Distinct cortical responses to Auditory Statistics: pre-attentive discriminations based on local and global representations

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ABSTRACT

The auditory system relies on local and global representations, depending on the amount of entering temporal details. When local information exceeds system constraints, acoustic details are summarized into a set of average statistics and global structure emerges. Whether computations subtending local and global representations of sounds can be distinguished at the cortical level is unknown. A computational auditory model was employed to extract auditory statistics from natural sound textures, such as fire, wind, and rain, and generate synthetic exemplars in which we had control of local and global properties. Participants were passively exposed to auditory streams with triplets of sounds including two standards and an oddball while the EEG was recorded. In Local Discrimination (exp 1) the oddball sound varied from standards only for its local features; in Global Discrimination (exp 2), it varied for its global structure. Different sound durations were employed to manipulate the amount of acoustic information and statistical variability between standards and oddballs. We expected short and long sounds to engage local (exp 1) or global (exp 2) representations, respectively. As predicted, neural responses associated with local discriminations exceeded global ones for short sounds, whereas the opposite pattern emerged for longer sounds. Electrical source estimates revealed that local discriminations mainly engaged auditory regions of the right hemisphere, while global discriminations of the left hemisphere. These findings revealed distinct neural correlates of acoustic discriminations guided by local or global structures. Ultimately results demonstrated that the auditory system developed a functional architecture to automatically detect changes occurring in the environment based on these two modes of sound representation.

SIGNIFICANT STATEMENT

Prior to this study, it was not known whether it was possible to directly measure auditory cortical representations of sound discriminations depending on local or global acoustic properties. Results unveiled the existence of a mechanisms which pre-attentively determines at which timescale (local or global) a change in a stream occurred based on statistical variability between sound excerpts. By performing source reconstruction, we additionally revealed that the response to local change detection pertains to different cortical structures as compared to global one, displaying also hemispheric asymmetries. These findings expand our knowledge on fundamental mechanisms characterizing auditory system functioning.

INTRODUCTION

The human auditory system is capable of discriminating sounds based on both local and global properties (McAdams, 1993; Griffiths, 2001). Local analysis relies on extracting and retaining fine-grained details to detect transient changes and amplitude modulations over time (Plomp, 1964; Dau, Kollmeier, and Kohlrausch, 1997). These temporal variations characterize different sound objects and help the system discerning across acoustic sources. However, environmental inputs typically comprise long lasting sounds in which the number of local features to be retained exceed sensory storage capacity. This prohibits discrimination based on local analysis to give way to global representations (McDermott, Schemitsch, and Simoncelli, 2013). In other words, as the duration of the entering sounds increases, global acoustic representations are built upon temporal features to condense information into a more compact, and retainable structure (Yabe et al., 1998; McDermott, Schemitsch, and Simoncelli, 2013). For stationary sounds (such as sound textures, e.g., rain, fire, waterfall, typewriting; Saint-Arnaud and Popat, 1995), characterized by a constant repetition of similar events over time, this form of compression consists of computing a set of auditory statistics which comprises time-averaged acoustic details. Consequently, local features are no longer retained after their average global representation emerges (McDermott, Schemitsch, and Simoncelli, 2013).

Computational synthesis approaches proved being fundamental for the characterization of local and global auditory analysis. The basic assumption derives from information theories (Barlow, 1961) and suggests that the brain represents a sensory input with a set of measurements. This would imply that signals containing values matching those measurements will be perceived as the same. Furthermore, computational approaches allow to extract auditory statistics from original recordings and impose them to synthetically produced sounds (McDermott and Simoncelli, 2011). By doing so, they provide the opportunity to create synthetic audio excerpts which sound like the original natural sounds, while controlling the embedded statistics. Previous behavioral studies have used this type of synthetic stimuli to characterize the temporal dynamics of the two computational modes, local and global representations, respectively (McDermott, Schemitsch, and Simoncelli, 2013; McWalter and McDermott, 2018). Two main questions remain unsolved. First, it is unclear if the two computational modes can occur automatically. Previous investigations (McDermott, Schemitsch, and Simoncelli, 2013; Berto et al., 2021) relied on psychophysics and required that participants paid attention to the stimuli throughout the experimental session to make deliberate judgments over the heard sounds. Based on this evidence alone, it is not possible to make assumptions whether the engagement of these modes can occur during passive exposure, i.e., automatically or require individual effort. Second, it is unknown whether the two basic auditory computations rely or not on the same neural correlates and subtend to similar cortical activations. That is, whether different neural fingerprints to the emergence of local and global representation can be detected. We hypothesized that the switch between the two modes of representation rely on different cortical networks in the auditory system.

