

Auditory memory for random time patterns in cochlear implant listeners

HiJee Kang^{1*}

Olivier Macherey²

Stéphane Roman³

Daniel Pressnitzer¹

1. Laboratoire des Systèmes Perceptifs, Département d'études cognitives, École Normale Supérieure, PSL University, CNRS, 29 rue d'Ulm, 75005, Paris, France
2. Aix-Marseille University, CNRS, LMA, 4 impasse Nikola Tesla, CS 40006, Centrale Marseille, France
3. Dept. of Pediatric Otolaryngology and Neck Surgery, Aix-Marseille University, 264 rue Saint Pierre, 13005, Marseille, France

Email: hijee kang@gmail.com

Running title: Memory for time patterns in CI listeners

Keywords: cochlear implant, temporal pattern, learning, memory

*Also at: Department of Neuroscience, City University of Hong Kong, Hong Kong

Abstract

Learning about new sounds is essential for cochlear-implant and normal-hearing listeners alike, with the additional challenge for implant listeners that spectral resolution is severely degraded. Here, a task measuring the rapid learning of slow or fast stochastic temporal sequences (Kang et al., 2017) was performed by cochlear-implant ($N = 10$) and normal-hearing ($N = 9$) listeners, using electric or acoustic pulse sequences, respectively. Rapid perceptual learning was observed for both groups, with highly similar characteristics. Moreover, for cochlear-implant listeners, an additional condition tested ultra-fast electric pulse sequences that would be impossible to represent temporally when presented acoustically. This condition also demonstrated learning. Overall, the results suggest that cochlear-implant listeners have access to the neural plasticity mechanisms needed for the rapid perceptual learning of complex temporal sequences.

I. Introduction

To navigate realistic sound scenes, listeners must combine the acoustic cues reaching their ears with auditory knowledge arising from past experience: Am I hearing the voice of a familiar person? Is the timbre of my friend's voice relaxed or anxious? Which phonemes are being uttered? Over the last ten years, it has been shown that adult normal-hearing (NH) listeners can display a remarkable form of rapid auditory perceptual learning (Agus et al., 2010). Here, we used a similar paradigm to probe rapid learning in adult listeners using a cochlear implant (CI). To make a fair comparison, we used a variant of the paradigm relying purely on temporal cues (Kang et al., 2017; 2018), because such cues can be represented peripherally at least as well for CI listeners as for NH listeners. The aim of this study was two-fold: first, to ascertain whether or not rapid perceptual learning processes are available to post-lingually deafened CI listeners; second, to use direct electrical stimulation of the auditory nerve to better characterize the range of temporal cues amenable to rapid perceptual learning.

The original version of the rapid memory task used samples of noise to probe perceptual learning (Agus et al., 2010; Agus and Pressnitzer, 2013; Viswanathan et al., 2016). Briefly, listeners were presented with short trials (e.g., 1 s) containing either novel noises, or, unbeknownst to them, re-occurring noise samples that had been presented previously during an experimental block. An ancillary task was designed to measure unsupervised learning. Each trial could be either a full-duration sample of white noise, or a half-duration sample of noise seamlessly repeated to make up a full-duration trial. Overall, performance on this within-trial repetition detection task improved over the course of an experimental block for re-occurring noise samples, which was taken as evidence of a rapid learning of complex sounds in adult NH listeners. The learning process was robust and unsupervised, which would likely make it relevant to how listeners accumulate

knowledge about re-occurring sounds in realistic environments.

Learning novel sounds is arguably an even more acute need for CI listeners than for NH listeners. Post-lingually implanted adults have to transition from acoustic hearing to electric hearing, which must involve a thorough re-learning of the mapping between auditory cues and sound meaning. Furthermore, prelingually implanted children may receive cues that are transmitted via the implant but not available in acoustic hearing, such as fast electrical pulses in nominally low-frequency regions of the cochlea, and it is yet unclear whether such cues can be learnt. Previous studies have shown the importance of perceptual training for CI listeners to improve the outcome of implantation, in particular for speech perception (James et al., 2019; Schumann et al., 2014) or music perception (Fu and Galvin, 2007). On an even more basic level, the frequency-to-place mismatch arising from the uncertainty and limitations of electrode insertion must also be compensated by learning, which seems possible if it is not too severe (Rosen et al., 1999; Schumann et al., 2014; Svirsky et al., 2015).

With the exception of James et al.'s (2019) study, who showed that some of their best-performing CI subjects could exhibit relatively good speech reception only one day post activation, learning effects in CI listeners have mainly been documented over relatively long time scales. In particular, the time course of improvement in speech intelligibility seems to be generally slow, taking up to several months (Holden et al., 2013; James et al., 2019). This appears to contrast with the very fast perceptual learning observed with NH listeners for noise-vocoded speech, which can be viewed as a simulation of CI processing. For instance, Davis et al. (2005) reported that NH subjects improved their word intelligibility scores from near 0% to about 70% following the presentation of only 30 noise-vocoded sentences. Longer time courses for learning can also be observed using noise-vocoded speech when a frequency shift is introduced on spectral cues

(Faulkner et al., 2003; Rosen et al., 1999). These apparent discrepancies in the time course of perceptual learning for CI listeners and NH subjects may be due to several factors.

First, CI listeners experience various amounts of auditory deprivation before being implanted, so it is possible that such deprivation impairs the underlying neural mechanisms recruited by rapid perceptual learning. The available neurophysiological evidence is not sufficient to draw firm conclusions about this hypothesis. In NH listeners, brain imaging studies using magnetoencephalography (MEG; Luo et al., 2013), functional magnetic resonance imaging (fMRI; Kumar et al., 2014) or electroencephalography (EEG; Andrillon et al., 2015) have implicated sensory regions in the rapid learning process, more specifically secondary auditory cortex. Rapid plasticity in sensory regions may thus complement the well-established involvement of the hippocampus in auditory sequence learning (Barascud et al., 2016; Bianco et al., 2020; Jablonowski et al., 2018; Kumar et al., 2014). In CI listeners, implantation has been shown to trigger a cascade of neural plasticity processes in adult listeners, from sensory to language or even visuo-motor areas (Giraud et al., 2001; see Glennon et al., 2020 for a recent review). It is nevertheless unclear whether such wide-reaching changes are enabled by intact perceptual learning abilities, or rather, if they compensate for reduced underlying perceptual learning abilities.

Second, there are differences between the peripheral patterns of neural activity produced by acoustic and electric stimulation, because of neural degeneration in CI users and of the neural recruitment properties of electrical stimulation. It is, for instance, well-known that listening through an implant severely reduces the accuracy of spectral information (e.g., Henry and Turner, 2003). The possibility thus exists that the cues provided by an implant are difficult to learn for an auditory system attuned to acoustic stimulation. Most of the previous studies probing rapid perceptual learning (e.g., Agus et al., 2010, 2013; Andrillon et al., 2015) used Gaussian noise as

the stochastic stimulus to be learned. Noise obviously contains both spectral and temporal cues, from which the spectral cues would be differently represented in CI and NH listeners. This would possibly favor NH listeners if performance was compared across populations, even with underlying identical rapid learning abilities. One solution to this issue is to focus on temporal information. Indeed, temporal amplitude modulation seems largely preserved in CI listeners, at least for modulation rates up to about 300 Hz (McKay et al., 2000; Shannon, 1985; Zeng, 2002). There is further evidence that the performance of CI listeners is similar to that of NH listeners in temporal processing tasks such as gap detection or musical rhythm perception (Gfeller and Lansing, 1991; Kong et al., 2004; Penner, 1977; Phillips-Silver et al., 2015; Shannon, 1989). On a neural level, the encoding of cortical responses to temporal cues is also similar between electric and acoustic hearing (Nourski et al., 2013). Interestingly, training was shown to be able to improve the accuracy of the neural temporal cues in the auditory cortex in animal models, for acoustic hearing (Schnupp et al., 2006) or electric hearing (Vollmer and Beitel, 2011; Vollmer et al., 2017). Therefore, focusing on temporal cues, which are likely to be highly relevant for CI listeners, seems appropriate to probe perceptual learning processes for CI listeners.

