinpflug et al., 2018)(Bondanelli et al., 2021) as well as *de novo* generation (Solyga and Barkat, 2021)(Akimov et al., 2017), thus leading to a dual pathway (Scholl et al., 2010)(Liu et al., 2019). If only little is known about their origins, the most accepted hypothesis relies on a post-inhibitory rebound phenomenon due to ionic mechanisms ((Takahashi et al., 2004)(Kopp-Scheinpflug et al., 2011), see (Bondanelli et al., 2021) for a model at the network level). It is now clear that these responses have important consequences at the behavioral level, notably for sound duration perception (Qin et al., 2009), gap detection (Weible et al., 2014)(Threlkeld et al., 2008)Anderson and Linden (2016), and at a higher level for communication (Kopp-Scheinpflug et al., 2018). Recent optogenetic studies in mice notably established that suppressing offset responses resulted in a performance drop on sound duration discrimination (Li et al., 2021) and sound termination detection (Solyga and Barkat, 2021) tasks.

Despite this now established importance of auditory off-

set responses, only a few computational models took them into account. While some of them suffered from a high level of complexity(Fishbach et al., 2001)(Bondanelli et al., 2021), others were constrained to low-level processes (Kopp-Scheinpflug et al., 2011), or were difficult to interpret in terms of biological mechanisms because they were based on deep-learning black-box(Deneux et al., 2016)(Pennington and David, 2023b). Besides, even fewer studies have made the connection between OFF responses and adaptation, sustained responses, and ON responses, although they might not be independent from each other (Hillyard and Picton, 1978) and some auditory neurons display all these types of behaviour (Kasai et al., 2012);(Phillips et al., 2002)(Xu et al., 2014)(Anderson and Linden, 2016). For instance, Willmore et al. (2016) proposed a frequency-wise model of adaptation inspired from electrophysiological measurements in the inferior colliculus (IC) of anaesthetized ferrets. If their approach increased the response-fitting ability of a linear-nonlinear (LN) model, they did not test whether it generalized to other types of models, nor if it also provided better fits on data collected in other species. Also, this work focused only on the phenomenon of adaptation, even if their model is capable of extracting –without segregation– onsets and offsets. In the study performed by Anderson and Linden (2016), authors proposed a simple computational model of auditory ON and OFF responses with split pathways to explain pathological deficits of gap detection in ectopic mice. Despite their convincing results, their model was applied to raw sound level, and therefore cannot generalize to responses to separated frequency bands, nor to interactions between them.

To adress these shortcomings, We propose here a new and unified theoretical framework to model neural responses in the mammal auditory pathway. Our model is composed of two linear filters (one for ON and the other for OFF responses) that capture the sustained and transient properties of auditory inputs within each frequency band (see the 'Model' section). We demonstrate that this model accurately reproduces previous biological findings such as the dependence of OFF responses on the stimulus fall time and on the preceding sound duration (see the 'Results' section). We also demonstrate that our filtering approach greatly improves neural fitting performances of a large variety of models of the auditory pathway, going from simple linear models to state-of-the-art multi-layer convolutional neural networks. This is done across three datasets (collected in different mammal species and under different experimental conditions) to permit robust estimations of the performances and hence more reliable conclusions. All the data, models, processing and pre-processing codes are publicly available on our github repository (`https://github.com/urancon/deepSTRF`).

Model

Two filters to capture the onsets and offsets of auditory inputs

Neural responses in the mammal auditory cortex depend on both the sustained and transient properties of input sounds and rapidly adapt their firing rates to intensity modulations (Dean et al., 2005)(Dean et al., 2008). In order to take into account these properties, our model is based on a pair of filters that we call *AdapTrans* (for *"Adaptation and Transients"*) which efficiently computes ON and OFF responses to sound onsets and offsets. These filters also maintain a sensitivity to the raw amplitude of sounds in different frequency bands, as observed in biology (Dean et al., 2008)(Rabinowitz et al., 2011). Inspired by a previous study which modelled visual processes in the retina Wohrer et al. (2007) and similar to the model of auditory processing proposed by Willmore et al. (2016), our approach consists in partially high-pass temporal filtering operations on the cochleagram with frequency dependent exponential kernels. However, instead of using only one set of filters, we use two in order to separately compute the responses to the sound onsets and offsets, as it is done in the auditory cortices of rats (Scholl et al., 2010) and mice (Liu et al., 2019). In signal processing theory, our filters can be categorized as causal, first order, biphasic, and with infinite impulse responses (IIR). These IIRs (or *"kernels"*) are shown Figure 1A and can be formulated as:

$$\begin{cases} h_{ON}[n] = \delta[n] - C_{ON} w \sum_{d=1}^{+\infty} a_{ON}^{d-1} \delta[n-d] \\ h_{OFF}[n] = -w * \delta[n] + C_{OFF} \sum_{d=1}^{+\infty} a_{OFF}^{d-1} \delta[n-d] \end{cases} \quad \textbf{(1)}$$

with n the discrete time variable, δ the Kronecker delta function

$$\delta[n] = \begin{cases} 1 & \text{if } n = 0 \\ 0 & \text{otherwise} \end{cases} \quad \textbf{(2)}$$

and $a \in [0,1]$ a real-valued parameter relative to the time constant τ (in timesteps) of the exponential part of the kernel ($a = exp(-1/\tau)$), $w \in [0,1]$ a real-value parameter, and C a normalization factor such that elements of the exponential sum to 1. Specifically, for an infinite exponential part (i.e., IIR filter):

$$\begin{aligned} C &= \frac{1}{\sum_{k=0}^{+\infty} a^k} \\ &= \frac{1}{\frac{1}{1-a}} \qquad \text{(sum of an infinite geometric series)} \\ &= 1 - a \end{aligned} \quad \textbf{(3)}$$

Essentially, these kernels compute a weighted difference between the current value of the signal and its exponential moving average (EMA) in a recent past. With this formulation, the a parameter is related to the

time constant of the exponential: the closer to 1, the higher (i.e., slower) the time constant. Meanwhile, the w parameter allows to control the ratio between current (stem) and past (EMA) signal values. Equivalently, it can be interpreted as the ratio between permanent and transient features that are computed by the filter: with a value of 0, the ON-response only accounts for the raw signal; with a value of 1 it only accounts for its derivative. Given the equations above, our filters have the following properties (see Figure 1B): 1) sound onsets on the ON channel lead to the same amplitude as sound offsets on the OFF channel, 2) sound offsets on the ON channel lead to the same amplitude as sound onsets on the OFF channel, 3) sustained sounds lead to the same amplitude on the ON and OFF channels in permanent regime and 4) the output of the filters is null when there is no auditory input. Importantly, although our two filters do not introduce a bias toward one of the two polarities, they are asymmetrical and linearly independent from each other (see Figure 1A), as documented in several studies on the auditory pathway ((Qin et al., 2007) (Deneux et al., 2016) (Phillips et al., 2002)). In the next section, we further describe the influence of the filter parameters on their responses.

Parametric frequency analysis

The transfer function of both filters can be obtained as the Z-Transform of their impulse responses (derivation in Supplementary Note 1):

$$\begin{cases} H_{ON}(z) = \dfrac{1-(a+w-aw)z^{-1}}{1-az^{-1}} \\ H_{OFF}(z) = \dfrac{-w+(1-a+aw)z^{-1}}{1-az^{-1}} \end{cases} \quad \textbf{(4)}$$

The frequency responses of our filters can be better characterized with their Bode diagrams which are shown on Figure 1C (see the Supplements for the associated analytic formula). Both filters are generally high-pass. The cutoff frequency of the ON filter depends on the time constant a, while w acts as gain tuner: the closer to 1 the higher the high-pass effect. With $w = 0$, the exponential part of the ON kernel vanishes, thereby reducing it to a single Kronecker delta function and leaving any auditory input unchanged. This is reflected in the Bode diagram with a flat magnitude-frequency curve. With $w = 1$, ON and OFF kernels are opposite and thus have the same frequency response, which is not efficient from a computational point of view. Interestingly, the OFF kernel can also turn into a low pass-filter for low w. This analysis confirms that the proposed family of paired filters actually highlights the transient properties of input acoustic stimuli. As hinted above, it provides a simple interpretation to both parameters, a regulating the “adaptation" part (i.e., the time constant with which to compute the exponential average of past inputs) and w the “transient“ part (i.e., the relative importance of current with respect to previous inputs).

A frequency-wise application

In our framework, we apply the pair of filters independently on each frequency band of the cochleagram. This choice is motivated by electrophysiological observations of animal responses to multi-frequency components (Solyga and Barkat (2021), see also our results in the next section). Another argument for this multi-frequency filtering is that auditory neurons can display both different frequency and polarity tuning (Sollini et al., 2018). Therefore, we used different sets of AdapTrans parameters (w, a_{ON}, a_{OFF}) for each cochlear frequency. Given that auditory neurons tend to have larger time constants for lower frequencies (Dean et al., 2008), we initialized the time constants of our model following a biologially-plausible logarithmic function that was fitted on experimental data (Willmore et al., 2016):

$$\tau(f) = 500 - 105\log(f) \quad \textbf{(5)}$$

with τ in milliseconds and f in Hertz. We initialized w to 0.75 for all frequencies. This value close to 1 is justified by the fact that onset-sustained-offset neurons in the auditory cortex display small, yet nonzero, sustained activity upon presentation of a sound.

Implementation

In the present study, for computational efficiency and parallelization on modern GPU hardware, we truncated the IIR, such that our implementation of the AdapTrans filters was based on a kernel with a finite number of elements. Its length was euqla to $3 \times \tau_{max} + 1$, τ_{max} being the time constant of the lowest cochleagram frequency band (see Figure 1A). In this case, approximately 95% of the exponential part of AdapTrans is properly represented. As indicated above, we normalized the exponential part by computing C such that the terms respectively sum to 1 and $-w$ for ON and OFF polarities, respectively. We padded the input spectrogram to its left (past) in 'replicate' mode (i.e., using the left-most value, see PyTorch documentation) before the convolution operation in order to avoid any downsampling along the time dimension. Our repository (available at `https://github.com/urancon/deepSTRF/`) contains an easy-to-use dedicated PyTorch class for AdapTrans.