We used a computational auditory model to extract auditory statistics from natural sounds and generate synthetic excerpts controlling local and global properties; we acquired the EEG of twenty-four participants being passively exposed to a stream composed by triplets of sounds presented at a fast stimulation rate (one sound every 500ms). Sounds were randomly drawn from a large set of different synthetic excerpts. Within the triplet, the first two sounds were identical (standards), while the third one (oddball) was a different one.

Two experiments were designed. In Local Discrimination, the oddball sound could vary for its local features with unaltered global structure; in Global Discrimination, the

oddball differed for global (and thus also local) properties as compared to standard

sounds. As statistical variability is expected to vary as a function of sound duration

(McDermott, Schemitsch, and Simoncelli, 2013), in separate blocks, stimuli of

different lengths (40, 209 and 478ms) were presented. Participants were performing

an orthogonal task so that any difference between experiments may be interpreted

as automatic discriminative responses to the statistical variability in the oddball and

the auditory mode elicited by it (local vs. global; see Materials and Methods).

MATERIALS AND METHODS

Participants

Twenty-four normal-hearing right-handed young adults (F= 12; mean age= 27.13

years, std= 2.83) took part in the experiment. This sample size was estimated

through simulations. We used the procedure described in Wang and Zhang (2021;

for details on sample size estimation see Supplementary Expanded Methods in

appendix 1 and Figure S1). All participants were healthy, fully informed on the

scopes of the experiment, signed a written informed consent prior to testing, and

received a monetary compensation. The study was approved by the regional Ethical

Committee (CEAVNO protocol n 24579) and protocol adhered to the guidelines of

the Declaration of Helsinki (2013).

Experimental design and statistical analyses

Stimuli

Stimuli were synthesized with a previously validated computational auditory model

(McDermott and Simoncelli, 2011; Figure 1A). A set of statistics which emulates

basic auditory computations at the level of the cochlea (envelope, marginal moments

and cross-correlation) and mid-brain (modulation power and two correlations) were

extracted from original recordings of sound textures (Table 1) and imposed in an

iterative way on four white noise samples. This allowed to generate different sounds

varying for their local features but including the same long-term statistics (global

structure). Synthetic sounds derived from the same original sound texture but built

on different white noise samples, were referred to as *exemplars* of the same sound

texture and were perceptually very similar. As long-term statistics represent

averages of local features over time (McDermott, Schemitsch, and Simoncelli, 2013),

statistical similarity among exemplars of the same sound texture increases with

duration. On the other hand, exemplars of different sound textures were derived from

different original recordings and diverged for both local features and long-term

statistics (Figure 1B and C).

This computational synthesis approach provides an unprecedented level of control

over the statistics embedded in the sounds and allows to disentangle local features

processing from their statistical averaging.

Synthesis toolbox is available here: http://mcdermottlab.mit.edu/downloads.html

To create experimental stimuli, exemplars were cut into excerpts of different lengths,

equally spaced on a logarithmic scale, either 40, 209, and 478ms. Stimuli were

equalized to the same root mean square (RMS= 0.1) and had a sampling rate of

20kHz.