The present study focused on the rapid perceptual learning of purely temporal cues. Such rapid learning may only be part of the learning processes involved for instance in the improvement of speech intelligibility over time, but could play a crucial role in non-speech tasks such as timbre identification or sound source recognition (Agus et al., 2019). Importantly, such rapid learning tasks have not yet been systematically studied for CI listeners. Among the previous studies that used the rapid memory task, Kang et al. (2017) showed that rapid perceptual learning was observed for pulse trains delivering primarily timing information in NH listeners, over a broad range of temporal inter-pulses intervals (from milliseconds to hundreds of milliseconds). The paradigm has

also been extended to other sensory modalities, by using light flashes or tactile impulses to carry time intervals, with again an observation of rapid perceptual learning (Kang et al., 2018). Here, we probe yet another modality, electric hearing, by using direct stimulation of the auditory nerve of CI listeners through the research interface of the implant. We used electrical pulses transmitted quasi-simultaneously to four electrodes of the CI, covering the useful frequency range of the device for each participant. A comparison group of NH listeners was also tested, using acoustic click trains with the same temporal characteristics as those presented to the CI group (the acoustic click trains were also high-pass filtered to prevent spectral cues, see Methods for details). Two average click rates, 10 Hz (Slow) and 40 Hz (Fast), were tested in both groups. The average rates were chosen to ensure that the early representation of the acoustic cues would be accurate for both CI and NH participants. An additional pulse rate, 300 Hz (Ultra-Fast), was used for the CI group only, a situation testing temporal cues that would be impossible to experience acoustically because such ultra-fast click rates would induce accompanying spectral cues in NH listeners, due to cochlear filtering. The experiments thus aimed to evaluate the rapid learning of temporal sequences in CI listeners, and to compare its characteristics with the rapid learning expected in NH listeners for similar stimuli (Kang et al., 2017).

II. Experiment

A. Participants

A total of ten CI listeners of Med-EL devices took part in the experiment (age range: 38 – 77 years, $M = 59.8$, $SD = 15.3$, 5 male, c.f. Table 1 for details). All participants were unilateral CI listeners with 12 electrode channels, except one bilateral user of the same device (M004 in the table below). CI listeners were recruited in the Marseille area from a pool of CI listeners regularly tested in the laboratory. The CI branch of the experiment consisted of two different test sessions.

Nine and eight participants, out of ten participants overall, took part in Test session 1 and Test session 2, respectively, and seven of them took part in both test sessions. The experiment with CI listeners was approved by a local research ethics committee (Eudract 2012-A00438-35).

Table 1. Details for all CI participants.

Subject ID	Age	Duration of CI usage (y)	Etiology of deafness	Duration of profound bilateral deafness (y)	Electrode array	Type of implant	Sessions participated
M004	77	9	Unknown	10	standard long	sonata ti100	1 and 2
M005	39	5	Congenital hereditary	20	standard long	concerto	1
M010	38	9	Congenital	16	standard long	sonata ti100	1 and 2
M012	69	7	Unknown	2	standard long	pulsar 100	1
M013	75	4	Unknown	1	standard long	sonata ti100	1 and 2
M014	61	3	Auto-immune disease	1	flex 28	concerto	1 and 2
M015	51	3	Unknown	15	flex 28	concerto	1 and 2
M016	45	3	Congenital hereditary	20	flex 28	concerto	1 and 2
M017	70	2	Unknown	3	flex 28	concerto	1 and 2
M018	73	1	Otosclerosis	6	flex 28	synchrony	1 and 2

Nine NH listeners were recruited in the Parisian area for the comparison group. There was no attempt to match the CI and NH groups in age or any other factor such as gender or education. The age range for the NH group was between 18 – 35 years ($M = 22.5$, $SD = 0.7$, 2 male). Audiometry was performed for all NH listeners at 125, 250, 500, 1000, 2000, 4000, and 8000 Hz. All participants had audiometric thresholds better or equal to 20 dB HL in both ears. The experiment with NH listeners was approved by a local ethics committee (CERES, IRB: 20154000001072). All participants from both groups provided written consent and were compensated for their participation by a small monetary payment (NH and CI listeners) and travel reimbursement (CI listeners).

B. Stimuli

Stimuli consisted of sequences of electrical (CI) or acoustical (NH) pulses separated by

random inter-pulse-intervals (IPIs). The IPIs were drawn from a Poisson distribution with a refractory period. The refractory period was introduced to enforce a minimum IPI, intended to prevent spectral cues potentially caused by auditory filter ringing when the stimuli were presented acoustically in the NH group. For a fair comparison, the same refractory period was applied to the pulse sequences used for both the CI and NH groups. The rate parameter of the Poisson distribution was varied to generate different stimulus conditions, with no maximum IPI enforced. Three rate conditions were used with mean pulse rates of 10 (Slow), 40 (Fast), and 300 Hz (Ultra-Fast). The total stimulus duration was either 2 s for Slow and Fast rates conditions or 3 s for the Ultra-Fast rate condition. The refractory periods were 10 ms for the Slow and Fast conditions, and 0.3 ms for the Ultra-Fast condition. Simulations showed that 95% of all IPIs were shorter than 300 ms, 60 ms, and 9.2 ms in the Slow, Fast, and Ultra-Fast conditions, respectively.

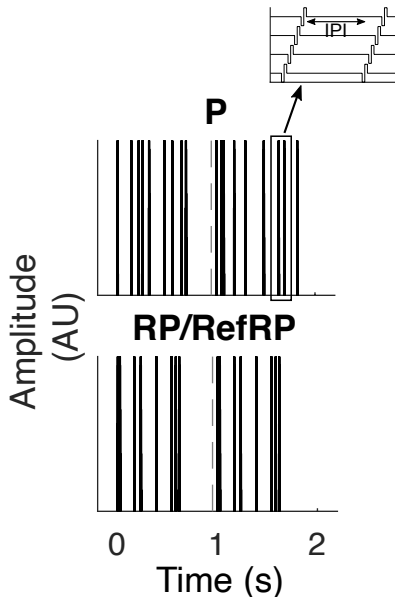


Figure 1. Illustration of the stimuli. An example of a fully random pulse train (P, top) and a repeated pulse train (RP or RefRP, bottom) for the Slow (10 Hz) rate condition. Inter-pulse intervals were drawn from a Poisson distribution with a 10-ms refractory period. Dashed lines indicate the midpoint of the click trains. For CI listeners, such stimuli were presented with direct stimulation of the implant. IPIs were delineated by symmetric biphasic electric pulses with duration of 45 μ s, presented almost simultaneously to 4 equally spaced electrodes (100 μ s delay between pulses, IPI exactly enforced within each electrode, see inset). For NH participants, the

pulse sequences were presented as high-pass acoustic click trains accompanied by low-pass masking noise (see Methods and Kang et al., 2017).

For the CI group, electrical stimulation was achieved through the research interface of the implant. Each pulse consisted of four monopolar cathodic-first symmetric biphasic pulses transmitted quasi-simultaneously to four different electrodes (Fig. 1). Each pulse had a phase duration of 45 μ s and the delay between the offset of one pulse and the onset of the following pulse (presented on another electrode) was 100 μ s to avoid direct electrical field summation (de Balthasar et al., 2003). The four electrodes were stimulated from apex to base and were regularly spaced across the electrode array to cover a large range of the neural population excited by the CI. Electrodes 1, 4, 7, and 10 were chosen for seven participants. For the remaining three participants, some of these electrodes were switched off clinically, so stimulation was as follows: electrodes 1, 4, 7, and 9 (participants M013 Ultra-Fast rate only, M014); 1, 4, 6, and 8 (M012); 2, 4, 7, and 10 (M004). Loudness was adjusted individually using the procedure described in section II.C.

For the NH group, pulses were acoustic clicks with similar temporal characteristics to the Slow and Fast rate conditions used for the CI group. Each click had a nominal duration of 50 μ s. The random click trains, generated with the same Poisson distributions as for the CI group, were then high-pass filtered using an 8th-order Butterworth filter with a 1-kHz filter cut-off to minimize spectral cues arising from cochlear filtering. Low-pass pink noise at -20 dB root-mean square level relative to the click train (i.e., 45 dB SPL) was added between 50 Hz and 1 kHz to mask any possible distortion products (Kang et al., 2017). The sound level was kept at an overall level of 65 dB SPL A-weighted for both rate conditions, calibrated using the procedure described in section C.