Integration within larger models of audition

We explain here how our framework can be easily integrated into larger models of auditory processing, going from simple and gold-standard linear models to state-of-the-art convolutional neural networks. This integration is illustrated in Figure 3. Assuming an input sound waveform converted into its spectro-temporal representation in an initial processing step (e.g., using a gammatone filter bank), our AdapTrans filters are applied on each frequency band (see above). The output of this filtering process is a 2-channel, ON-OFF spectrogram with transient and adaptive sustained activities. This tensor can then be fed to standard auditory neural response mod-

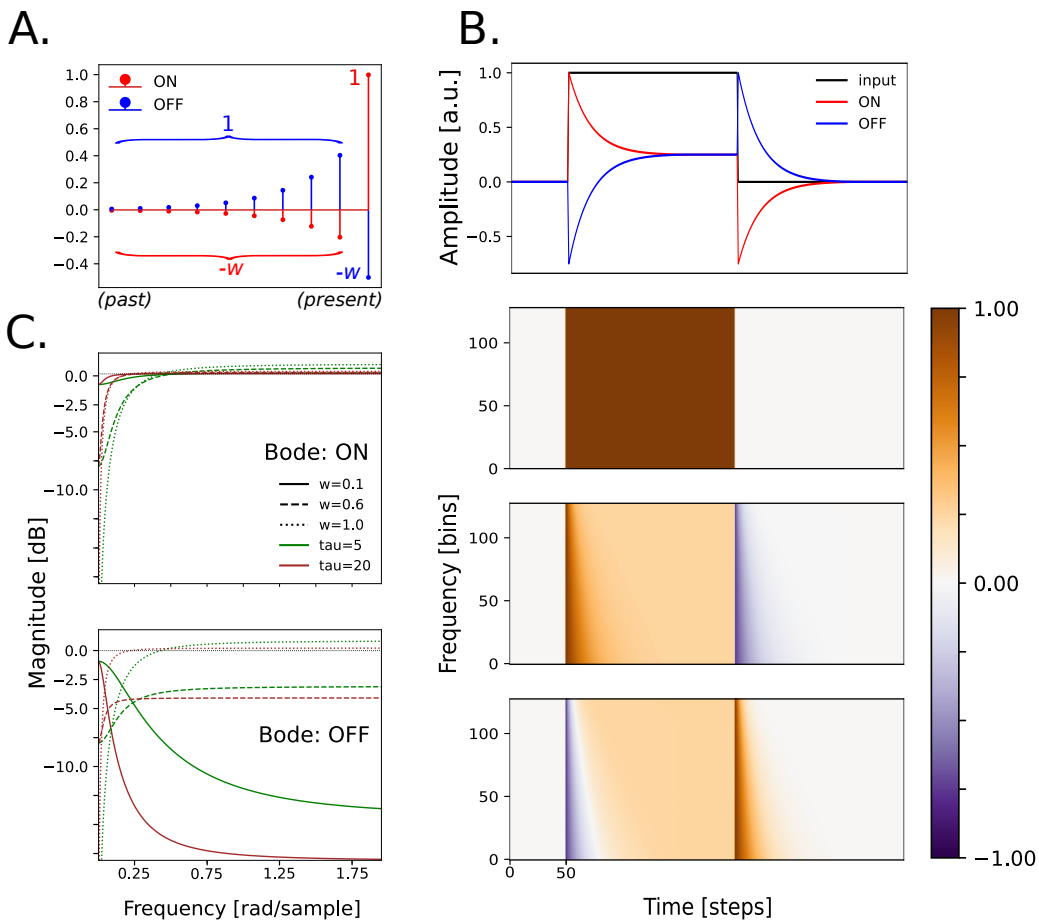

Figure 1. Presentation of AdapTrans filters. (**A.**) ON and OFF kernels of an AdapTrans filter of size 10, with $w = 0.5$ and $a = 0.6$. Most recent time-steps are represented on the right. Each kernel is temporally convolved with a cochleagram spectral band from left to right, thereby computing a weighted difference between the current value of the signal and an exponential average of its recent past. Importantly, the output of the OFF channel is not the opposite of the output of the ON channel, since both kernels are linearly independent. (**B.**) Example ON and OFF outputs for a dummy input spectrogram composed of 128 frequency bands. All frequency bands of the latter bear the same signal: a rectangle function with one onset, one permanent regime, and one offset *(top)*. The ON channel responds positively to the onset and negatively to the offset, while the OFF channel does the opposite. The ON channel has an initial onset response of 1 –the value of the step in the input signal– and a negative offset response of $-w$; similarly the OFF channel has a negative onset response of $-w$ and an offset response of 1. Importantly, both polarities share the same sustained activity. For this particular input, the permanent response in both channels equals $1 - w$. Time constants are logarithmically distributed along the frequency axis, therefore producing slower responses for lower cochlear bands *(bottom 2 sub-panels)*. (**C.**) Bode plots of the ON and OFF filters, for different sets of parameters τ and w.

els, such as Linear (L) or Linear-Nonlinear (LN) by doubling the number of input channels, in order to be compatible with the ON and OFF channels of AdapTrans. As a result, the number of learnable parameters in the input layer of the response model is doubled, which is not an issue because in multi-layer neural network algorithms like deep Convolutional Neural Networks (CNN), the input layer only constitutes a negligible fraction of the total number of learnable parameters in the model. Most importantly, in our framework, these added parameters remain fully interpretable (weights for each frequency bin become weights for each time-frequency-polarity bin).

In practice, the (a_{ON}, a_{OFF}, w) parameters of AdapTrans can be optimized for each frequency bin during the fitting process of the biological data through gradient descent. Note that this approach is very general and encompasses a large variety of cases (including the identity transform, which would let the raw spectrogram unchanged for $w = 0$, or the derivative for $w = 1$).

Results

The aim of this work is to propose a model of auditory ON/OFF responses and adaptation, which can reproduce actual neural responses and properties measured from electrophysiological recordings in a wide range of animals, brain areas, and stimulus types.

Dependence of OFF responses on stimulus fall time

Several studies have empirically demonstrated a dependence of offset responses on the stimulus fall time, in a variety of animal species and in different cortical areas: mouse MGB and AAF (Solyga and Barkat, 2021), rat AAF, A1 and VAF (Takahashi et al., 2004). This property of offset responses is well captured by our model as abrupt down steps in the input stimuli elicit higher OFF responses than slow descending ramps of the same amplitude .

To prove it, we simulated the AdapTrans OFF response to a single-channel stimulus composed of a ramp of variable duration (see Figure 2A). We systematically

computed the maximal offset response at sound termination as a function of fall time, and we searched for the a_{OFF} and w parameters that yielded the best fit with Solyga and Barkat (2021) data (see Figure 2A). Beyond the validation of the biological plausibility of our model, this simulation also illustrates that our framework easily permits to test any property. For instance, we can easily extract the latency of offset responses as a function of ramp duration (see Supplementary Figure S1). To our knowledge, it has not been tested in previous experiments. We hope future studies will explore whether the predictions of our model are correct in this case.

Dependence of OFF responses on preceding sound duration

Another well-established property of auditory offset responses in the mammal brain is their dependency on preceding sound duration. This dependency takes the form of a saturating exponential (Solyga and Barkat, 2021) (Scholl et al., 2010) (He, 2002). In order to test whether AdapTrans can reproduce this relationship, we fed the OFF channel of our filter with auditory stimuli consisting in binary steps. Figure 2B shows the maximum amplitudes of the responses to the offsets of these stimuli. These values can also be computed from AdapTrans OFF impulse response. If T is the number of discrete timesteps of the step stimulus, the offset response amplitude at sound termination is:

$$A_{OFF}(T,a,w) = (1-a)\sum_{d=1}^{T} a^{d-1} \qquad \textbf{(6)}$$

Note that A_{OFF} is an exponential function depending only on T and a (not w) and saturating to a maximum value as the preceding stimulus gets longer (i.e., in the limit of infinite T). Indeed, longer step stimuli can build up bigger exponential moving averages (left part of AdapTrans kernels in Figure 1A), leading to a bigger difference between present and past values and therefore to a bigger response when it stops. To further demonstrate the ability of AdapTrans to capture this biological property, we fitted this function on data collected in two auditory areas of the mouse cortex (Solyga and Barkat, 2021). Results are reported in Figure 2B. The predictions of our model match remarkably well with experimental data (R^2 = 0.94). This is notably the case for data collected in the Medial Geniculate Body (MGB, in green) which are less favourable to offset responses than measurements made in cortical areas such as the Anterior Auditory Field (AAF, in orange). (Solyga and Barkat, 2021).

The multi-frequency processing scheme of AdapTrans is in line with experimental data

Auditory neurons in areas MGB and AAF of the mouse auditory cortex can detect the offsets of different frequency components with a rich spectral stimulus (Solyga and Barkat, 2021). To test whether our approach can reproduce these results, we designed an artificial binary stimulus composed of three spectral bands with activations set to 1 and turned down to 0 at different time instants (respectively 0.3, 0.4, and 0.5 s in simulation time, $dt = 1$ ms, see figure 2) and filtered through adapTrans, using different ON and OFF time constants

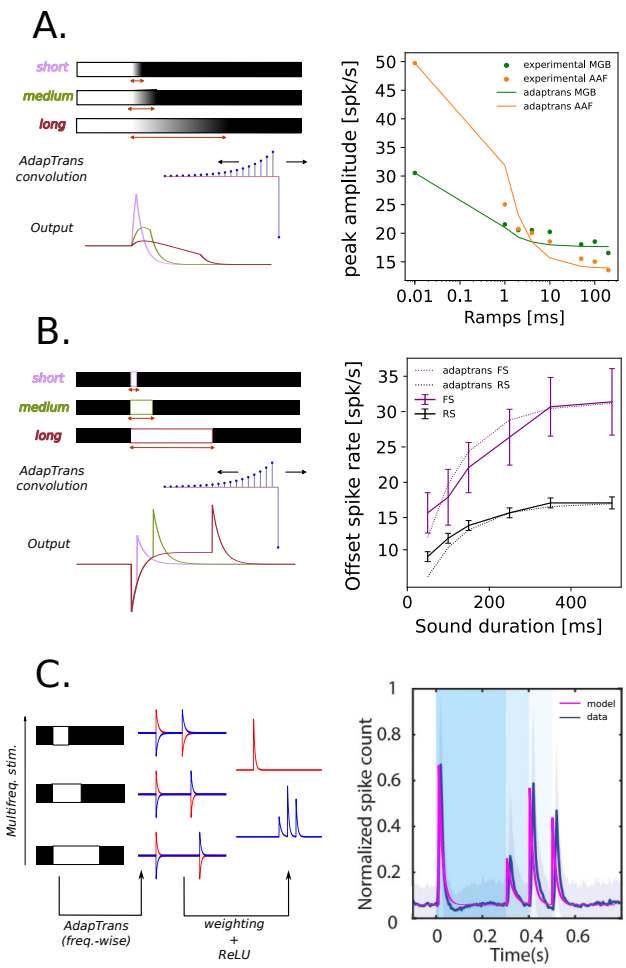

Figure 2. Comparison between OFF responses predicted by our model and neurobiological data. Experimental measurements were performed in the mouse medial geniculate body (MGB) and anterior auditory field (AAF)(see Solyga and Barkat (2021)). Despite a lesser effect of preceding sound duration than in AAF, MGB responses also follow a saturating exponential function. We argue that the latter could perhaps become even more evident if probed with smaller sound durations (i.e., less than 50 ms), as neurons in earlier relays of the auditory pathway tend to have shorter time constants than cortical neurons. Thus, it could be that authors tested sounds too short compared to MGB time constants, resulting in a directly saturated effect. (**A.**) Adaptrans reproduces the decrease in offset response amplitude as a function of preceding fall-ramp duration. The experimental setup *(left)* simply consisted of a convolution of an AdapTrans kernel over 1D fall-ramp stimuli; the maximum offset responses over the whole time course were then reported and the AdapTrans parameters were empirically optimized to best fit biological data *(right)* (**B.**) Similarly, offset response amplitude increases as an exponential function of preceding sound duration, measured in regular spiking (RS) and fast spiking (FS) neurons. The simulation setup was the same as for the previous panel, except for the stimuli, which were steps of infinite ramp and variable durations. (**C.**) Biological responses to multi-frequency stimulus can be accurately replicated *(right)* by a simple model *(left)* built upon the frequency-wise AdapTrans scheme. The latter processed each spectral component with its own version of AdapTrans, each with 3 parameters (a_{ON}, a_{OFF}, w); after a rectification (ReLU) stage, ON and OFF traces for each spectral component were then weighted and combined into a single final channel (3 bands $\times$ 2 polarities $=$ 6 additional parameters).

(parameter a) and w for each frequency band. Each output channel was then rectified and the final neural response was readout at each timestep through weighted summation of each frequency-polarity bin, following the addition of a bias accounting for baseline neural activity. This simple 15-parameter model was finally fitted to reproduce experimental data averaged over a large number of thalamic and cortical neurons.

The resulting model activity closely matches the experimental data (see Figure 2C). This observation strongly supports the use of learnable time constants for each frequency band and polarity of the cochleagram, rather than the use of the raw sound waveform envelope. This experiment also demonstrates that AdapTrans can be used as a foundation or building block for larger models of audition.