Procedure

Participants were tested in an electrically shielded and sound isolated booth. After

reading instructions on a monitor, they listened to the sound in the absence of retinal

input (participants were blindfolded to prevent visual input).

A sound sequence lasting 108sec was presented. The sequence contained triplets of

sounds (n= 216), presented one after the other to form an almost continuous sound

stream in which each sound was comprised within a 500ms time-window (Figure

1D).

Two experiments were implemented. (1) In Local Discrimination, two sounds within a

triplet were identical (standards), while the third one, oddball, comprised different

temporal local features but same long-term statistics with respect to the other two;

namely, it was an excerpt drawn from a different exemplar of the same sound

texture. Thus, standards, and oddball were the same sound object but slightly

differed in their local structure (e.g., both standards and oddball sounds are the

sound of waterfall; see Table S1, column 1). (2) In Global Discrimination, oddball

sound deviated from the other two for both its local features and global properties

(auditory statistics) being it an excerpt extracted from an exemplar of a different

sound texture compared to the other two identical sounds. This means that the

oddball was a different sound object compared to the standards (e.g., standard is the

sound of a bulldozer, the oddball is waterfall).

All sounds were drawn from a large set of different synthetic excerpts of each

original sound texture (Table S1). Sound Textures pairs were combined as in Table

S1 (column 1 and 2).

In both experiments, excerpts were drawn from two exemplars randomly selected

out of the four synthetic sounds originated from the four possible white noise

samples. In this way, statistical variability within a triplet was kept constant but the

sound streams were always different across blocks. In other words, stimuli *per se*

were never the same between experiments, but the expected variability between

standards and oddball was and discriminative responses emerging by the contrast of

deviant and standard did not depend on specific properties (e.g., a change in

frequency) but only on by their local or global statistical change. Moreover, to

improve generalizability, the order of the triplets was shuffled for each participant. In

sum, this allowed to test the processing (local features processing and/or global

statistical averaging) independently from the specific stimuli that were presented,

increasing generalizability of results.

Moreover, in the two experiments, the statistical variability between standard and

oddball sounds changed as a function of sound duration in opposite directions:

decreasing with duration in Local Discrimination, while increasing in Global

Discrimination (Figure 1C).

Three different sound durations were used: short, intermediate, and long (40, 209, or

478ms, respectively). These sound lengths were chosen based on results in

previous behavioral investigations (Berto et al., 2021; McDermott, Schemitsch, and

Simoncelli, 2013).

A total of six conditions were employed, one for each of two experiments (Local and

Global Discrimination) presented with stimuli of each of the three sound durations

(40, 209, 478) separately. Two runs per condition (Experiment * Duration) were

presented, for a total of twelve runs. The order of runs was randomized across

participants and short breaks were foreseen in between runs. Disregarding sound

duration, the number of standards was kept constant in each run (two standards in

each triplet), to prevent potential differences in standard formation (i.e., Sussman

and Gumeyuk, 2005) and expectancy effects from accounting for results.

Participants had to listen to the sound stream but were asked to perform an

orthogonal task consisting of pressing a button when a beep sound appeared. The

beep was a pure tone higher in pitch and intensity compared to the sound textures

stream. The pure tone was 50ms in length, had a frequency of 2200Hz, an amplitude

of 50dB, a sampling rate of 20kHz, and RMS of 5. The beep appeared randomly

within the stimulation. The number of beeps varied randomly across runs, from zero

to three. Detection was considered valid when participant pressed the key within an

arbitrary window of 3 seconds from beep appearance (behavioral results are

reported in the Supplementary Expanded Methods in appendix 1 and Figure S2).