C. Task, Procedure, and Apparatus

The task was identical for the CI and NH groups, but there were minor differences in stimuli and procedure across groups. The Slow and Fast rate conditions were tested in a single session for the CI group and NH group. The Ultra-Fast rate condition was tested in a second session for the CI group only. We start by describing the main CI experiment (Slow and Fast rates), as all other cases are derived from it.

CI participants were tested in a quiet room. The procedure was programmed in Matlab and used the Research Interface Box (RIB2, University of Innsbruck) and a National Instruments card (PCI-6533, National Instruments, Austin, TX) connected to a PC to directly stimulate the implant. For the bilaterally implanted participant, the stimuli were presented to the ear with the longest duration of CI use.

Participants were told to report within-trial repeats, that is, to report pulse trains for which the first half was heard as identical to the second half. Even though there were only two possible responses, there were in fact three different stimulus types. For the first stimulus type, the pulse trains had fully random IPIs for the full 2-s duration of a trial (pulse train, P; Fig. 1 top). For the second stimulus type, a random, 1-s duration sequence of IPIs was generated and immediately repeated, identically, to create a 2-s repeated pulse train (RP; Fig. 1 bottom). For the third stimulus type, the generation procedure was identical to RPs. The only difference was that, without warning the participants about this possibility, the exact same sequence of IPIs was presented in a number of trials (20 trials, see below) over the course of an experimental block. This condition is termed reference repeated pulse trains (RefRP; Fig 1 right). All stimuli were generated afresh for each test block, so any given RefRP would have been heard in only one block by one participant. The main hypothesis of the study is that participants may be able to learn RefRP sequences as they re-occur throughout a block. Each test block comprised 80 trials, consisting of 40 Ps, 20 RPs, and 20 RefRPs.

The different types of stimuli were presented in a pseudo-random order during an experimental block, with the only constraint that no two successive trials should contain RefRPs. Listeners were asked to report repetitions after each trial. There was no feedback during the main experiment.

Most comfortable loudness levels (MCLs) were measured individually on each of the 4 electrodes, at a constant rate of 40 Hz. Current level was progressively increased, starting at a subthreshold level. Participants were asked to indicate the loudness of each sound using a 10-point loudness chart with MCL corresponding to a level labelled “6”. Once the MCLs for individual electrodes were collected, the 4-electrode stimulus was constructed by keeping fixed the relative level difference (in dB) across electrodes. Then, the MCL of the 4-electrode stimulus was measured once again, starting at subthreshold level and progressively increasing current level. We finally checked that the multi-electrode pulse train at the rate of 10 Hz with the same current levels as for 40 Hz was still clearly audible, which was the case for all subjects. The same current levels were, therefore, used in both the Slow and Fast conditions.

After the MCL adjustment, a training session was provided. The training session consisted of detecting repetitions for trials that contained more within-trial repeats than in the main experiment, to make the repetition-detection task easier. Four training phases were run in increasing level of predicted difficulty: 10, 4, 3, and 2 repetitions of a 1-s pulse train (Kang et al., 2017). Only P and RP stimulus types were included in these training blocks, in equal proportion. Note that no RefRP was included in the training. Each training block contained a total of 40 trials, except for the easiest 10 repetitions block which only contained 10 trials. Visual feedback on the correctness of the response was provided after each trial. No performance criterion was enforced but the experimenter ensured that the task was understood, mostly by checking that participants

varied their responses across a block. Four CI participants required more than one block (two to five blocks) to meet this condition.

Finally, the main experiment was performed. Four blocks for each of the Slow and Fast rate conditions were run. Participants were randomly assigned to start the main experiment with either the Slow or the Fast rate condition first. Two test blocks for each rate condition were presented as a first part of the main experiment. Then, an additional short training session (with 2 repetitions only) was provided for both rates, starting with the Slow condition. This was to reconfirm that participants were still engaged in the task. A second part of the main experiment again consisted of 2 test blocks for each rate condition, in a reversed order of the rate condition from the first part to counterbalance any possible order effects. The experiment lasted between 2.5h and 3h, which included ample time for breaks.

For the Ultra-Fast condition in the CI group, the same loudness adjustment procedure was performed anew for the 300 Hz pulse trains, to find the MCLs at this rate. Three repeats of a 1-s sequence were used for the RP and RefRP conditions, in an attempt to make the within-trial repetition detection task easier, leading to an overall stimulus duration of 3 s for all conditions. Training was similar but only included 3 blocks with 10, 4, and 3 repetitions of 1-s pulse train sequences, to match the number of within-trial repetitions in the main task. The experiment lasted for about 2h.

For the NH group, the procedure was identical except for two minor differences. First, no loudness adjustment was used; rather, the same level was used for all participants and conditions. Sound level was calibrated with a Bruel & Kjaer (2250) sound level meter on the “Slow” setting coupled to a Bruel & Kjaer ear simulator (4153). Because we chose to keep average level constant, this meant that peak level varied across (but not within) average rate conditions for the NH group.

Second, sounds were presented diotically for the NH group, to keep the procedure as in Kang et al. (2017). Training and testing procedures were the same as for the CI group in the Slow and Fast rate conditions. One participant required more than one block to pass the training phase. NH listeners were tested in a double-shielded booth (Industrial Acoustics). Sounds were presented over an RME Fireface soundcard and Beyerdynamics DT 770 Pro headphones, at a sample rate of 44.1 kHz and a 16-bit resolution. The experiment for NH listeners lasted about 2h. All participants were informally debriefed at the end of the experimental session, to gather their spontaneous comments about the experiment.

E. Statistical analyses

Performance in the within-trial repetition detection task was analyzed in terms of the sensitivity index d' from signal detection theory (Macmillan and Creelman, 2004). “Yes” responses for the RP and RefRP stimulus types were considered as hits, while “Yes” responses for the P stimulus type were considered false alarms.

A mixed-design analysis of variance (ANOVA) combining both CI and NH groups was run, with stimulus type (RP and RefRP) and rate condition (10 Hz and 40 Hz) as within subject factors, group (CI and NH) as between subject factors, and participant as a random factor. Mauchly’s test for sphericity confirmed that the data meet the assumptions required. F -values and p -values meeting a level of $p < 0.05$ were treated as statistically significant. Generalised eta squared (η^2_g) was also computed to estimate effect sizes (Lakens, 2013). In the Ultra-Fast rate condition, which was performed by CI listeners only, a paired t -test was conducted to compare the d' values for RP and RefRP conditions.

The time-course of performance was analyzed by considering the evolution of hit rates for each presentation of RefRP and RP, averaged over participants and test blocks, per rate conditions

and separately for NH and CI listeners. The hit rate values over time were fitted by the least-squares method to two different models: a constant, flat line (1 parameter: the intercept) and an exponential function (3 parameters: the starting point, the asymptote, and the time constant of the exponential). The statistical significance of the reduction in the fitting error obtained by introducing the more complex three-parameter model was then assessed using an F statistics (Motulsky and Christopoulos, 2004):

$$F = \frac{\left(\frac{ss1 - ss3}{df1 - df3}\right)}{\left(\frac{ss3}{df3}\right)}$$

where ss represents the sum of squares and df represent degrees of freedom, with the subscript identifying the one-parameter and three-parameter models.

Lastly, we tested for an influence of age on baseline performance (defined as d' in the RP condition). An analysis of covariance with baseline performance as the outcome variable, subject group (NH or CI) as the predictor variable and age as a covariate was performed (Bland and Altman, 1995). This was intended to remove any spurious influence of the average age differences between groups and different presentation modes across groups. A correlation was finally computed between baseline performance and duration of deafness for the CI group. Note that one CI subject who only participated in the Ultra-Fast condition was not included in these analyses.