AdapTrans filtering enhances the neural fitting performances of a large spectrum of models

In order to test whether our framework can constitute a valuable extension to gold-standard models of auditory processing, we trained several computational pipelines, with and without AdapTrans, on electrophysiological data collected in auditory areas (Harper et al., 2016)(Asari et al., 2009)(Pennington and David, 2022) (see Materials and Methods, Datasets). This training was performed with supervision using back-propagation in order to predict new single-unit activity (see the 'Task and Evaluation of Performance' section). Figure 3 gives an overview of the proposed processing pipeline when the Adaptrans filters are used. The architecture of the different models of the auditory pathway wihch were implemented is detailed in the Methods (see the 'Computational Neuron Models' section). For each model and each dataset, we report in Table 2 the cross-validated raw and normalized Pearson correlation coefficients (CC_{raw} and CC_{norm}) between the predicted and groundthuth neural responses, averaged over all units of the dataset.

Overall, using AdapTrans significantly increase fitting performances. As an illustration, figure 4 shows the predicted responses for different neurons sampled from the three datasets. Predictions using our approach are better (see the associated correlation coefficients on the upper-right parts of the panels). On average, this increase in performances with AdapTrans reaches 0.041 in CC_{raw} and 0.063 in CC_{norm} (mean absolute delta between all baseline and adaptrans models accross datasets). Importantly, for each dataset, the best correlation coefficients were obtained using our method (see the underlined scores in the tables). This was true for both correlation coefficients (CC_{raw} and CC_{norm}). Increases in CC were generally higher for smaller models (L, LN) but significant improvements were also found for NRF, DNet and 2D-CNN models (see the values in bold). Interestingly, we noticed that the improvements brought by AdapTrans on the "Wehr" dataset were close to 50%, even among the more sophisticated models (DNet, 2D-CNN). This dataset was the only one containing whole-cell current clamp recordings and was characterized by a very low inter-trial variability inneural recordings. Despite this high quality, it was associated with rather poor fits. It could be that this nature of recording is intrinsically more difficult to capture. In any way, the decomposition of the cochleagram into ON and OFF spectrogramms performed by our approach greatly improve the predictions of neural responses in this case.

In order to test whether AdapTrans provides a prefiltering of the input spectrogram that is more beneficial to the neural response fitting task than previous approaches, we also trained downstream models using the method described by Willmore et al. (2016). The associated performances are provided in table 2. Correlation scores are systematically better (mean absolute delta between IC adaptation and AdapTrans models: 0.062 in CC_{raw} and 0.098 in CC_{norm}) using our framework, with the exception of the values obtained with the L model for the Wehr dataset. These results were expected given that the processing performed by IC adaptation are less general than those of adapTrans (i.e., IC adaptation does not segregate ON and OFF responses, discards all sustained information, and does not treat adaptation time constants as free, learnable parameters). More surprisingly, we were unable to reproduce the results of Willmore et al. (2016) who reported that the neural predictions obtained with an LN model on the NS1 dataset were better with IC adaptation than when no filtering was applied. This might be because these authors overfitted their approach on their experimental data. This hypothesis is supported by the rather low general performances obtained with IC adaptation on the large set of neural data used in the present study (N.B.: IC adaptation nonetheless leads to interesting improvements of the correlation scores on the Wehr dataset). This demonstrates the importance of testing methods on different datasets in order to properly validate their robustness.

In brief, AdapTrans was shown to provide a simple first preprocessing layer that performs an efficient decomposition of input stimuli into dual features. The use of ON and OFF spectrograms almost systematically improve the predictions of neural responses, despite the wide variability in the datasets which contain different temporal (5-10 ms) and spectral (18-49 bins) resolutions of input cochleagrams, different animal species (rat, mouse, ferret) and areas (A1, AAF, PEG), different natures of recordings (spike sorted extracellular activity, patch-clamp).

Parameters of the model after optimization

Here we show that AdapTrans parameters learnt through the neural response fitting process described above (see the 'AdapTrans filtering enhances the neural fitting performances of a large spectrum of models' subsection) converged towards values that are in line with electrophysiological recordings.

Model		Dataset							
		NS1		Wehr		NAT4			
						PEG		A1	
Backbone	Prefiltering	CC_{raw}	CC_{norm}	CC_{raw}	CC_{norm}	CC_{raw}	CC_{norm}	CC_{raw}	CC_{norm}
L	None	22.8	31.6	0.8	0.8	19.3	32.7	23.4	37.6
	IC Adaptation	24.7	35.1	**7.2**	**7.3**	16.0	26.0	17.5	28.0
	AdapTrans	**30.6**	**45.2**	5.0	5.0	**21.2**	**36.6**	**25.7**	**41.8**
LN	None	23.6	32.8	16.0	16.2	24.5	42.5	28.8	48.4
	IC Adaptation	13.1	18.0	15.7	15.9	20.8	36.4	22.4	38.6
	AdapTrans	**27.1**	**38.9**	**16.3**	**16.4**	**25.5**	**45.1**	**30.0**	**50.6**
NRF	None	38.1	56.1	15.0	15.2	**26.0**	**44.1**	**30.3**	**49.5**
	IC Adaptation	31.4	45.6	23.3	23.5	19.1	26.0	21.7	34.2
	AdapTrans	**42.2**	**63.4**	**26.0**	**26.3**	25.5	42.6	30.2	48.2
DNet	None	29.2	42.4	13.5	13.6	26.7	46.2	31.2	51.5
	IC Adaptation	29.5	42.3	21.3	21.5	23.1	39.3	25.7	42.6
	AdapTrans	**36.9**	**54.8**	**25.3**	**25.5**	**29.5**	**51.0**	**34.2**	**57.0**
2D-CNN	None	42.4	63.1	11.3	11.4	29.8	51.3	34.4	56.4
	IC Adaptation	36.2	53.4	17.3	21.5	26.9	46.8	30.1	49.7
	AdapTrans	**43.7**	**65.3**	**24.4**	**24.6**	**32.6**	**56.9**	**37.2**	**62.4**

Table 2. Performances of the models with various prefiltering conditions on the datasets. Correlation coefficients (CC) and normalized correlation coefficients are given in %. **Bold font** indicate the best prefiltering for a given model backbone, while underlined scores indicate the best among all models on a given dataset. All bold entries were deemed statistically significant with unilateral paired t-tests (best versus second best, $p = 0.05$).

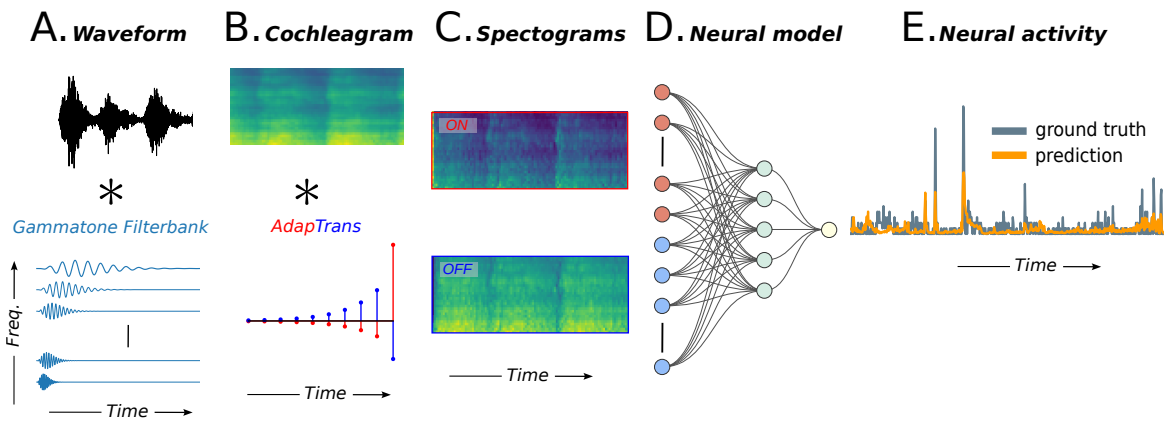

Figure 3. Overview of the proposed processing pipeline. (**A.**) Its inputs are given by a spectrogram representation of the sound stimulus (e.g. obtained from a Gammatone filterbank). (**B.**) Two AdapTrans filters are convolved to each frequency band along the temporal dimension, effectively accounting for transient and permanent features of the stimulus. (**C.**) The filter outputs consist of a 2-channel, ON-OFF spectrogram that is further processed by conventional models as found in the litterature. (**D.**) Such models can be separated into several classes, depending on whether they are based on a single and large spectro-temporal receptive field (STRF), a cascade of convolutions with small-sized kernels (CNNs), or recurrent neural networks (RNNs)(the architectures of the models used in this study are shown in Figure 6). (**E.**) All models output the predicted neural activity as a time series that can be compared to a groundtruth recording.

Figure 5 provide the average distributions (across neural units, models and datasets) of the w and a parameters. It is interesting to observe that optimal values for w remain high (i.e., in the $[0.5, 1]$ interval) in all the frequency bands (see panel A). It suggests that neural responses in auditory areas are more strongly modulated by the transient rather than by the sustained properties of the input sounds. Time constants (i.e., parameter a, see panel B) remain overall close to their initialization values which were directly inspired from biological findings (see equation 5). It is nonetheless remarkable to observe that the optimization process led to greater values for the OFF channel rather than for the ON channel. This was true in the three datasets and for all the models. This result is in line with the findings of previous electrophysiological studies ((Qin et al., 2007), (Hartley et al., 2011)) and could reflect statistical differences between the onsets and offsets of natural sounds ((Kopp-Scheinpflug et al., 2018), (Cavaco and Lewicki, 2007)).

Discussion

In this paper, we describe a new theoretical framework to model neural responses in the mammal auditory pathway. Our model is composed of two linear filters that capture the sustained and transient properties of auditory inputs (see (Wohrer et al., 2007) for an illustration of this concept in the visual domain). Con-