Figure 1. Synthetic stimuli and Experimental Protocol.
(A) Example of sound synthesis. Sound waveform of 7s original recording of a fire cracking sound (left panel) and of 5s synthetic excerpt originated from the same recording by extracting the set of auditory statistics with an Auditory Texture model (McDermott and Simoncelli, 2011). Spectrograms of each sound are displayed below for comparison. (B) Auditory statistics extracted from two original recordings (in this example, waterfall and bulldozer) are imposed to two white noise samples (their spectrograms are represented on the left). The outcomes of the imposition are displayed as spectrograms on the right. The two synthetic sound excerpts containing the *same set of statistics* have the same global structure but differ for their local properties as they are derived from different white noise samples. On the other hand, when *different statistics* are imposed on the same white noise both local and global structures vary. Stimuli with the same auditory statistics will be perceptually very similar and identified as the same sound object (i.e., both are instances of a bulldozer sound); different set of auditory statistics will generate a different sound object (i.e., bulldozer in one case, waterfall in the other). (C) Average standard deviation of auditory statistics between oddball and standard for each experiment at each sound duration. Variability increases with duration in Global Discrimination, as global structure emerges, and decreases in Local. (D) Experimental protocol. Triplets of sounds were presented at a fast rate (one sound every 500ms). Two sounds were identical (standard), while the third was different (oddball) and could vary for its local or its global properties, depending on the experiment (Local or Global Discrimination). Since statistical variability changes as a function of sound length, three sound durations equally spaced logarithmically (40, 209, and 478ms) were employed to tap into each auditory mode separately (local vs. global processing).

EEG recording

Electroencephalography (EEG) was recorded from an EGI's HydroCel Geodesic Sensor Net with 65 EEG channels and a Net Amps 400 amplifier (Electrical Geodesics, Inc., EGI, USA). Acquisition was obtained via EGI's Net Station 5 software (Electrical Geodesics, Inc., EGI, USA). Central electrode E65 (Cz) was used as reference. Four electrodes were located above the eyes and on the cheeks to capture eye movements. Electrode impedances were kept below 30 kΩ. Continuous EEG signal was recorded throughout the whole session with a sampling rate of 500Hz.

Experimental sounds were played from a stereo speaker (Bose Corporation, USA) positioned in front of the participant and at one meter distance from their eyes; sounds loudness was kept constant across participants and runs. The experiment ran on MATLAB (*R2018b*; Natick, Massachusetts: The MathWorks Inc.); written instructions were displayed only at the beginning of the experimental session, via Psychtoolbox version 3 (Brainard and Vision, 1997; PTB-3; http://psychtoolbox.org/).

EEG Data Analysis

Preprocessing

Data were preprocessed with a semi-automatic pipeline implemented in MATLAB (see Stropahl et al., 2018; Bottari et al., 2020). Preprocessing was performed using EEGLAB (Delorme and Makeig 2004; https://sccn.ucsd.edu/eeglab/index.php). Data were loaded excluding electrode E65 (Cz) which was the reference channel of our EEG setup (thus included only zero values).

To remove slow drifts and DC offset, a high-pass filter (windowed sinc FIR filter, cut-off frequency 0.1 Hz, filter order 500) was applied to the continuous signal. Signal was then re-sampled to 250Hz to reduce computational time of further analyses steps.

A first segmentation in time was performed, by epoching the signal according to event onset. To avoid boundary artifacts, for each run, the signal was cut two seconds before its onset event and until two seconds after the end of the presentation (thus, from -2 to +114 sec). For each participant, epochs were then merged in a single file containing only the parts of the signal referring to significant stimulation (thus excluding breaks in between trials).

Independent Component Analysis (ICA) (Bell and Sejnowski, 1995; Jung et al., 2000a,b) was used to attenuate artifacts. To improve ICA decomposition, beforehand data were high-pass filtered (windowed sinc FIR filter, cut-off frequency 1Hz, filter order 500), low-pass filtered (windowed sinc FIR filter, cut-off frequency 40Hz, filter order 100) and segmented into consecutive dummy epochs of 1sec in order to spot non-stereotypical artifacts. Epochs with joint probability larger than 3 standard deviations were rejected (Bottari et al., 2020). PCA rank reduction was not applied prior to ICA, to avoid compromising its quality and effectiveness (Artoni, Delorme, and Makeig, 2018).