III. Results

A. Rationale for the analyses

The data analysis contains three successive steps. First, an overall test of rapid learning for the two groups of participants, CI and NH, is performed on average performance. Second, the

distribution of performance across blocks is visualized to identify blocks with or without learning. Third, for those blocks where learning is hypothesized, a characterization of the change in performance over time is achieved through model fitting. Previous studies have used a highly similar experimental paradigm for NH participants (Kang et al., 2017; 2018). The analysis plan used here was thus identical to that used in Kang et al. (2017), which was itself derived from Agus et al. (2010) and Agus and Pressnitzer (2013).

The first and main step of the analysis tests whether learning improved the average performance for RefRP compared to RP in the within-trial repetition detection task. Such an effect on performance is expected because implicit or explicit recognition of a RefRP exemplar provides additional cues to perform an otherwise difficult task (Agus and Pressnitzer, 2013). The effect on average performance is quantified by comparing sensitivity in the task for RefRP and RP trials, using the d' measure from signal detection theory. Sensitivity is computed over the whole duration of a block, and averaged over all blocks, without exclusion, for all CI and NH participants.

The second step measures the documented variability across experimental blocks with the rapid learning paradigm, with only some blocks expected to display rapid perceptual learning among other blocks with essentially random performance. The distribution of performance over all blocks is tested against the null hypothesis of a random distribution. If the normality assumption is violated, clusters of high-performance blocks are selected, and termed “good blocks”. Good blocks may arise because of specific patterns in the stimulus, differences across listeners, or an interaction between the two (Agus et al., 2010; Andrillon et al., 2015).

Third, the time course of performance is characterized for the good blocks. By construction, RefRP and RP sequences are novel to the listener at the onset of a block. Because they are drawn from the same random process, they should thus initially produce equivalent performance. But, as

the RefRP exemplar receives increased exposure, this should increase performance for RefRP over time. Note that performance changes associated with learning can also manifest themselves as decreases in performance for RP. Such decreases are predicted by criterion shifts, because participants become less likely to report a repetition for the comparatively more difficult RP trials as learning progresses (Agus et al., 2010). Changes in performance over time are tested by comparing the fits for the trial-by-trial data obtained with a constant-line model versus an exponential change model (Agus et al., 2010). In summary, even though one type of measure would be already strongly indicative of learning, we used three complementary looks at the dataset to evidence and characterize perceptual learning.

B. Average performance

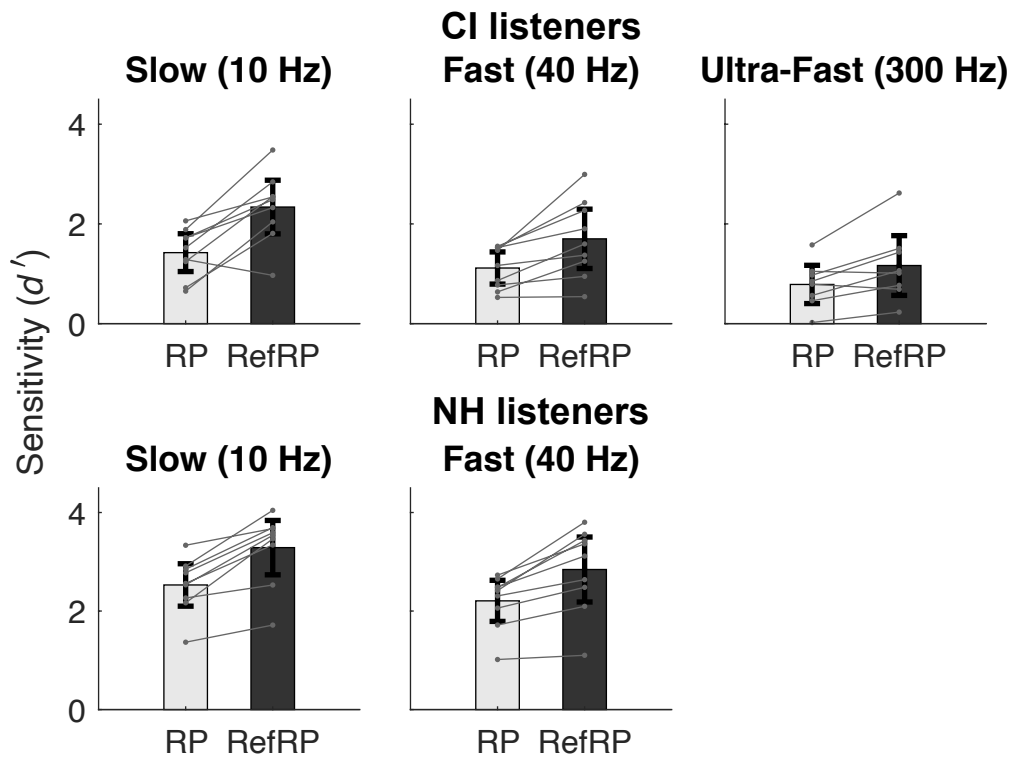


Figure 2. Average results for all experiments. Performance (d') is plotted for the different stimulus types (RP, light grey, and RefRP, black), in panels corresponding to the different rate conditions (Slow, Fast, or Ultra-Fast). Results are shown for the CI group (top) or the NH group (bottom). Individual data points are indicated as dots, paired for each participant with connecting lines

between RP and RefRP. Error bars represent 95% confidence intervals.

The results of the main experiment are shown in Fig. 2. Qualitatively, the NH group showed higher performance (d' values) overall than the CI group. In addition, both groups showed higher performance for the Slow than for the Fast rate condition. However, as detailed in the Rationale section, the critical comparison for perceptual learning consists in comparing the RP *versus* RefRP performance. Here, the pattern of results was similar for the CI and NH groups. Importantly, in all cases, RefRP performance was higher than RP performance, suggesting that the task was performed more accurately for the re-occurring sounds that may have provided an opportunity for learning.

The statistical analyses confirmed these qualitative observations. The mixed-design ANOVA combining both groups and Slow and Fast rate conditions showed a significant effect of group on performance ($F(1,16) = 25.73, p < 0.001, \eta^2_g = 0.49$), confirming the difference in overall performance across groups. Significant effects of stimulus type (RP vs RefRP, $F(1,16) = 57.07, p < 0.001, \eta^2_g = 0.24$) and rate conditions (Slow vs Fast, $F(1,16) = 30.80, p < 0.001, \eta^2_g = 0.15$) on performance were also confirmed. Importantly, no interaction was observed between group and stimulus type ($F(1,16) = 0.60, p > 0.05, \eta^2_g = 0.003$), nor between group and rate condition ($F(1,16) = 0.17, p > 0.05, \eta^2_g = 0.001$). This indicates that, even if baseline RP performance was better in NH listeners compared to CI listeners, there were similar benefits of increased exposure to RefRP in both groups of participants. Thus, for both groups, there was a performance advantage for RefRP over RP, which was equivalent for both rate conditions. Finally, for the Ultra-Fast rate condition, which was performed by CI listeners only, a paired t -test showed that RefRP produced higher performance than RP (300 Hz: $t(7) = -2.9, p < 0.05$).

C. Distribution of performance over blocks

It has been repeatedly observed that not all test blocks show learning of RefRPs (Kang et al., 2017; 2018). This observation could be related to acoustic properties of the RefRPs, to variability across listeners, or to an interaction between the two (Agus et al., 2010; Andrillon et al., 2015). This variability should result in a non-normal distribution of performance across blocks when the last trials of a block are considered, for which learning has sometimes occurred and sometimes not (e.g., Agus et al., 2010; Kang et al., 2017; 2018).