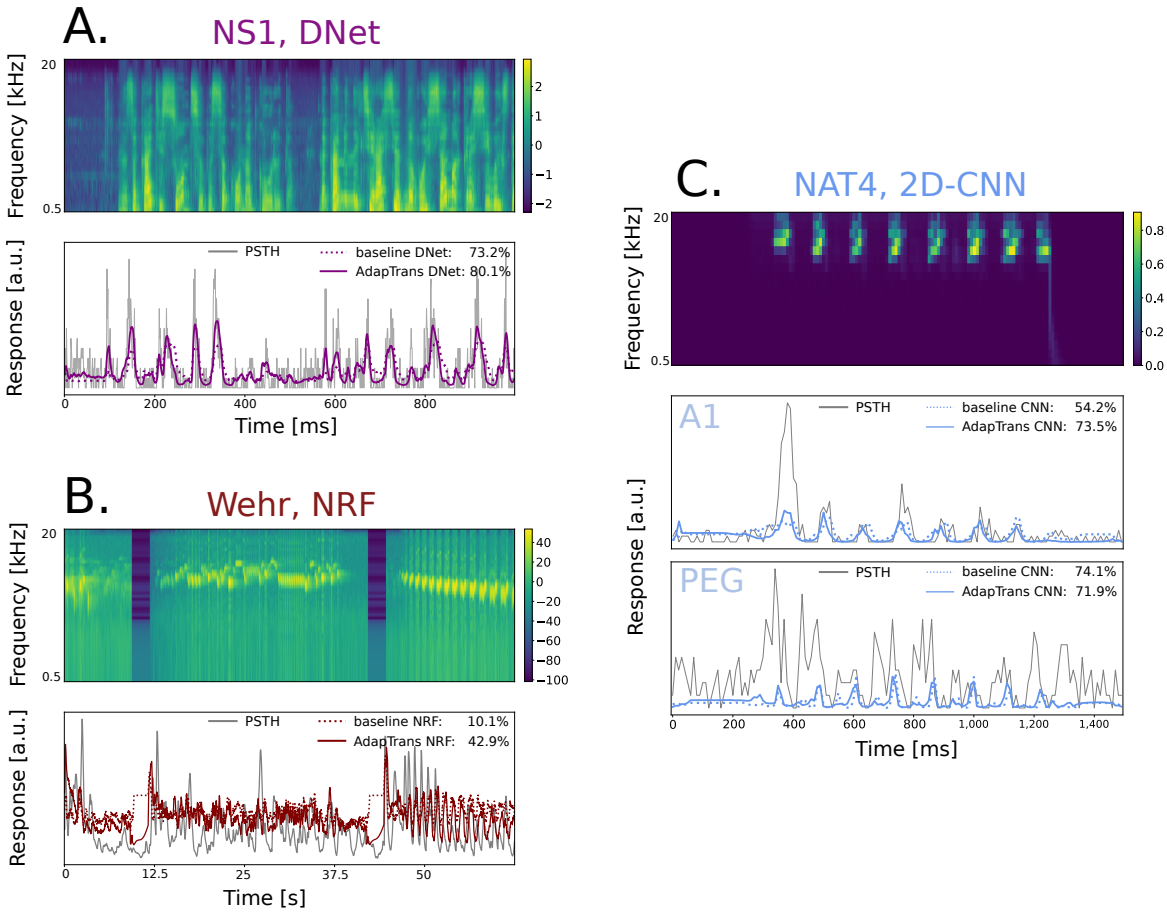

Figure 4. Various deep learning models fitting auditory neural responses: model prediction versus actual neural activity. Top of each panel: stimulus spectrogram from the test set, used to evaluate the performances of each model. Bottom: comparison of groundtruth and model predictions, with and without AdapTrans. Indicated percentages represent the normalized correlation coefficients of the corresponding models for these clips. (**A.**) DNet model predictions on NS1 Dataset (ferret A1 spikes). AdapTrans models often better capture transient variations of activity, in particular the height of peaks. (**B.**) Network Receptive Field (NRF) model benefits from AdapTrans on Wehr Dataset (rat A1 potentials). In contrast to its baseline counterpart, the AdapTrans-enhanced model was able to predict a peak at initial sound onset and a decrease in activity during inter-stimulus intervals. (**C.**) 2D-CNN model on NAT4 Datasets (ferret A1 and PEG spikes). This example shows that in some cases, baseline and AdapTrans models can have equivalent responses; here, both are able to produce predictions time-locked with the input stimulus, despite missing the peaks, due to noisy data.

trarily to most previous modeling works, it takes into account both the ON and OFF responses and processes them independently within each frequency band (see the 'Model' section). This segregation is justified by the results of previous studies which established that separating the ON and OFF systems improves sensory coding and actually provides a better code for extracting meaningful information by a downstream decoder (see e.g., Gjorgjieva et al. (2014). We demonstrated here that our framework accurately reproduces known properties of neural responses in the auditory cortex such as the dependence of OFF responses on the stimulus fall time and on the preceding sound duration (see the 'Dependence of OFF responses on stimulus fall time' and 'Dependence of OFF responses on preceding sound duration' subsections). By combining data from numerous studies collected in different animal models and auditory areas (see Table 3), we also demonstrated that AdapTrans almost systematically improves neural fitting performances of a large gamut of models of the auditory pathway (higher correlation scores were observed in 18 cases over 20), going from simple linear models to state-of-the-art convolutional neural networks (see Table 2 and Figures 3 and 6). The overall increase of normalized correlation scores was above 0.063 in across all datasets tested (see the 'Results' section). For each of these datasets, the best models used AdapTrans.

One of the interests of our framework is that the optimal distribution of the model parameters (τ and w) can be directly derived from experimental data through the neural fitting process (see the 'AdapTrans parameters follow biologically-plausible distributions after learning' section). For all the tested models, we encouraged time-constants (parameter τ) to decrease as frequency increase (see Figure 5) through an initialization in line with previous biological findings (Dean et al., 2008). Interestingly, in addition to remaining close to that initial distribution, we found that optimal time constants were significantly higher for OFF than for ON responses. This result is in agreement with previous measurements in the ferret (Hartley et al., 2011) and cat (Qin et al., 2007) auditory cortices and might reflect an efficient encoding of statistics in natural sounds where offsets are usually slower and less salient than onsets (Cavaco

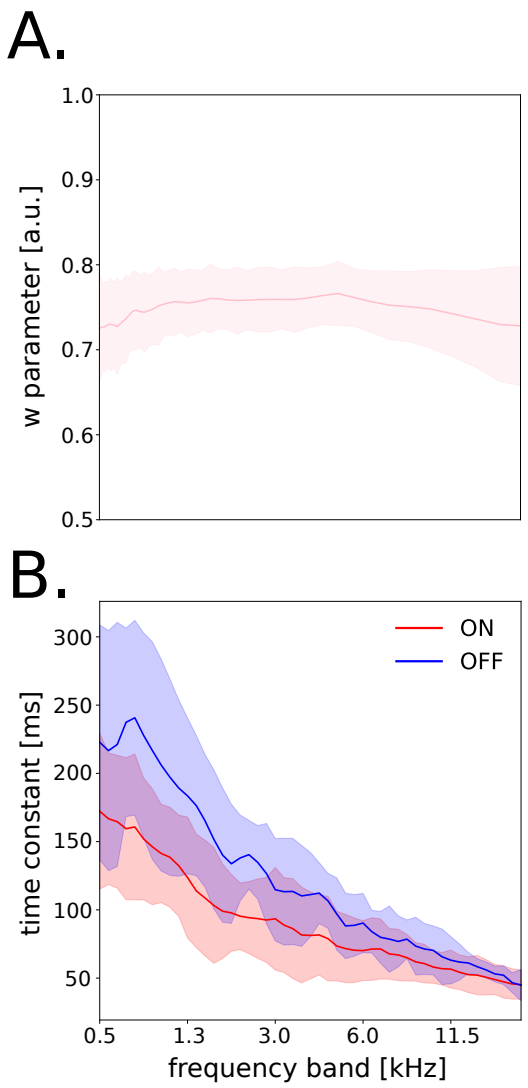

Figure 5. Distribution of AdapTrans parameters learned during the neural fitting process as a function of frequency. Values were averaged across neural units, models and datasets. The errobars correspond to $\pm$ the standard deviations across datasets. (**A.**) w remains at high values even after learning, thus favoring transient over sustained responses. (**B.**) ON and OFF time constants. These constants decrease with frequency. Values obtained for OFF responses are systematically higher than those observed for ON responses.

and Lewicki, 2007); (Kopp-Scheinpflug et al., 2018). In addition, our approach also predicts that the optimal w ranges between 0.5 and 1, which confirms that auditory responses are better captured when both the transient and sustained parts of auditory inputs are taken into consideration, in line with biological findings (see e.g., Kasai et al. (2012)). Finally, we also found that this optimal w remains stable across frequencies. Thus, we predict that the relative contribution of transient versus sustained responses is frequency independent. To our knowledge, this hypothesis has never been tested in animal models. We hope that future experimental works will explore this lead.

Two previous studies proposed models that shared properties with our framework (Willmore et al., 2016); (Anderson and Linden, 2016). Willmore et al. (2016) modeled adaptation to mean sound level in the auditory midbrain using a high-pass filter with frequency-dependent time constants. However, they did not segregate between the ON and OFF pathways and their model can thus only capture whether the sound intensity has changed in a given frequency band but not whether this modification reflects an increase or a decrease. In addition, their model only considers transients and completely discards the sustained properties of the auditory inputs. As we saw it, our framework is more general as it segregates ON and OFF responses and considers both sustained and transient properties whose relative contributions are controlled with the w parameter (see equation 1 in the 'Model' section). Note that fixing this parameter to one and processing the ON and OFF responses in a single channel followed by a full-wave rectification (i.e., absolute value) actually brings our model back to the one proposed by Willmore et al. (2016)). It is thus not surprising that the correlation scores obtained with AdapTrans are systematically higher than those obtained with the method described in Willmore et al. (2016) (see Table 2).

Anderson and Linden (2016) proposed a model based on divisive normalization that takes into account ON and OFF responses, although these two channels are ultimately merged together. Their method uses the 1D sound envelope and thus does not process each frequency band separately. AdapTrans is based on subtractive normalization and is more general as it is applied on the 2D sound spectrogram of the auditory inputs and relies on parameters that are frequency dependent. By learning from experimental data, our approach permits to optimize the relative contributions of the ON and OFF channels for each frequency band, whereas this relative contribution is fixed and global in Anderson and Linden (2016). Also, our method is more biologically plausible as it keeps separated the ON and OFF channels along the entire hierarchy of the auditory cortex.

There are still biological properties that our approach cannot properly capture in its current form. For example, some asymmetries (i.e., in amplitude, latency, spectral tuning) commonly observed between ON and OFF STRFs do not seem to emerge implicitly from training on a machine learning task such as response fitting. This issue could however be easily resolved by explicitly parameterizing ON and OFF weights subsequent to AdapTrans altogether. Another example is given by the non-instantaneous buildup times of ON/OFF responses which are currently not well predicted by our model. This could also be easily sorted out by replacing the initial Kronecker delta function (see Figure 1A) by a growing exponential, at the cost of one extra parameter (i.e., the time constant of this added exponential part). These leads will be explored in future works from our team.

Altogether, we present here a unifying framework that

encompasses previous approaches (Willmore et al. (2016); Anderson and Linden (2016)) and permits to improve our understanding of computations performed in the mammal auditory pathway. AdapTrans can serve as a transparent primitive and a key layer of computation (Deneux et al., 2016) to account for the broad range of neural response patterns observed in the mammal auditory cortex such as ON, OFF, ON-sustained-OFF, inhibition-OFF, among others (Kasai et al., 2012);(Phillips et al., 2002)(Xu et al., 2014)(Anderson and Linden, 2016). Such a wide algorithmic-level model (in opposition to Marr's implementation level, see Marr (1982)) has been lacking so far in the field. We hope it will inspire new modelling works at the mechanistic level in order to clarify what might be the biophysical implementations of the computations described here (in the terminology of Wang et al. (2020) and Sadagopan et al. (2023)). Beyond audition, we think our approach could also account for processing in other sensory modalities and notably in the visual system where the segregation between ON and OFF luminance information has been documented at multiple stages of processing, starting from the retina (Westheimer, 2007);(Jin et al., 2008). Applying AdapTrans in a pixel-wise manner to temporal image sequences could thus improve the bio-plausibility of existing models of the early visual pathway. In terms of applicative researches in artificial intelligence, the integration of our framework within state-of-the-art deep learning models could improve performances in numerous sensory-based tasks, such as sound classification or object detection. In this sense and in order to facilitate the reproduction of our results and the use of our approach in future studies, we provide all the data, models, processing and pre-processing codes used in the present work at the following github repository. We also provide user-friendly Pytorch Dataset classes for each source of data.

Materials and Methods

In this section, we first describe the datasets (audio stimuli and neural recordings) that were used in our study. Next, we provide details about the models of the auditory pathway that were combined to our pair of adapTrans filters to predict neural responses. Finally, we described our methodology to characterize the performances. Note that because our theoretical framework is an essential part of the present study, it is presented in a separate section which precedes the results (see the 'Model' section).

Sound datasets

To demonstrate the generalization ability of our approach, we chose audio data collected in different cortical areas (ferret A1, ferret AAF, ferret PEG, rat MGB) and at different temporal resolutions (1, 5 and 10 ms). These data come from recent studies (Asari et al. (2009), Harper et al. (2016), Pennington and David (2022)) and are freely available on the internet. We only report here the main steps for their acquisition and preprocessing (see also table 3 for an overview of their main characteristics). More details can be found in the corresponding papers. The preprocessed data, ready for Pytorch development, are all freely available on our GitHub.