For each subject, ICA weights were computed using EEGLAB runica algorithm and assigned to the corresponding original raw (unfiltered) dataset. Topographies for each component were plotted for visual inspection. Artefacts associated to eye movements and blinks were expected. CORRMAP algorithm (Viola et al., 2009) was used to semi-automatically remove components associated to such artefacts. Component representing eye movements and blinks were manually identified from a single dataset and used as template. CORRMAP algorithm clusters ICA components

with similar topography across all datasets to highlight the similarity between the IC
template and all the other ICs. A correlation of the ICA inverse weights was
computed, and similarity allocated, with a threshold criterion of correlation coefficient
being higher or equal to 0.8 (default value of CORRMAP; Viola et al., 2009). For all
participants, on average 1.79 components were removed (std= 0.72; range= 0-3).
Cleaned data were re-loaded and bad channels were interpolated after visual
inspection. For most participants, a maximum of four channels were interpolated,
except for one participant in which several noisy channels required interpolation
(mean number of interpolated electrodes per participant= 1.67; std= 2.01; range= 0-
8). Bad channels were interpolated via superfast spherical interpolation implemented
in EEGLAB.
Finally, the channel E65 (Cz) was included back in the EEG data of each participant
and datasets were re-referenced to average reference across channels.
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Time-domain analysis
Preprocessed data were low pass filtered (windowed sinc FIR filter, cut-off
frequency= 40Hz, filter order= 100). Consecutive epochs (from -0.1 to 0.5sec) were
generated, including segments of either the oddball sounds or the second standard
of the triplets for each participant and condition. Joint probability was used to prune
non-stereotypical artifacts (i.e., sudden increment of muscular activation); rejection
threshold was 4 standard deviations (Stropahl et al., 2018). For oddballs, on average
10.51 epochs per participant were removed (std=3.55; range 3-22) out of the 144
concatenated epochs that each Experiment * Duration comprised; for standards, on
average 10.71 epochs were removed (std= 3.81; range 3-21), again out of 144 trials
per each condition.
Datasets were converted from EEGLAB to FieldTrip (Oostenveld, Fries, Maris, and
Schoffelen, 2011; http://fieldtriptoolbox.org). Grand averages across participants
were computed for each experiment, duration, and stimulus type (either standard or
oddball). Data across trials were averaged to compute event-related potentials
(ERPs) at central electrodes (Cz and FCz). Before displaying results, the data were
baseline corrected using the −0.1 to 0 sec pre-stimulus period.
Since all stimuli in the triplets were never the same across runs, we assessed
whether differences exist between experiments (Local and Global) at sound duration
by subtracting from the response to the oddball sound the response to the preceding

standard in each triplet. This was done to ensure that any potential difference in the
perceived oddball sound between experiments, for each sound duration, was not
driven by idiosyncratic differences in the stimuli that were presented in that specific
run, but by the statistical difference to their preceding standards.
ERPs and grand-average topographies to oddball and standard sounds (prior to
subtraction) are also available in the Supplementary information (Figure S3).
A non-parametrical permutation test was performed to check significances between
experiments (Local vs. Global), for each duration (short, intermediate, and long) in
the so-formed oddball – standard epochs. Each participant's data were summarized
in an array of condition-specific averages (experiment*duration). Permutation test
was carried out under the null hypothesis that probability distributions across
condition-specific averages were identical across experiments. Noticeably, statistical
analysis between experiments were performed only within duration, to control for
refractoriness effects related to different interstimulus intervals (ISI) at long and short
durations.
Thus, the contrasts of interest were: (1) Local short vs. Global short; (2) Local
intermediate vs. Global intermediate; (3) Local long vs. Global long.
A series of cluster-based permutation tests (Maris and Oostenveld, 2007; cluster
alpha threshold of 0.05 (two-tailed); 1000 permutation; minimum neighboring
channels = 2) was performed. Cluster-based permutation analyses were performed
without a priori assumptions regarding specific regions of interest, thus, including all
channels. Based on extensive literature on auditory change detections, effects of
Local and Global Discriminations were expected to occur around N1 and P200
components of auditory evoked potentials (see Näätänen et al., 2007 for review).
Thus, cluster-based permutations were carried including all timepoints within the 0.1
to 0.3 s time-window. Significant positive clusters would indicate grater response at
sensor level to Local as compared to Global Discrimination; significant negative
clusters would imply the opposite trend, with grater response to Global as compared
to Local.
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Source Reconstruction
Source reconstruction was performed using the Brainstorm toolbox (Tadel et al.
2011; http://neuroimage.usc.edu/brainstorm) and following a validated pipeline
(Stropahl et al., 2018; Bottari et al., 2020). This analysis was driven by results in the