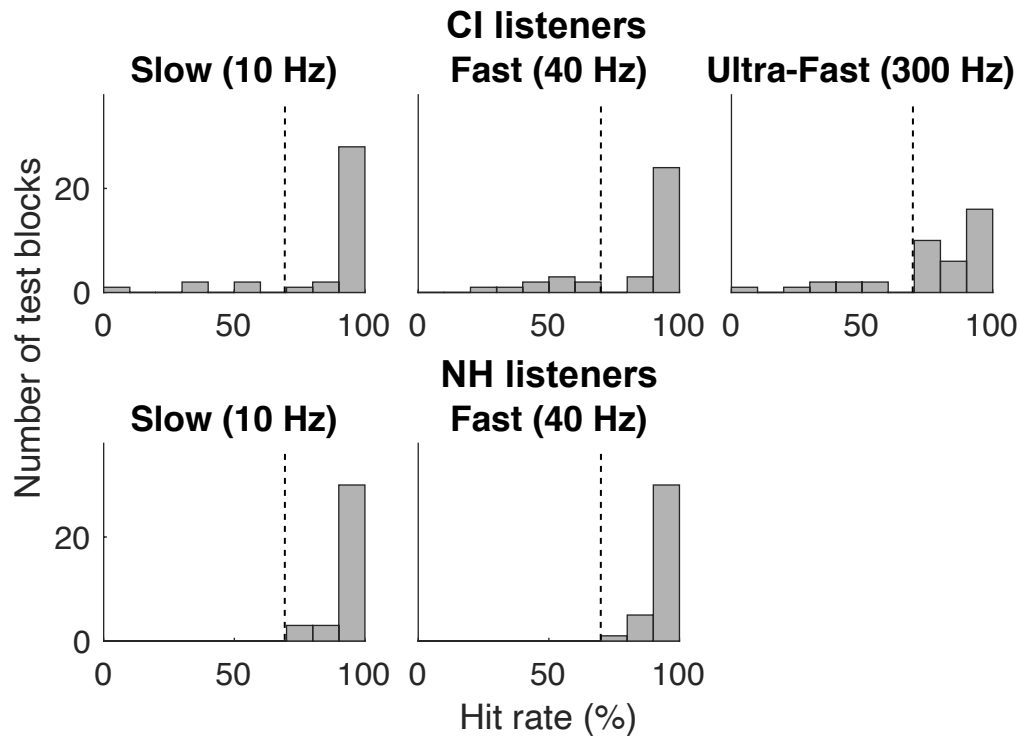


Figure 3. Distributions of hit rate for the RefRP stimulus condition, averaged over the last 10 presentations, for all RefRP experimental blocks across all participants. Distributions are shown for CI (top) and NH participants (bottom), and for the different rate conditions. Dashed vertical lines indicate the criterion for selecting “good blocks” (see text).

Figure 3 shows the distribution over all blocks of the average hit rates for the RefRPs over the last 10 RefRP trials of a block. In general, there was a substantial proportion of blocks with near to ceiling performance, and some remaining blocks with lower performance. For the CI group,

the average hit rates during the last 10 trials for RefRPs were not normally distributed, as shown by one-sample Kolmogorov-Smirnov tests (Slow: $D(36) = 0.62, p < 0.001$; Fast: $D(36) = 0.60, p < 0.001$; Ultra-Fast: $D(40) = 0.57, p < 0.001$). The same analysis for the NH group also showed a deviation from normality (one-sample Kolmogorov-Smirnov tests, Slow: $D(36) = 0.76, p < 0.001$; Fast: $D(36) = 0.76, p < 0.001$).

Based on this outcome, we selected the high-performance blocks for which learning is suspected. We set a selection criterion of hit rate above 70% to define so-called good blocks. This criterion value is lower than what we used in previous studies using similar stimuli (Kang et al., 2018; Kang et al. 2017) but it visually separates the good performance blocks from the rest of the distribution for both the CI and NH groups, in spite of the difference in baseline performance. For the CI group, this led to 86%, 75%, and 80% good blocks in the Slow, Fast, and Ultra-Fast conditions, respectively. For the NH group, this led to 100% of good blocks in both the Slow and Fast conditions.

D. Time course

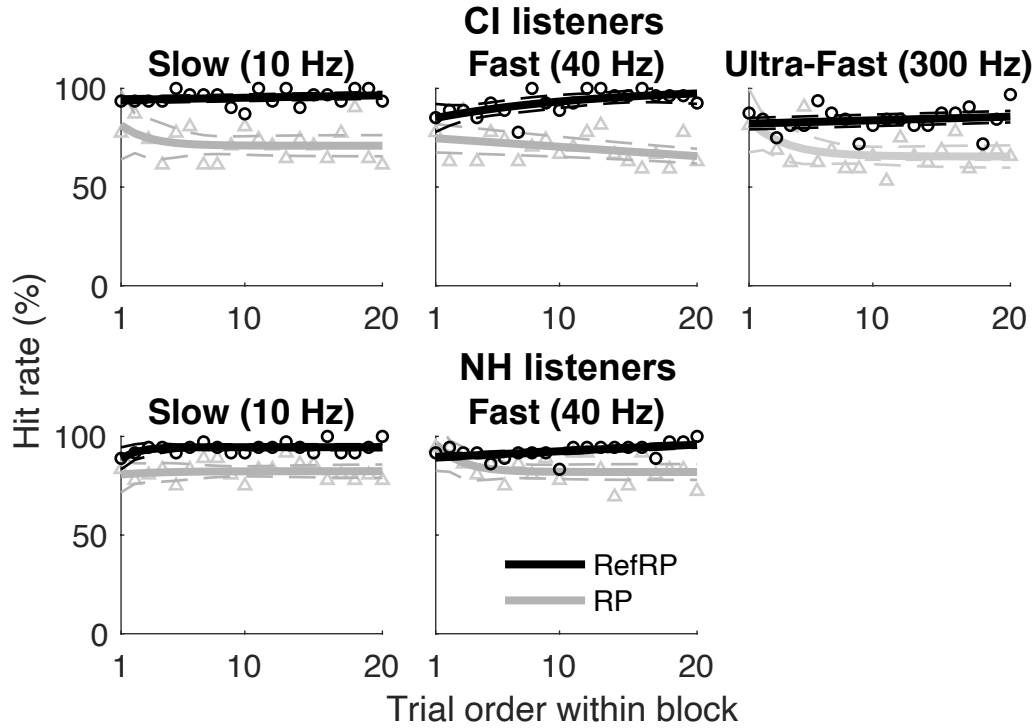


Figure 4. Time course of performance for CI (top) and NH (bottom) participants. The group-average hit rate is plotted as a function of presentation order within a block, for RP (grey triangles) and RefRP (black circles) stimulus types. The analysis is restricted to “good blocks” for which learning was hypothesized (see text). Dashed lines indicate 95% confidence intervals.

Figure 4 shows the time course of hit rate for RP and RefRP stimulus types, for good blocks only which are those where learning is suspected. A constant flat-line and exponential change model were fitted to the trial-by-trial data. The exponential fit indicated increases in RefRP performance over time in all cases except for the Slow condition in both groups of participants. It also indicated decreases in performance for RP except in the Slow condition for NH participants. Such increases in performance for RefRP and decreases for RP are what is expected with learning in the task (Agus et al., 2010).

To ascertain statistically whether the exponential change model was warranted, its fit was compared to the flat-line model taking into account the increased numbers of parameter required for the exponential (see Methods). The outcomes of the statistical comparisons were less clear-cut

than the qualitative description. Only the Fast rate condition for the CI group showed a significant advantage of the exponential model for RefRP ($F(1,16) = 5.95, p = 0.011$). No other test passed the significance criterion.

Another check that can be made from the time course analysis is that performance should be matched at the outset of a block between RefRP and RP, as by construction, both were generated by the same process and no learning could have taken place on the first presentation. A difference would indicate a chance selection of easy RefRPs. In all cases, the confidence intervals of the model fits overlap for the first presentation.

E. Correlations with age

One unintended feature of our dataset was that the average age and the age range differed between the CI group and the comparison NH group. To test whether this could explain the observed difference between groups on the baseline RP condition, we performed two additional analyses.

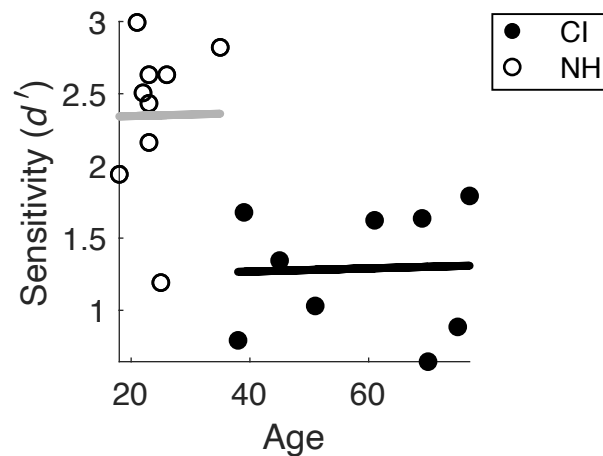


Figure 5. Baseline performance (d' for the RP condition) as a function of age. Each symbol indicates a participant (filled circles: CI; empty circles: NH). Grey and black lines indicate regression lines for each group with a common slope enforced, equivalent to a covariance analysis (Bland and Altman, 1995, see Methods).