NS1 dataset. This dataset comprises single-unit extracellular electrophysiological recordings performed in the primary auditory cortex (A1) and anterior auditory field (AAF) of 6 anesthetized pigmented ferrets exposed to natural stimuli. Natural sound clips (n = 20) included either birdsong, ferret vocalizations, human speech and environmental noises (e.g. wind, water). Each clip last 5 s and was presented 20 times to each animal at a sample rate of 48,828.125 Hz. A Klustawik-based spike-sorting algorithm (Kadir et al., 2013) isolated a total of 73 single units that matched a certain noise ratio threshold, allowing the construction of their peri-stimulus time histograms (PSTH) by first counting spikes in 5 ms temporal windows, then averaging over repeats, and smoothing by convolution with a Hanning window. This yielded supra-threshold (i.e. firing probability) response profiles with a temporal resolution of 5 ms for each unit and sound clip.
Stimuli were first processed into a 34 band mel spectrogram of 5 ms time bins with frequencies ranging from 500 to 22,627 Hz. The log of each time-frequency bin was then computed, and values below a fixed threshold were set to that threshold. The resulting cochleagrams were finally normalized to zero mean and unit variance. This dataset is available online on the Open Science Framework (OSF) website[1], at the repository associated to its original article (Harper et al., 2016). Please refer to the latter for more details on the acquisition and preprocessing of the data.

NAT4 datasets. The following dataset (Pennington and David, 2023a) was acquired from the primary auditory cortex (A1) and secondary auditory field (PEG) of 5 awake ferrets exposed to a wide range of natural sound samples. Spiking activity was collected extracellularly through micro-electrode arrays (MEA) and single- and multi-units were isolated from raw traces using the Kilosort 2 spike sorter (Pachitariu et al. (2016)). In total, 849 units were identified in A1 (including 567 single-units) and 398 in PEG (314 single-units).
All of the 595 stimuli were 1 s long, and were presented with a 0.5 sec interval of silence. 15% were congenital vocalizations and noises recorded inside the animal facility, while the remaining 85% were taken from a public library of human speech, music and environmental sounds (Mcdermott et al., 2013). 577 of these sounds were repeated only once, and 18 were repeated

[1] https://osf.io/

		Dataset			
		NS1	Wehr	NAT4	
				PEG	A1
Literature	original paper	Harper et al. (2016)	Machens et al. (2004)	Pennington and David (2022)	
	others	Rahman et al. (2019), Rahman et al. (2020)	Asari and Zador (2009)	Pennington and David (2023b)	
Recordings	animal model	ferret	rat	ferret	
	brain areas	A1, AAF	A1	PEG	A1
	# valid neurons	73	20	777	339
	mean CC_max	89%	96%	59%	61%
Stimuli	sound type	natural			
	duration	5 s	7.5 - 15 s	1 s	
	sounds $\times$ repeats	20$\times$20	3-63$\times$1-25	577$\times$1 + 18$\times$20	
	time bins	5 ms	5 ms	10 ms	
	# frequency bins	34	49	18	

Table 3. Review of the datasets used in this study. Mean CC_{max} was computed accross neurons and stimuli for responses with more than 1 repeat. Please refer to main text or their original study for additional details.

20 times.
These data are available in online open-access on the Zenodo platform[2], on a dedicated repository associated to its original paper (Pennington and David, 2022).

Wehr dataset. In this last dataset (Asari et al., 2009), pure tones and natural stimuli were presented to anesthetized Sprague Dawley rats while membrane potentials of neurons in their primary auditory cortex (A1) were recorded using a standard blind whole cell patch-clamp technique, in current-clamp mode ($I = 0$, sampling frequency: 4,000 Hz). Action potentials were pharmacologically prevented by the administration of a sodium channel blocker, therefore allowing large PSPs at most. For each of the 25 cells recorded in this study, the frequency tuning curve was determined thanks to the presentation of short pure tone stimuli (20 ms duration with a 5 ms cosine-squared ramp or 75 ms a 20 ms ramp) which were sampled and delivered at 97.656 kHz in a pseudo-random sequence. Natural sounds with various durations (7.5 - 15 sec with 20 ms cosine-squared ramps at onset and offset) originally sampled at 44.1 kHz were upsampled and delivered at 97.656 kHz. These natural stimuli were a selection of 122 commercially available clips of environmental noises and animal vocalizations, and covered frequencies from 0 to 22 kHz. Depending on neurons and experiments, these natural stimuli were repeated up to 25 times. Recorded neural responses in this dataset are characterized by very low variability and are therefore very reliable.
Similarly to previously described data, stimulus spectrograms resulted from a simple short-term Fourier transform (STFT) in which the frequency axis was logarithmically discretized into $F = 49$ spectral bands (12 / octave); temporal resolution was set to $dt = 1$ ms for our analysis. The resulting energy density spectrum of the sound pressure wave was passed to a log-compression function and then further multiplied by a factor 20.

[2] https://zenodo.org/

This dataset is freely available online on the Collaborative Research in Computational Neuroscience (CRCNS) website[3], and constitutes the first half of the "CRCNS-AC1" dataset. More details are available in its original article (Machens et al., 2004).

Computational Neuron Models

We review here the computational response models used in this study. Unless stated otherwise, we do not parameterize the spectro-temporal kernels of these network, nor regularize them using weight decay. All model architectures are shown in Figure 6, and Table 4 compiles the hyperparameters used on each dataset.

Auditory Periphery. To facilitate present and future comparisons with previous methods, and to limit as much as possible the introduction of biases due to different data pre-processings, we directly used the cochleagrams provided in each of the associated datasets. They were all obtained following similar principles, that is, a short-term spectro-temporal decomposition from windowing functions, followed by a compressive nonlinearity. However, despite their overall resemblance and for the sake of completeness, we briefly review here the main computations which were performed (more details can be found in the associated papers). Table 3 partly summarizes the waveform-to-spectrogram encoding for each dataset.
In the NS1 dataset (Harper et al., 2016), 10 ms Hanning windows (overlap: 5 ms) were used to compute the short-term amplitude spectrum of auditory stimuli which was subsequently transformed into a spectrogram using a set of 34 mel filters logarithmically spaced along the frequency axis (500 - 22,627 Hz). Finally, a logarithmic function was applied to each time-frequency bin, any values below a manually-defined threshold was set to that threshold, and the cochleagrams were normalized

[3] https://crcns.org/

Model Backbone	Dataset Prefiltering	NS1 (dt=5ms) F	T	H	#params	Wehr (dt=5ms) F	T	H	#params	NAT4 (dt=10ms) F	T	H	#params
L / LN	None / Willmore	34	41	1	1,395	49	21	1	1,030	18	21	1	379
	AdapTrans				2,891				2,206				811
NRF	None / Willmore	34	41	20	27,961	49	21	20	20,661	18	21	20	7,641
	AdapTrans				55,943				41,388				15,237
DNet	None / Willmore	34	5	20	3,502	49	5	20	5,002	18	5	20	1,902
	AdapTrans				7,004				10,049				3,756
2D-CNN	None / Willmore	15	6	90	36,274	7	6	90	39,694	3	7	90	15,484
	AdapTrans				37,276				40,261				15,748

Table 4. Technical details for each model investigated in this study. Hyperparameters, such as the temporal span, could vary between datasets for a given model, due to the fact that the time-step could vary between datasets (e.g., 5 ms for NS1 and 10 ms for NAT4). As a result, same models could have a variable number of learnable parameters, depending on the dataset they were trained on. However, as a general rule and for fair comparison, for a given dataset, all models had access to the same temporal span.

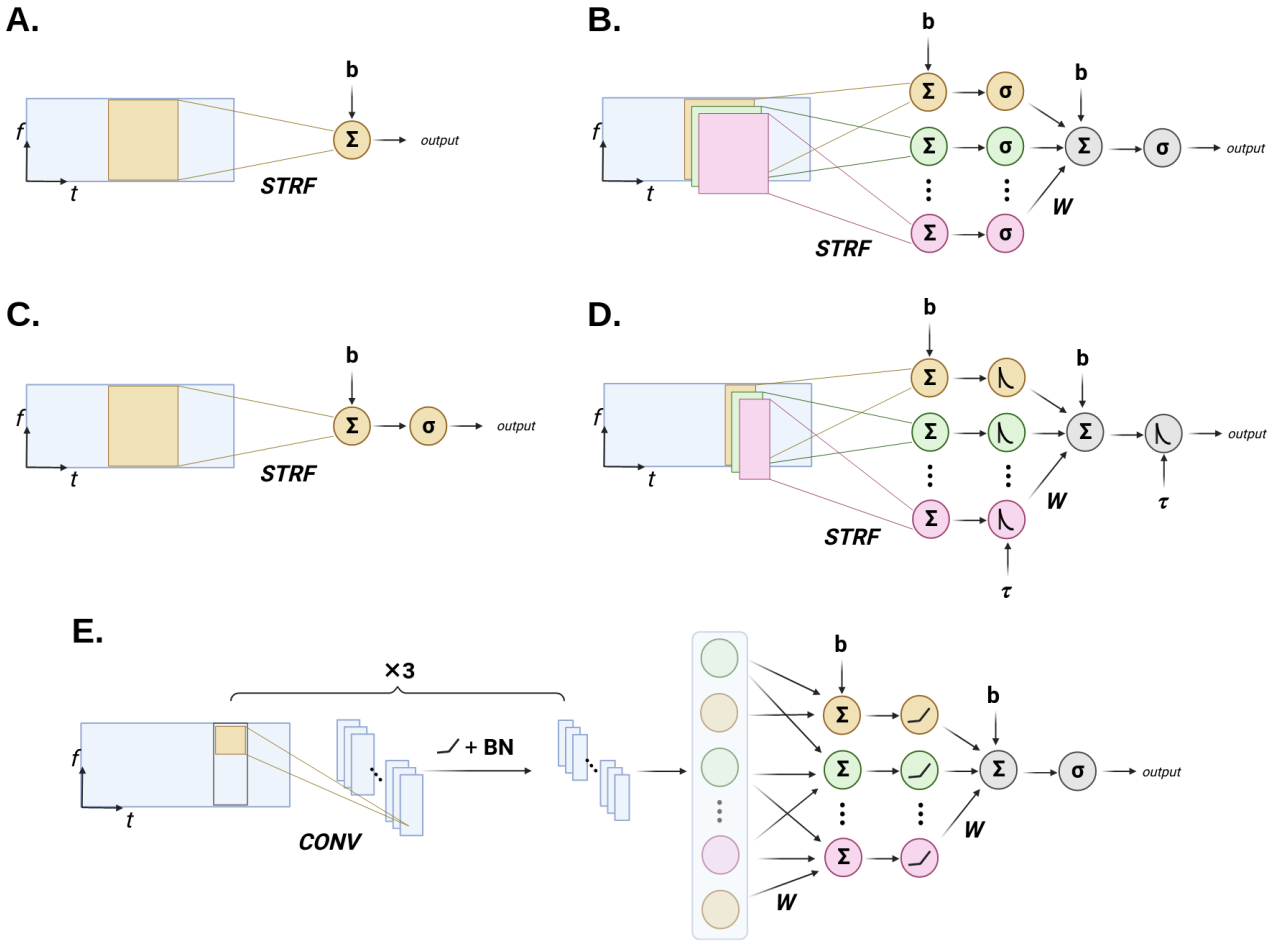

Figure 6. Schematic expliciting the architecture of the different auditory response models used in combination to AdapTrans. See main text and associated papers for a detailed description of each. (**A.**) L model. (**B.**) NRF model. (**C.**) LN model. (**D.**) DNet model. (**E.**) 2D-CNN model.

to zero mean and unit variance accross the training set.

In the NAT4 dataset (Pennington and David, 2022), sound waveforms were converted into cochleagrams with a gammatone filterbank of 18 filters whose central frequencies were logarithmically distributed from 200 Hz to 20 kHz. After a log-compression stage, the temporal resolution was downsampled to 10 ms.

Finally, stimulus spectrograms from the Wehr dataset (Asari et al., 2009) were obtained using a short-term Fourier transform with a Hamming window, followed by a log function. The resulting cochleagrams have a temporal resolution of 5 ms, while the frequency axis is discretized into 49 logarithmically-scaled spectral bins.

Linear Model (L). The canonical Linear (L) model consists of a spectro-temporal window spanning all frequency bands and a large set of temporal delays that is convoluted over the temporal dimension of the stimulus spectrogram. The output of this model at each time step (i.e., the time-step of the most recent delay) is simply a linear projection of past spectro-temporal bins into

a scalar value, to which a bias term is added to account for spontaneous activity. The set of weights associated with each input coefficients is also known as the *Spectro-Temporal Receptive Field* or STRF. Therefore, for a spectro-temporal window spanning F frequency bins and T delays, the number of parameters is $F \times T + 1$. Different parametrizations exist to reduce this number of free parameters (Thorson et al., 2015)(David et al., 2007)(Simon et al., 2007), which we did not adopt to illustrate the performances of the simplest implementation of this model. For the same reasons, we did not apply any regularization technique like ridge regression (Hastie et al., 2001)(Machens et al., 2004) or L1 penalty (Willmore and Smyth, 2003)(Rahman et al., 2019) by setting weight decay to 0. These methods allow to mitigate the high-frequency patterns appearing during optimization on unregularized STRFs, but require computationally intensive and often time-consuming hyperparameter tuning, as in Rahman et al. (2019). Furthermore, we noticed that they did not necessarily prove beneficial in terms of performance in our setup. This observation could be due to our usage of gradient descent, whereas previous literature tended to use order-0 optimization algorithms like boosting (Thorson et al., 2015) (David et al., 2007) to fit these simple models.

Linear-Nonlinear Model (LN). The LN model differs from the L model in that the output of the convolution is passed through a static nonlinearity in the form of a sigmoid:

$$y = \frac{1}{1 + exp(-x)} \tag{7}$$

where x is the output of the Linear model and y is the output of the nonlinearity. Other forms of activation functions are commonly used, such as 4-parameter parameterized sigmoids (Willmore et al., 2016)(Rahman et al., 2019), or double exponentials (Pennington and David, 2023b)(Thorson et al., 2015), but our preliminary results with the latter did not necessarily yield better results than with the standard sigmoid function.

Network Receptive Field (NRF). This model, proposed in Harper et al. (2016), extends the LN model by replacing its unique spectro-temporal weighting windows by several. After a pass through a standard sigmoid activation, the features extracted by each of these channels are then combined into a single output scalar forming the final prediction at the current timestep. With its multi-filter paradigm, authors argued that this model fitted much better actual electrophysiological recordings, due to the fact that auditory neurons react to several spectro-temporal patterns, and not just one.

Dynamic Network (DNet) Model. Rahman et al. (2019) further extended the NRF model by constraining its hidden and output units to follow a recurrent, exponentially decaying relationship over time, similar to a non-spiking Leaky Integrate-and-Fire (LIF) neuron. Authors showed that this replacement of the sigmoid activation by a simple stateful dynamic observed in biology, allows to reduce the span of the STRF windows to a more biologically plausible range, without sacrificing performance. Implementation-wise, removing the spiking condition allows to emulate the leaky recurrence by simply convolving an exponential kernel along the time dimension of each layer's output. We parametrize the exponential kernel the same way as AdapTrans filters, and let automatic differentiation learn the time constant, which we express as follows for numerical stability:

$$\frac{1}{\tau} = \frac{1}{1 + d^2} \tag{8}$$

We mark a difference with these authors, in that we allow the network to learn a different time constant for each hidden unit, instead of a single one that is shared accross the layer.

2D Convolutional Neural Network (CNN). Also based upon convolution operations on the stimulus spectrogram, this last model differs from the preceding in that it is a fully-fledged, deep neural network, with a larger number of stacked convolutional layers of small kernels (i.e. that do not span the entire range of frequencies). Introduced by Pennington and David (2023b) among other CNN-based models, it displayed superior performances on the task of elecrophysiological response fitting, despite its higher number of learnable parameters. Our PyTorch re-implementation aimed at being as close as possible from the original architecture: a feature extraction backbone constituted in a series of three 2D convolutions alternating with nonlinear activations, followed by a prediction head composed of two fully connected layers. Nevertheless, we added a minor update by incorporating batch normalization (BatchNorm) between each convolution and nonlinear activation (LeakyReLU with a negative slope of 0.1), as it constitutes a well appreciated solution to mitigate overfitting among the deep learning community (Ioffe and Szegedy, 2015). Similar to the original paper, we chose to maintain 10 hidden channels within the convolutional backbone, and 90 hidden units in the last layer, the size of penultimate layer being determined by flattening the downsampled spectrogram out of the convolution backbone.

Task and Evaluation of Performance

the Optimization Process. All models were trained using gradient descent and backpropagation, with AdamW optimizer (Loshchilov and Hutter (2019)) and its default PyTorch hyperparameters ($\beta_1 = 0.9$, $\beta_2 = 0.999$). We used a batch size of 1 and a constant learning rate of 10^{-3}, as we empirically found that these values led to better results. We explored different strategies to reduce overfitting in our modelling, e.g. by using weight decay (L2 regularization), Dropout or data augmentation (TimeMasking and FrequencyMasking). As none of

these strategies significantly improved our results, we did not consider them further. At the completion of each training epoch, models were evaluated on the validation set and if the validation loss had decreased in comparison to the previous best model, the new model was saved. Models were trained until there were no improvement during consecutive 50 epochs on the validation set, at which point the training was stopped, the last best-performing model was saved and evaluated on the test set.

Performance metrics. The neural response fitting ability of the different models has been reported using the raw correlation coefficient (Pearsons' r), noted CC_{raw}, between the model's predicted activity and the ground-truth PSTH. However, due to noisy signals and limited number of takes, perfect fits (i.e. $CC_{raw} = 1$) are impossible to get in practice. As a result, in order to give an estimation of the best reachable performance given neuronal and experimental trial-to-trial variability, several metrics have been proposed, such as the normalized explained signal power (Sahani and Linden, 2002) (Machens et al., 2004) or the normalized correlation coefficient CC_{norm}, as defined in Hsu et al. (2004) and Schoppe et al. (2016); we report the latter in this paper. However, contrarily to previous works, which computed a general normalization factor for each neuron and that was applied to all of its stimuli, we decided to normalize *per neuron and per stimulus*, as there can be a variability in the responses depending on both of these factors. Thus, for each neuron and each stimulus, we first computed the CC_{half}, defined as the mean correlation coefficient between the PSTH made from one half of the trials and the PSTH made from the over half, with different splits (up to 126, to follow Willmore et al. (2016)). From this, we can compute the CC_{norm} for this neuron and this stimulus, as:

$$CC_{max} = \sqrt{\frac{2}{1 + \frac{1}{|CC_{half}|}}} \tag{9}$$

Finally, the normalized correlation coefficient can be computed as:

$$CC_{norm} = \frac{CC_{raw}}{CC_{max}} \tag{10}$$

In the extreme case of only one trial being available, we set $CC_{max} = 1$, corresponding to the best-case scenario of a fully repeatable recording, therefore preventing any overestimation of performances by giving a lower bound of the latter, in absence of data.

Cross-validation methodology. We split the dataset into three training, validation and test sets respecting a 70-10-20% ratio. As indicated in the 'Optimization Process', the model is fitted on the training set for a limited number of epochs. At the end of each epoch, the loss over the validation set is computed, and the model with the lowest validation loss is saved at the end of the fitting procedure. The number of training epochs was determined manually such that more epochs would not further decrease the validation loss. Finally, the saved model was evaluated on the test set. This procedure was repeated 10 times for different train-valid-test data splits and model parameters initializations, and the test metrics were averaged across splits.

Note that this model validation method differs from the one employed in Rahman et al. (2019), which is not a "cross-validation" *per se*. In this study, authors kept a fixed (i.e. always the same) subset of data for testing, and used the rest for training and validation. Because of the very small dataset size on NS1 (20 stimulus-response pairs), we found that this methodology was not robust to the selection of the test set, and often resulted in overestimated performances.

Another methodological difference with this study concerns the normalization of correlation coefficients. Authors computed a single CC_{max} coefficient for each unit and for all stimuli presented, giving an average idea of the variability and noise of that unit. With the concern of evaluating models with maximum precision, we instead computed one CC_{max} coefficient per unit and per stimulus. Therefore, during evaluation, raw CCs between our model's prediction and actual PSTHs were normalized by the factor corresponding to these particular neurons and sounds. Again, we found that Rahman et al. (2019)'s method of normalization overestimated the CC_{norm} of models. We believe that the neural response fitting task is inherently difficult, and that our validation method, by being more pragmatic, increases the margin for improvement on this task. Indeed, in absolute and with a well normalized CC, a CC_{norm} of 1 is reachable; it is only a matter of data-preprocessing and model –the latter guided by knowledge in neuroscience and machine learning– to bridge the remaining gap.

Reproducibility

Our simulations were done in Python using the popular automatic differentiation library PyTorch. Upon publication of this article, we will make our code freely available on Github at the following address: `https://github.com/urancon/deepSTRF`. A code example is provided in Supplementary Note 2, to showcase its simplicity and encourage other researchers to build upon it. Jobs required less than 2 GiB and were executed on Nvidia Titan V GPUs, taking 10 to 15 hours on NS1, depending on the complexity of the model.

Electrophysiology datasets openly available in this field often come in a variety of formats that each necessitates a specific pre-processing. Research teams also use their own performance metric, without systematically comparing their results to those reported in previ-

ous papers. We identify at least three drawbacks due to this lack of harmonization, that could hinder the development of new quality research:

- First, a lack of harmonization could induce errors and biases, as pre-processing methods could differ from one dataset to another
- Each team has its own preferences for tools; some use MATLAB, which is proprietary, others prefer Python (open-source). Switching from one to the other can be unreasonably costly, both in terms of time and money.
- Finally, this heterogeneity can be very overwhelming and deterring from publishing quality research, because of poor reproducibility.

For these particular reasons, there have been a few attempts to federate the scientific community around data hubs such as the Neural Prediction Challenge[4] or software toolkits like the NEMS library[5]. However, we found that the latter can be outdated, not maintained anymore, or not adapted to the current standards of machine learning workflows.
As a result, we are committed to openly publishing all major codes that led to the results presented in this paper. Because Python is open-source and has become the language of choice for machine learning over the recent years[6], our simulations were done using the popular automatic differentiation library PyTorch[7]. In addition to our models and scripts to train them, we provide more user-friendly PyTorch Dataset classes for each source of data used in this study. By building this repository, our constant goal has been to make an easy-to-use software material that is as plug-and-play as possible. We hope that the code architecture we have adopted will inspire other researchers by easing the development of future work, and ultimately contribute to make the bridge between experimental and theoretical research.

Acknowledgments

Our thanks go to Céline Cappe for her valuable insights on the mammalian auditory system, and to Corentin Nivelet-Etcheberry for his help on pre-processing the datasets and fitting the models.