Figure 5 shows the performance in the baseline RP condition as a function of age for all participants. Best performance was achieved by younger participants, but it is important to note that those younger participants are also all part of the NH group. To test for the statistical relationship between age and baseline, an analysis of covariance was performed, with age as a covariate. This is equivalent to fitting regression lines to each group of participants, while enforcing a common slope for the regression (Bland and Altman, 1995, see Methods). No significant correlation was observed ($\rho = 0.09$, $p > 0.05$; Fig. 5). An additional analysis was performed for the CI group by correlating baseline performance and years of profound deafness. Here again, no significant relationship was detected ($\rho = 0.30$, $p > 0.05$), even though it should be noted that this analysis had limited power due to the limited number of data points ($N = 9$).

IV. Discussion

The present study tested for rapid perceptual learning of temporal patterns in CI listeners, comparing their performance to NH listeners. Stimuli were stochastic sequences of electric pulses for the CI group and high-pass filtered click trains for the NH group, sharing the same temporal characteristics, with the aim that such temporal sequences would be equally well represented by CI and NH listeners. However, CI listeners usually experience degraded auditory input for some time before implantation, followed by drastically modified input after implantation, which is known to trigger a cascade of compensatory neural changes (Giraud et al., 2001; Glennon et al., 2020). It was therefore unclear whether rapid perceptual learning would be comparable for CI and NH listeners. Results showed highly similar patterns of behavioral performance in both participants' groups. In particular, the only stimulus condition that was amenable to perceptual learning, because of multiple exposure, was also the one that induced consistently better

performance. Furthermore, an additional experimental condition ran with CI listeners only and using fast temporal cues unavailable to the non-implanted auditory system also followed this pattern of results. In this discussion, after considering alternative interpretations, we argue that these results show that the auditory plasticity mechanisms required by rapid perceptual learning are largely preserved in CI listeners.

A. What was learned by CI and NH listeners?

A first important point is that the experimental results cannot be interpreted in terms of procedural learning. Participants were presented with sounds that either occurred on single trials (RP) or on re-occurred over several trials (RefRP). Importantly, the task was the same for two conditions, and there were an equal number of RefRP and RP trials over a block and over the whole experiment, randomly interspersed with no feedback. Also, all sounds were generated from the same random process with identical long-term statistics. Therefore, procedural learning, if present, should improve performance on RefRP and RP trials in an identical manner. In contrast, our main result was that performance was consistently better for the RefRP condition compared to the RP condition.

One other interpretation is that multiple exposures to the same temporal sequence in the RefRP condition induced rapid perceptual learning. What kind of cues could be learned with such complex, stochastic sequences, to distinguish the “reference” sequence in a block from all of the other sequences drawn from the same random process? Kang et al. (2017), who used similar stimuli, suggested that listeners may learn distinctive changes in the distribution of IPIs in a sequence, such as short gaps or modulations in roughness. Such an interpretation was motivated by previous findings about rhythm and temporal pattern perception, where “runs” or “motifs” have been shown to provide discrimination cues (Ross and Houtsma, 1994; Povel and Essens, 1985;

Goossens et al., 2008). The present results are consistent with such an interpretation. Because CI listeners have preserved performance in rhythm tasks (e.g., Kong et al., 2004) or temporal discrimination tasks (e.g., Gaudrain, Deeks, and Carlyon, 2017), at least over the range of IPIs tested here, the auditory cues hypothesized to have been learned by NH listeners would also be available to CI listeners.

B. Difference in baseline performance

While the pattern of results was similar across CI and NH listeners, performance was overall lower for CI listeners. It is unclear what caused this baseline difference in performance. We did not make any attempt to match the mean age or age range of the CI and NH groups, for practical reasons, so age may be a candidate explanation. There are documented impairment of temporal processing with aging that are at least partly unrelated to elevated detection thresholds due to hearing loss and so plausibly relevant to CI listeners. In particular, gap detection thresholds have been found to worsen with age (Strouse et al., 1998), which is reflected in electrophysiological measures of neural synchrony (Harris and Dubno, 2017). For CI listeners specifically, a deleterious effect of age on temporal processing tasks has been shown. Poorer performance with advancing age has been observed for pulse rate discrimination, at least for fast rates (Johnson et al., 2021). Word categorization based on a temporal cue (the duration of a silent gap) also degrades with age for high levels of stimulation (Xie et al., 2019). As our task involved the comparisons of temporal sequences with short silent gaps between clicks, an impairment in gap or pulse rate processing could plausibly lead to worse performance for the older CI group compared to the younger NH group.

However, when testing for a possible relationship between age and baseline performance in the data, a covariance analysis showed no statistically reliable effect. A first possible interpretation

for this could be the limited power available to the test. Also, beyond age, there also other cognitive factors that impact performance on perceptual tasks for CI listeners, such as working memory or non-verbal intelligence (O'Neill et al., 2019). These factors were not controlled for in our study. Finally, the experiment was generally longer for CI listeners, because of the loudness matching procedure, which may have led to more fatigue and poorer overall results in the CI group.

In any case, it is important to note that the baseline difference in RP was also reflected in the RefRP performance, as there was no interaction between group and stimulus type in the performance analysis. The main learning effect, that is, the difference between RefRP and RP, was observed in both groups whatever the cause of the baseline difference between groups.

C. Effect of rate

Overall, performance was better for Slow rates than Fast rates or Ultra-Fast rates, for both CI listeners and NH listeners. This is consistent with previous studies reporting a decrease in performance with increasing rate in various temporal tasks with CI listeners, such as rate discrimination or temporal jitter detection (Gaudrain et al., 2017; Johnson et al., 2021; Macherey et al., 2011; Vandali and van Hoesel, 2012). Thus, it is likely that our observation of a decrease in overall performance with rate can be accounted for by mechanisms independent of the learning process. Consistent with this, the performance gain associated with learning (the RefRP advantage over RP) did not statistically interact with the performance change with rate.

D. Time course of learning

When using the planned analyses replicating exactly the methodology of our own previous studies of rapid learning, a significant change in performance associated with learning was only observed in the Fast condition for both groups of listeners. So, the most conservative interpretation of the current results is that we formally demonstrated rapid learning in CI listeners only for fast

temporal sequences. This in itself would be enough to unequivocally confirm that temporal cues alone can support rapid perceptual learning (Kang et al., 2017), as our broadband electric stimulation procedure could not involve any spectral cues.

However, several aspects of the data suggest that this interpretation may be overly conservative. First, much to our surprise, baseline performance was high in the task, even for the CI group. This could have led to ceiling effects obscuring potential changes in performance over time. Second, it is noticeable that we failed to find evidence for changes in performance over time for the NH group in the Slow condition, even though previous studies showed precisely such an effect for near-identical stimuli (Kang et al., 2017; 2018). Third, even though the model comparison statistics did not always reach our significance criterion, all trends but one (so 9 out of 10 model fits) went in the expected direction: a matched initial performance, an increase in performance for RefRP and a decrease for RP. Finally, it would seem extremely unlikely that a chance sampling of RefRPs produced the pattern of results observed, with a consistent advantage of RefRP over RP in all groups and conditions. This would mean that, for the 19 participants and 5 conditions in the study, RefRPs were selected by chance alone so as to produce better performance than the average RP.

In summary, we would speculate that perceptual learning occurred in all cases, as suggested by the performance gain always observed for re-occurring RefRP stimuli. Our failure to obtain statistically robust evidence for performance change over time in some conditions, which represents the second of two stringent criteria to ascertain learning, should perhaps be re-evaluated in follow-up studies, for instance by increasing the number of participants, varying baseline task difficulty, or collecting other behavioral measures such as reaction times (Andrillon et al., 2015; Bianco et al., 2020).