Fundings

This study was supported by a grant from the Agence Nationale de la Recherche (ANR-21-CE28-0021, ANR PRC ReViS-MD) and by a FLAG-ERA funding (Joint Transnational Call 2019, project DOMINO), both awarded to BRC.

[4] https://neuralprediction.org/npc/index.php
[5] https://github.com/LBHB/NEMS/tree/main
[6] for a quantitative comparison of utilization of major deep learning frameworks, see https://paperswithcode.com/trends
[7] https://pytorch.org/

Bibliography

Akimov, A. G., Egorova, M. A., and Ehret, G. (2017). Spectral summation and facilitation in on- and off-responses for optimized representation of communication calls in mouse inferior colliculus. *European Journal of Neuroscience*, 45(3):440–459. doi: https://doi.org/10.1111/ejn.13488.

Anderson, L. A. and Linden, J. F. (2016). Mind the gap: Two dissociable mechanisms of temporal processing in the auditory system. *The Journal of Neuroscience*, 36(6):1977–1995. doi: 10.1523/JNEUROSCI.1652-15.2016.

Asari, C. K., Hiroki andMachens, Wehr, M. S., and Zador, A. M. Auditory cortex and thalamic neuronal responses to various natural and synthetic sounds, (2009). URL https://crcns.org/data-sets/ac/ac-1/about.

Asari, H. and Zador, A. M. (2009). Long-lasting context dependence constrains neural encoding models in rodent auditory cortex. *Journal of Neurophysiology*, 102(5):2638–2656. doi: 10.1152/jn.00577.2009.

Bondanelli, G., Deneux, T., Bathellier, B., and Ostojic, S. (2021). Network dynamics underlying OFF responses in the auditory cortex. *eLife*, 10:e53151. doi: 10.7554/eLife.53151.

Cavaco, S. and Lewicki, M. S. (2007). Statistical modeling of intrinsic structures in impacts sounds. *The Journal of the Acoustical Society of America*, 121(6):3558–3568. doi: 10.1121/1.2729368.

David, S. V., Mesgarani, N., and Shamma, S. A. (2007). Estimating sparse spectro-temporal receptive fields with natural stimuli. *Network: Computation in Neural Systems*, 18(3):191–212. doi: 10.1080/09548980701609235.

Dean, I., Harper, N. S., and McAlpine, D. (2005). Neural population coding of sound level adapts to stimulus statistics. *Nature Neuroscience*, 8(12):1684–1689. doi: 10.1038/nn1541.

Dean, I., Robinson, B. L., Harper, N. S., and McAlpine, D. (2008). Rapid neural adaptation to sound level statistics. *Journal of Neuroscience*, 28(25):6430–6438. doi: 10.1523/JNEUROSCI.0470-08.2008.

Deneux, T., Kempf, A., Daret, A., Ponsot, E., and Bathellier, B. (2016). Temporal asymmetries in auditory coding and perception reflect multi-layered nonlinearities. *Nature Communications*, 7(1):12682. doi: 10.1038/ncomms12682.

Fishbach, A., Nelken, I., and Yeshurun, Y. (2001). Auditory edge detection: A neural model for physiological and psychoacoustical responses to amplitude transients. *Journal of Neurophysiology*, 85(6):2303–2323. doi: 10.1152/jn.2001.85.6.2303.

Gallego, G., Delbrück, T., Orchard, G., Bartolozzi, C., Taba, B., Censi, A., Leutenegger, S., Davison, A. J., Conradt, J., Daniilidis, K., and Scaramuzza, D. (2022). Event-based vision: A survey. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 44(1):154–180. doi: 10.1109/TPAMI.2020.3008413.

Gjorgjieva, J., Sompolinsky, H., and Meister, M. (2014). Benefits of pathway splitting in sensory coding. *The Journal of Neuroscience*, 34(36):12127–12144. doi: 10.1523/JNEUROSCI.1032-14.2014.

Harper, N. S., Schoppe, O., Willmore, B. D. B., Cui, Z., Schnupp, J. W. H., and King, A. J. (2016). Network Receptive Field Modeling Reveals Extensive Integration and Multi-feature Selectivity in Auditory Cortical Neurons. *PLOS Computational Biology*, 12(11):e1005113. doi: 10.1371/journal.pcbi.1005113.

Hartley, D. E. H., Dahmen, J. C., King, A. J., and Schnupp, J. W. H. (2011). Binaural sensitivity changes between cortical on and off responses. *Journal of Neurophysiology*, 106(1):30–43. doi: 10.1152/jn.01070.2010. _eprint: https://doi.org/10.1152/jn.01070.2010.

Hastie, T. J., Tibshirani, R., and Friedman, J. H. The elements of statistical learning. (2001). URL https://api.semanticscholar.org/CorpusID:58068920.

He, J. (2001). ON and OFF pathways segregated at the auditory thalamus of the guinea pig. *The Journal of Neuroscience*, 21(21):8672–8679. doi: 10.1523/JNEUROSCI.21-21-08672.2001.

He, J. (2002). Off responses in the auditory thalamus of the guinea pig. *Journal of Neurophysiology*, 88(5):2377–2386. doi: 10.1152/jn.00083.2002.

Henry, K. R. (1985). ON and OFF components of the auditory brainstem response have different frequency- and intensity-specific properties. *Hearing Research*, 18(3):245–251. doi: 10.1016/0378-5955(85)90041-3.

Henry, K. R. (1985). Tuning of the auditory brainstem OFF responses is complementary to tuning of the auditory brainstem ON response. *Hearing Research*, 19(2):115–125. doi: 10.1016/0378-5955(85)90115-7.

Hillyard, S. A. and Picton, T. W. (1978). ON and OFF components in the auditory evoked potential. *Perception & Psychophysics*, 24(5):391–398. doi: 10.3758/BF03199736.

Hsu, A., Borst, A., and Theunissen, F. (2004). Quantifying variability in neural responses and its application for the validation of model predictions. *Network (Bristol, England)*, 15:91–109. doi: 10.1088/0954-898X/15/2/002.

Ioffe, S. and Szegedy, C. (2015). Batch normalization: Accelerating deep network training by reducing internal covariate shift. *CoRR*, abs/1502.03167.

Jin, J. Z., Weng, C., Yeh, C.-I., Gordon, J. A., Ruthazer, E. S., Stryker, M. P., Swadlow, H. A., and Alonso, J.-M. (2008). On and off domains of geniculate afferents in cat primary visual cortex. *Nature Neuroscience*, 11(1):88–94. doi: 10.1038/nn2029.

Kadir, S. N., Goodman, D. F. M., and Harris, K. D. High-dimensional cluster analysis with the masked em algorithm, (2013).

Kasai, M., Ono, M., and Ohmori, H. (2012). Distinct neural firing mechanisms to tonal stimuli offset in the inferior colliculus of mice in vivo. *Neuroscience Research*, 73(3):224–237. doi: 10.1016/j.neures.2012.04.009.

Kopp-Scheinpflug, C., Tozer, A., Robinson, S., Tempel, B., Hennig, M., and Forsythe, I. (2011). The sound of silence: Ionic mechanisms encoding sound termination. *Neuron*, 71(5):911–925. doi: 10.1016/j.neuron.2011.06.028.

Kopp-Scheinpflug, C., Sinclair, J. L., and Linden, J. F. (2018). When sound stops: Offset responses in the auditory system. *Trends in Neurosciences*, 41(10):712–728. doi: 10.1016/j.tins.2018.08.009.

Li, H., Wang, J., Liu, G., Xu, J., Huang, W., Song, C., Wang, D., Tao, H. W., Zhang, L. I., and Liang, F. (2021). Phasic off responses of auditory cortex underlie perception of sound duration. *Cell Reports*, 35(3):109003. doi: 10.1016/j.celrep.2021.109003.

Liu, J., Whiteway, M. R., Sheikhattar, A., Butts, D. A., Babadi, B., and Kanold, P. O. (2019). Parallel processing of sound dynamics across mouse auditory cortex via spatially patterned thalamic inputs and distinct areal intracortical circuits. *Cell Reports*, 27(3):872–885.e7. doi: 10.1016/j.celrep.2019.03.069.

Loshchilov, I. and Hutter, F. Decoupled weight decay regularization. In *7th International Conference on Learning Representations, ICLR 2019, New Orleans, LA, USA, May 6-9, 2019*. OpenReview.net, (2019). URL https://openreview.net/forum?id=Bkg6RiCqY7.

Machens, C. K., Wehr, M. S., and Zador, A. M. (2004). Linearity of Cortical Receptive Fields Measured with Natural Sounds. *The Journal of Neuroscience*, 24(5):1089–1100. doi: 10.1523/JNEUROSCI.4445-03.2004.

Marr, D. *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information*. Henry Holt and Co., Inc., New York, NY, USA, (1982). ISBN 0716715678.

Mcdermott, J., Schemitsch, M., and Simoncelli, E. (2013). Summary statistics in auditory perception. *Nature neuroscience*, 16. doi: 10.1038/nn.3347.

Pachitariu, M., Steinmetz, N., Kadir, S., Carandini, M., and D., H. K. (2016). Kilosort: realtime spike-sorting for extracellular electrophysiology with hundreds of channels. *bioRxiv*. doi: 10.1101/061481.

Pennington, J. and David, S. Auditory cortex single unit population activity during natural sound presentation – dataset, (2023). URL https://doi.org/10.5281/zenodo.7796574.

Pennington, J. R. and David, S. V. Can deep learning provide a generalizable model for dynamic sound encoding in auditory cortex? preprint, Neuroscience, (2022). URL http://biorxiv.org/lookup/doi/10.1101/2022.06.10.495698.

Pennington, J. R. and David, S. V. (2023). A convolutional neural network provides a generalizable model of natural sound coding by neural populations in auditory cortex. *PLOS Computational Biology*, 19(5):e1011110. doi: 10.1371/journal.pcbi.1011110.

Phillips, D., Hall, S., and Boehnke, S. (2002). Central auditory onset responses, and temporal asymmetries in auditory perception. *Hearing Research*, 167(1):192–205. doi: https://doi.org/10.1016/S0378-5955(02)00393-3.

Qin, L., Chimoto, S., Sakai, M., Wang, J., and Sato, Y. (2007). Comparison between offset and onset responses of primary auditory cortex on – off neurons in awake cats. *Journal of Neurophysiology*, 97(5):3421–3431. doi: 10.1152/jn.00184.2007.

Qin, L., Liu, Y., Wang, J., Li, S., and Sato, Y. (2009). Neural and behavioral discrimination of sound duration by cats. *The Journal of Neuroscience*, 29(50):15650–15659. doi: 10.1523/JNEUROSCI.2442-09.2009.

Rabinowitz, N. C., Willmore, B. D., Schnupp, J. W., and King, A. J. (2011). Contrast gain control in auditory cortex. *Neuron*, 70(6):1178–1191. doi: 10.1016/j.neuron.2011.04.030.

Rahman, M., Willmore, B. D. B., King, A. J., and Harper, N. S. (2019). A dynamic network model of temporal receptive fields in primary auditory cortex. *PLoS Comput Biol*, 15(5): e1006618. doi: 10.1371/journal.pcbi.1006618.

Rahman, M., Willmore, B. D. B., King, A. J., and Harper, N. S. (2020). Simple transformations capture auditory input to cortex. *Proceedings of the National Academy of Sciences*, 117 (45):28442–28451. doi: 10.1073/pnas.1922033117.

Rhode, W. S. and Smith, P. H. (1985). Characteristics of tone-pip response patterns in relationship to spontaneous rate in cat auditory nerve fibers. *Hearing Research*, 18(2): 159–168. doi: 10.1016/0378-5955(85)90008-5.

Sadagopan, S., Kar, M., and Parida, S. (2023). Quantitative models of auditory cortical processing. *Hearing Research*, 429:108697. doi: 10.1016/j.heares.2023.108697.