E. Ultra-Fast rates

Another aspect of the results is the advantage of RefRP over RP observed for the Ultra-Fast rates. Given the caveats discussed above, we would argue that CI listeners were able to learn the Ultra-Fast sequences. Such sequences consisted in part of temporal cues unavailable to the unaided human auditory system: very fast timing cues in low-frequency tonotopic channels, unaccompanied by any corresponding spectral cues.

It is already known that fast temporal cues can be discriminated by CI listeners (McKay et al., 2000), but it is unclear whether cues that are not available to the typical auditory system can be learned. Computational models of rapid plasticity such as spike-dependent plasticity (Masquelier et al., 2008) hypothesize generic mechanisms, which have no reason to be tied to the specific temporal limits imposed by peripheral cochlear filtering. If the Ultra-Fast cues transmitted by the implant to the auditory nerve were to be represented in cortical regions implicated in auditory learning, then it is plausible that they would also be amenable to learning. This interpretation is consistent with our experimental results.

Alternatively, it is also possible that CI listeners ignored the low-frequency electrodes and exclusively relied on higher-frequency electrodes to learn the ultra-fast temporal cues, hence relying on temporal cues available in acoustic hearing. Such an alternative interpretation cannot be ruled out for the present data. It would also be hard to completely rule out in future studies, as stimulating only low frequency electrodes would only partially control for the issue, because of possible current spread to neighbouring sites, and as further increasing the stimulation rate would impair the peripheral representation of temporal cues.

F. Clinical considerations

Behavioural training and its underlying neural plasticity mechanisms are increasingly

recognized as crucial to improving the outcome of implantation (for a recent review, Glennon et al., 2020). Our results are encouraging in this respect. For our limited sample of CI listeners, we observed fully preserved rapid perceptual learning abilities compared to NH listeners. Learning was equivalent across baseline task difficulty, which should make the underlying mechanisms relevant to a broad range of real-life situations. Also, as the Ultra-Fast condition further suggests, CI listeners may even be able to learn cues that they may not have been exposed to pre-implantation. Of course, perceptual learning alone cannot support complex function such as speech comprehension, which is known to improve only slowly over time for most CI recipients (Holden et al., 2013; James et al., 2019). Nevertheless, we would speculate that rapid perceptual learning could be relevant for the initial re-mapping of acoustic to electric phonemic cues in CI listeners, as is observed in NH listeners with vocoded speech (Davis et al., 2005). Moreover, such learning could be leveraged in non-verbal tasks related to timbre perception and sound source recognition (Agus et al., 2019).

Another aspect of our paradigm is that learning was fully unsupervised: participants were not told about the possibility to learn some of the stimuli, and even if they guessed that this would be the case, they could not predict which trials contained the sounds to be learned as presentation was fully randomized. This does not necessarily show that learning was implicit. Indeed, during the informal debriefing, some participants (both NH and CI) reported that they felt there was a re-occurring sound, especially for the Slow rate condition. However, previous studies with NH listeners showed that learning of noise in our experimental paradigm could occur with diverted attention (Andrillon et al., 2015) or even during some sleep phases (Andrillon et al., 2017), strongly suggesting at least partially implicit learning. Intriguingly, in an animal model of electric hearing, neural plasticity for the coding of temporal cues was observed with passive exposure subcortically

and to a lesser extent cortically (Vollmer et al., 2017). Our results thus further suggest that implicit auditory learning, which is arguably an important part of real-life learning, may be available to CI listeners.

V. Conclusions

CI and NH listeners performed a task designed to probe the rapid perceptual learning of temporal sequences (Kang et al., 2017). Both groups showed highly similar patterns of results, strongly suggesting preserved learning abilities for CI listeners. Being able to map or remap the auditory cues provided by electric hearing to the acoustic world is clearly an essential part of the efficient auditory process for CI recipients. Our findings suggest that, at least for an unsupervised and likely implicit learning task, the perceptual learning abilities of CI listeners are essentially intact.

Acknowledgements

This work was funded by the ANR-17-EURE-0017, ANR-11-PDOC-0022, and Fondation Fyssen.

References

- Agus, T. R., and Pressnitzer, D. (2013). “The detection of repetitions in noise before and after perceptual learning,” *J. Acoust. Soc. Am.*, **134**, 464–473.
- Agus, T. R., Suied, C., and Pressnitzer, D. (2019). Timbre Recognition. In: Kai Siedenburg, Charalampos Saitis, Stephen McAdams, Arthur N. Popper, Richard N. Fay. “*Timbre: Acoustics, Perception, and Cognition*”. Springer Handbook of Auditory Research Series (SHAR). pp 59-85. Springer Nature Switzerland.
- Agus, T. R., Thorpe, S. J., and Pressnitzer, D. (2010). “Rapid formation of robust auditory memories: Insights from noise,” *Neuron*, **66**, 610–618.
- Andrillon, T., Kouider, S., Agus, T., and Pressnitzer, D. (2015). “Perceptual learning of acoustic noise generates memory-evoked potentials,” *Curr. Biol.*, **25**, 2823–2829.
- Andrillon, T., Pressnitzer, D., Léger, D., and Kouider, S. (2017). “Formation and suppression of acoustic memories during human sleep,” *Nature Communications*, **8**, 1-15.
- Barascud, N., Pearce, M. T., Griffiths, T. D., Friston, K. J., and Chait, M. (2016). “Brain responses in humans reveal ideal observer-like sensitivity to complex acoustic patterns,” *Proc Natl Acad Sci USA*, **113**, E616–E625.
- de Balthasar, C., Boëx, C., Cosendai, G., Valentini, G., Sigrist, A., and Pelizzone, M. (2003). “Channel interactions with high-rate biphasic electrical stimulation in cochlear implant subjects,” *Hearing Research*, **182**, 77–87.
- Bianco, R., Harrison, P. M., Hu, M., Bolger, C., Picken, S., Pearce, M. T., and Chait, M. (2020). “Long-term implicit memory for sequential auditory patterns in humans,” *eLife*, **9**, e56073.
- Bland, J. M., and Altman, D. G. (1995). “Calculating correlation coefficients with repeated observations: Part 2—Correlation between subjects,” *BMJ*, **310**, 633.

- Davis, M. H., Johnsrude, I. S., Hervais-Adelman, A., Taylor, K., and McGettigan, C. (2005). “Lexical information drives perceptual learning of distorted speech: evidence from the comprehension of noise-vocoded sentences,” *Journal of Experimental Psychology: General*, **134**, 222.
- Faulkner, A., Rosen, S., and Stanton, D. (2003). “Simulations of tonotopically mapped speech processors for cochlear implant electrodes varying in insertion depth,” *J. Acoust. Soc. Am.*, **113**, 1073-1080.
- Fu, Q.-J., and Galvin, J. J., III (2007). “Perceptual learning and auditory training in cochlear implant recipients,” *Trends in Amplification*, **11**, 193–205.
- Gaudrain, E., Deeks, J. M., and Carlyon, R. P. (2017). “Temporal regularity detection and rate discrimination in cochlear-implant listeners,” *J. Assoc. Res. Otolaryngol.*, **18**, 1-11.
- Gfeller, K., and Lansing, C. R. (1991). “Melodic, rhythmic, and timbral perception of adult cochlear implant,” *J. Speech Lang. Hear. Res.*, **34**, 916–920.
- Giraud, A. L., Truy, E., and Frackowiak, R. (2001). “Imaging plasticity in cochlear implant patients,” *Audiol. Neurotol.*, **6**, 381–393.
- Glennon, E., Svirsky, M. A., and Froemke, R. C. (2020). “Auditory cortical plasticity in cochlear implant users,” *Curr. Opin. Neurol.*, **60**, 108–114.
- Goossens, T., van de Par, S., and Kohlrausch, A. (2008). “On the ability to discriminate Gaussian-noise tokens or random tone-burst complexes,” *J. Acoust. Soc. Am.*, **124**, 2251-2262.
- Harris, K. C., and Dubno, J. R. (2017). “Age-related deficits in auditory temporal processing: unique contributions of neural dyssynchrony and slowed neuronal processing,” *Neurobiology of aging*, **53**, 150-158.