Sahani, M. and Linden, J. F. How linear are auditory cortical responses? In *Neural Information Processing Systems*, (2002). URL https://api.semanticscholar.org/CorpusID:14075981.

Scholl, B., Gao, X., and Wehr, M. (2010). Nonoverlapping sets of synapses drive on responses and off responses in auditory cortex. *Neuron*, 65(3):412–421. doi: 10.1016/j.neuron.2010.01.020.

Schoppe, O., Harper, N. S., Willmore, B. D. B., King, A. J., and Schnupp, J. W. H. (2016). Measuring the Performance of Neural Models. *Front. Comput. Neurosci.*, 10. doi: 10.3389/fncom.2016.00010.

Simon, J. Z., Depireux, D. A., Klein, D. J., Fritz, J. B., and Shamma, S. A. (2007). Temporal symmetry in primary auditory cortex: Implications for cortical connectivity. *Neural Computation*, 19(3):583–638. doi: 10.1162/neco.2007.19.3.583.

Sollini, J., Chapuis, G. A., Clopath, C., and Chadderton, P. (2018). ON-OFF receptive fields in auditory cortex diverge during development and contribute to directional sweep selectivity. *Nature Communications*, 9(1):2084. doi: 10.1038/s41467-018-04548-3.

Solyga, M. and Barkat, T. R. (2021). Emergence and function of cortical offset responses in sound termination detection. *eLife*, 10:e72240. doi: 10.7554/eLife.72240.

Suga, N. (1964). Single unit activity in cochlear nucleus and inferior colliculus of echolocating bats. *The Journal of Physiology*, 172(3):449–474. doi: 10.1113/jphysiol.1964.sp007432.

Takahashi, H., Nakao, M., and Kaga, K. (2004). Cortical mapping of auditory-evoked offset responses in rats. *NeuroReport*, 15(10):1565–1569. doi: 10.1097/01.wnr.0000134848.63755.5c.

Thorson, I. L., Liénard, J., and David, S. V. (2015). The essential complexity of auditory receptive fields. *PLOS Computational Biology*, 11(12):e1004628. doi: 10.1371/journal.pcbi.1004628.

Threlkeld, S., Penley, S., Rosen, G., and Fitch, R. (2008). Detection of silent gaps in white noise following cortical deactivation in rats. *Neuroreport*, 19:893–8. doi: 10.1097/WNR.0b013e3283013d7e.

Tian, B., Kuśmierek, P., and Rauschecker, J. P. (2013). Analogues of simple and complex cells in rhesus monkey auditory cortex. *Proceedings of the National Academy of Sciences*, 110(19):7892–7897. doi: 10.1073/pnas.1221062110.

Wang, X.-J., Hu, H., Huang, C., Kennedy, H., Li, C., Logothetis, N., Lu, Z.-L., Luo, Q., Poo, M.-m., Tsao, D., Wu, S., Wu, Z., Zhang, X., and Zhou, D. (2020). Computational neuroscience: a frontier of the 21st century. *National Science Review*, 7. doi: 10.1093/nsr/nwaa129.

Weible, A. P., Moore, A. K., Liu, C., DeBlander, L., Wu, H., Kentros, C., and Wehr, M. (2014). Perceptual gap detection is mediated by gap termination responses in auditory cortex. *Current Biology*, 24(13):1447–1455. doi: 10.1016/j.cub.2014.05.031.

Westheimer, G. (2007). The ON–OFF dichotomy in visual processing: From receptors to perception. *Progress in Retinal and Eye Research*, 26(6):636–648. doi: 10.1016/j.preteyeres.2007.07.003.

Willmore, B. and Smyth, D. (2003). Methods for first-order kernel estimation: Simple-cell receptive fields from responses to natural scenes. *Network (Bristol, England)*, 14:553–77. doi: 10.1088/0954-898X/14/3/309.

Willmore, B. D., Schoppe, O., King, A. J., Schnupp, J. W., and Harper, N. S. (2016). Incorporating Midbrain Adaptation to Mean Sound Level Improves Models of Auditory Cortical Processing. *J. Neurosci.*, 36(2):280–289. doi: 10.1523/JNEUROSCI.2441-15.2016.

Wohrer, A., Kornprobst, P., and Viéville, T. (2007). Virtual retina: A biological retina model and simulator, with contrast gain control. *Journal of computational neuroscience*. doi: 10.1007/s10827-008-0108-4.

Xu, N., Fu, Z.-Y., and Chen, Q.-C. (2014). The function of offset neurons in auditory information processing. *Translational Neuroscience*, 5(4). doi: 10.2478/s13380-014-0235-5.

Supplementary Note 1: Mathematical derivation of AdapTrans properties

Transfer functions

We demonstrate here how to compute the formulas for the transfer functions of Eq.4. Since the principle is the same for each polarity, we only provide the example of the ON channel. The transfer function is the Z-transform of the discrete-time impulse response (Eq.1):

$$\begin{aligned}
H_{ON}(z) = Z\{h_{ON}[n]\} &= \sum_{n=0}^{+\infty} h_{ON}[n] z^{-n} \\
&= h[0] + \sum_{n=1}^{+\infty} h_{ON}[n] z^{-n} \\
&= 1 - Cw \sum_{n=1}^{+\infty} a^{n-1} z^{-n} \\
&= 1 - Cwa^{-1} \sum_{n=1}^{+\infty} (\frac{a}{z})^n \\
&= 1 - (Cwa^{-1} \sum_{n=0}^{+\infty} (\frac{a}{z})^n - Cwa^{-1}) \\
&= 1 + Cwa^{-1} - Cwa^{-1} \times \frac{1}{1 - \frac{a}{z}} \\
&= ... \\
&= \frac{1 - (a + w - aw) z^{-1}}{1 - a z^{-1}}
\end{aligned} \tag{S1}$$

Magnitude-frequency curves (Bode)

From the expression of the transfer function, the formula for the magnitude-frequency response (expressed in dB) follows:

$$\begin{aligned}
A_{ON}^{dB}(\omega) = 20\log(|H_{ON}(e^{j\omega})|) &= 10\log(|H_{ON}(e^{j\omega})|^2) \\
&= 10\log(\frac{|1 - (a + w - aw) e^{-j\omega}|^2}{|1 - a e^{-j\omega}|^2}) \\
&= 10\log(\frac{|(1 - a + w - aw)\cos(-j\omega) - \sin(-j\omega)|^2}{|(1 - a)\cos(-j\omega) - a\sin(-j\omega)|^2}) \\
&= 10\log(\frac{((1 - a + w - aw)\cos(\omega))^2 + ((a + w - aw)\sin(\omega))^2}{((1 - a)\cos(\omega))^2 + (a\sin(\omega))^2}) \\
&= ... \\
&= 10\log(\frac{1 + (a + w - aw)^2 - 2(a + w - aw)\cos(\omega)}{1 + a^2 - 2a\cos(\omega)})
\end{aligned} \tag{S2}$$

Poles and zeroes

AdapTrans filters have one pole and one zero, which can be read directly from the expression of the transfer function. For instance, in the case of the ON polarity, the pole is a and the zero is $a + w - aw$.

Recursive equation

From the expression of AdapTrans transfer functions, we can derive their corresponding discrete-time recursive equation:

$$\begin{cases} y_{ON}[n] = x[n] - (a + w - aw) \times x[n-1] + a \times y_{ON}[n-1] \\ y_{OFF}[n] = -w \times x[n] + (1 - a + aw) \times x[n-1] + a \times y_{OFF}[n-1] \end{cases} \tag{S3}$$

This recurrent formulation has the advantage of implementing an actual IIR filter, rather than a long FIR filter. IIR filters are particularly suited for real-time online processing on dedicated hardware such as Digital Signal Processors (DSPs) or Field-Programmable Gate Arrays (FPGAs).

Supplementary Note 2: Code demonstration

We demonstrate here the simplicity of our code, hosted at the url https://github.com/urancon/deepSTRF, by showing its basic Pytorch flow. As the code is continuously updated and has been simplified for pedagogical purposes, minor differences can exist between the following snippet and the online version.

```python
import torch
from torch.utils.data import DataLoader

from deepSTRF.datasets import NS1
from deepSTRF.model_zoo import DNet
from deepSTRF.metrics import performance_metrics

dataset = NS1(path='../datasets/NS1/data', stimuli=('nat',), neuron_indexes='all')
model = DNet(n_bands=49, temporal_window_size=5, n_hidden=20, adapTrans=True)

for neuron_idx in dataset.neuron_indices:

    dataset.select_neuron(neuron_idx)

    len_train, len_val, len_test = 0.7*len(dataset), 0.1*len(dataset), 0.2*len(dataset)
    train_set, valid_set, test_set = torch.utils.data.random_split(dataset, [len_train, len_val, len_test])
    train_dataloader = DataLoader(train_set, shuffle=True)
    valid_dataloader = DataLoader(valid_set, shuffle=False)
    test_dataloader = DataLoader(test_set, shuffle=False)

    for epoch in range(n_epochs):

        for spectrogram, responses, ccmax in train_dataloader:

            prediction = model(spectrogram)

            CCraw, CCnorm = performance_metrics(prediction, responses, ccmax)

            loss = MSE(prediction, responses)
            loss.backward()
            optimizer.step()
            optimizer.zero_grad()


```

Supplementary Note 3: AdapTrans offset response latencies as a function of ramp duration

The simulated experimental setup described in Figure 2A allows to extract the adapTrans offset response latency as a function of the ramp duration. Figure S1 below shows this relationship for different pairs of w parameter and OFF time constant (tau). Our model predicts that latency increases as fall ramps become less abrupt. To our knowledge, this has never been tested by electrophysiologists. We hope that future experimental studies will address this question.

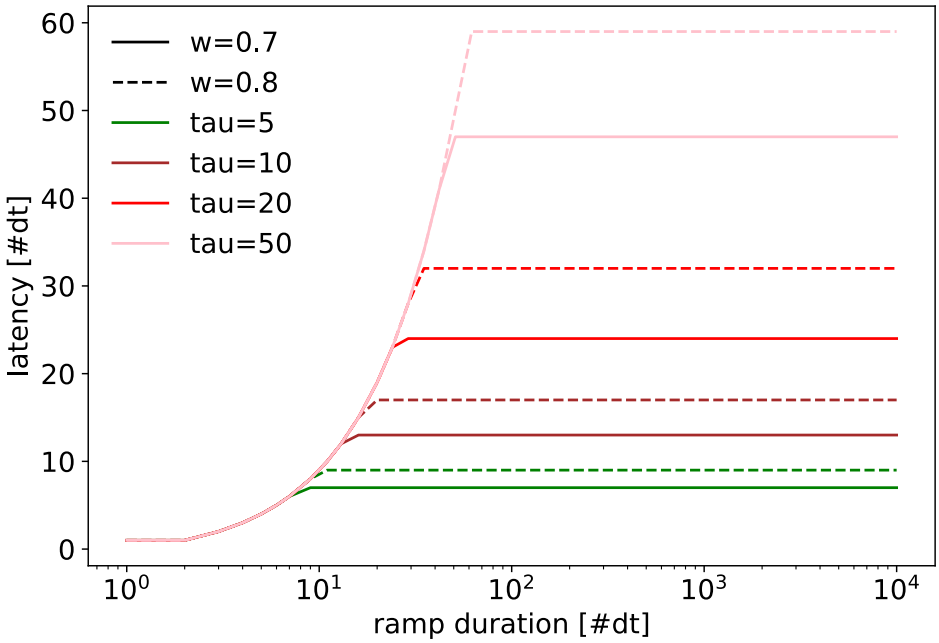

Figure S1. AdapTrans offset response latency as a function of ramp duration. Both are expressed in number of simulation timesteps.