- Henry, B. A., and Turner, C. W. (2003). “The resolution of complex spectral patterns by cochlear implant and normal-hearing listeners,” *J. Acoust. Soc. Am.*, **113**, 2861–2873.
- Holden, L. K., Finley, C. C., Firszt, J. B., Holden, T. A., Brenner, C., Potts, L. G., ... and Skinner, M. W. (2013). “Factors affecting open-set word recognition in adults with cochlear implants. *Ear & Hearing*,” **34**, 342-60.
- Jablonowski, J., Taesler, P., Fu, Q., and Rose, M. (2018). “Implicit acoustic sequence learning recruits the hippocampus,” *PLoS ONE*, **13**, e0209590–16.
- James, C. J., Karoui, C., Laborde, M. L., Lepage, B., Molinier, C., Tartayre, M., Escudé, B., et al. (2019). “Early sentence recognition in adult cochlear implant users,” *Ear & Hearing*, **40**, 905–917.
- Johnson, K. C., Xie, Z., Shader, M. J., Mayo, P. G., and Goupell, M. J. (2021). “Effect of Chronological Age on Pulse Rate Discrimination in Adult Cochlear-Implant Users,” *Trends in Hearing*, **25**, 1-15.
- Kang, H., Agus, T. R., and Pressnitzer, D. (2017). “Auditory memory for random time patterns,” *J. Acoust. Soc. Am.*, **142**, 2219–2232.
- Kang, H., Lancelin, D., and Pressnitzer, D. (2018). “Memory for random time patterns in audition, touch, and vision,” *Neuroscience*, **389**, 118–132.
- Kong, Y.-Y., Cruz, R., Jones, J. A., and Zeng, F.-G. (2004). “Music perception with temporal cues in acoustic and electric hearing,” *Ear & Hearing*, **25**, 173–185.
- Kumar, S., Bonnici, H. M., Teki, S., Agus, T. R., Pressnitzer, D., Maguire, E. A., and Griffiths, T. D. (2014). “Representations of specific acoustic patterns in the auditory cortex and hippocampus,” *Proc. Royal Soc. B*, **281**, 20141000.

- Lakens, D. (2013). "Calculating and reporting effect sizes to facilitate cumulative science: a practical primer for t-tests and ANOVAs," *Front. Psychol*, **4**, 863.
- Landsberger, D. M., Svrakic, M., Roland, T., Jr, and Svirsky, M. A. (2015). "The relationship between insertion angles, default frequency allocations, and spiral ganglion place pitch in cochlear implants," *Ear & Hearing*, **36**, e207–e213.
- Luo, H., Tian, X., Song, K., Zhou, K., and Poeppel, D. (2013). "Neural Response Phase Tracks How Listeners Learn New Acoustic Representations," *Curr. Biol.*, **23**, 968–974.
- Macherey, O., Deeks, J. M., and Carlyon, R. P. (2011). "Extending the Limits of Place and Temporal Pitch Perception in Cochlear Implant Users," *J. Assoc. Res. Otolaryngol.*, **12**,
- Macmillan, N. A., and Creelman, C. D. (2004). *Detection theory: A user's guide*, Psychology Press.
- Masquelier, T., Guyonneau, R., and Thorpe, S. J. (2008). "Spike timing dependent plasticity finds the start of repeating patterns in continuous spike trains," *PLoS ONE*, **3**, e1377–9.
- McKay, C. M., McDermott, H. J., and Carlyon, R. P. (2000). "Place and temporal cues in pitch perception: are they truly independent?," *Acoustics Research Letters Online*, **1**, 25–30.
- Motulsky, H., and Christopoulos, A. (2004). *Fitting models to biological data using linear and nonlinear regression*, Oxford University Press, New York.
- Nourski, K. V., Etler, C. P., Brugge, J. F., Oya, H., Kawasaki, H., Reale, R. A., Abbas, P. J., et al. (2013). "Direct recordings from the auditory cortex in a cochlear implant user," *J. Assoc. Res. Otolaryngol.*, **14**, 435–450.
- O'Neill, E. R., Kreft, H. A., and Oxenham, A. J. (2019). "Cognitive factors contribute to speech perception in cochlear-implant users and age-matched normal-hearing listeners under vocoded conditions," *J. Acoust. Soc. Am.*, **146**, 195-210.

- Penner, M. J. (1977). "Detection of temporal gaps in noise as a measure of the decay of auditory sensation," *J. Acoust. Soc. Am.*, **61**, 552–557.
- Phillips-Silver, J., Toiviainen, P., Gosselin, N., Turgeon, C., Lepore, F., and Peretz, I. (2015). "Cochlear implant users move in time to the beat of drum music," *Hearing Research*, **321**, 25–34.
- Povel, D. J., and Essens, P. (1985). "Perception of temporal patterns," *Music perception*, **2**, 411–440.
- Rosen, S., Faulkner, A., and Wilkinson, L. (1999). "Adaptation by normal listeners to upward spectral shifts of speech: Implications for cochlear implants," *J. Acoust. Soc. Am.*, **106**, 3629–3636.
- Ross, J., and Houtsma, A. J. (1994). "Discrimination of auditory temporal patterns," *Perception & Psychophysics*, **56**, 19–26.
- Schnupp, J. W., Hall, T. M., Kokelaar, R. F., and Ahmed, B. (2006). "Plasticity of temporal pattern codes for vocalization stimuli in primary auditory cortex," *Journal of Neuroscience*, **26**, 4785–4795.
- Schumann, A., Serman, M., Gefeller, O., and Hoppe, U. (2014). "Computer-based auditory phoneme discrimination training improves speech recognition in noise in experienced adult cochlear implant listeners," *International Journal of Audiology*, **54**, 190–198.
- Shannon, R. V. (1985). "Threshold and loudness functions for pulsatile stimulation of cochlear implants," *Hearing Research*, **18**, 135–143.
- Shannon, R. V. (1989). "Detection of gaps in sinusoids and pulse trains by patients with cochlear implants," *J. Acoust. Soc. Am.*, **85**, 2587–2592.
- Stakhovskaya, O., Sridhar, D., Bonham, B.

- H., and Leake, P. A. (2007). "Frequency Map for the Human Cochlear Spiral Ganglion: Implications for Cochlear Implants," *J. Assoc. Res. Otolaryngol.*, **8**, 220–233.
- Strouse, A., Ashmead, D. H., Ohde, R. N., and Grantham, D. W. (1998). "Temporal processing in the aging auditory system," *J. Acoust. Soc. Am.*, **104**, 2385-2399.
- Svirsky, M. A., Talavage, T. M., Sinha, S., Neuburger, H., and Azadpour, M. (2015). "Gradual adaptation to auditory frequency mismatch," *Hearing Research*, **322**, 163–170.
- Vandali, A. E., and van Hoesel, R. J. M. (2012). "Enhancement of temporal cues to pitch in cochlear implants: Effects on pitch ranking," *J. Acoust. Soc. Am.*, **132**, 392–402.
- Viswanathan, J., Rémy, F., Bacon-Macé, N., and Thorpe, S. J. (2016). "Long term memory for noise: Evidence of robust encoding of very short temporal acoustic patterns," *Front. Neurosci*, **10**, 490.
- Vollmer, M., and Beitel, R. E. (2011). "Behavioral training restores temporal processing in auditory cortex of long-deaf cats," *J Neurophysiol*, **106**, 2423–2436.
- Vollmer, M., Beitel, R. E., Schreiner, C. E., and Leake, P. A. (2017). "Passive stimulation and behavioral training differentially transform temporal processing in the inferior colliculus and primary auditory cortex," *J Neurophysiol*, **117**, 47–64.
- Xie, Z., Gaskins, C. R., Shader, M. J., Gordon-Salant, S., Anderson, S., and Goupell, M. J. (2019). "Age-related temporal processing deficits in word segments in adult cochlear-implant users," *Trends Hear.* **23**, 1-19.
<https://asa.scitation.org/doi/10.1121/1.5116009>
- Zeng, F.-G. (2002). "Temporal pitch in electric hearing," *Hearing Research*, **174**, 101–106.