time-domain at the sensor level, thus only performed for those conditions which

yielded to significant differences after cluster-based permutation (see below and

Figure 2). Preprocessed, epoched, and pre-stimulus baseline subtracted datasets

were imported in Brainstorm. Electrode location was assigned, projected on the

scalp, and MRI registered to a default anatomy (ICBM152; Fonov et al. 2009).

We computed noise covariance matrix (using a pre-stimulus period between -0.1 and

-0.002 sec) and we averaged all epochs for each participant. The cortex surface was

computed using OpenMEEG BEM (Gramfort et al. 2010); since default anatomy was

used, this was done only for the first participant, and subsequently the head model

was applied to all others. Sources were extracted using the minimum norm imaging

inverse method and the dSPM inverse measure (Dale et al. 2000) with constrained

(normal to cortex) dipole orientations. Subtraction (oddball – standard) was then

performed in the source domain.

To assess significant voxels, we performed non-parametric tests (Pantazis et al.,

2005a). Directionality of the tests and time window within which perform the statistics

were driven by results in cluster-based permutation performed at the sensor level,

that is to address the specific hypotheses yielded from time-domain analysis.

Wilcoxon signed ranked test (MacFarland and Yates, 2016) was performed in

Brainstorm to compare the two datasets at the whole brain level (across all voxels) to

calculate t-statistics with a critical alpha of 0.05 (one-tailed). A number of 1000

permutations was implemented. Results were time-corrected for False Discovery

Rate (FDR; Benjamini and Yekutieli, 2001); a cortical activation was considered only

if above a minimum voxel-size of 20mm. Activity-based ROIs were defined after

whole brain analysis. ROI selection was both data-driven according to the peak of

activity and based on previous knowledge on auditory cortex organization and

functioning.

RESULTS

Time-domain results

Cluster permutation revealed significant positive cluster for the short duration 40 (p =

0.02), lasting between 192ms and 224ms after stimulus onset. No significant cluster

was found for the intermediate duration 209 (all p > 0.17), while a significant negative

cluster was found for the long duration 478 (p < 0.001) lasting between 196ms and
300ms after stimulus onset. Grand-average topographies at relevant latencies are
displayed in Figure 2A. For visualization, we selected two central channels (Cz and
FCz) and plotted the grand-average event-related potentials (ERPs) of oddball minus
standard for all durations in each experiment (Figure 2B). These results support the
hypotheses based on behavioral data (i.e., Berto et al., 2021; McDermott,
Schemitsch, and Simoncelli, 2013) for which local processing is favored for brief
sound excerpts while global processing emerges at longer durations and show that
the same can hold even when participants are directly engaged to discriminate them.
Discriminative responses can emerge automatically (pre-attentively) from stimulus
properties as the amount of acoustic information changes.

A

Grand-average topographies (oddball – standard)

Time window (s)

B

Response to sound change at central electrodes (oddball – standard)

Time (s)

C

Average over time of response at central electrodes (oddball – standard)

Time-window (s)

Figure 2. Results of time-domain analysis at sensor level.
(A) Grand-average topographies of the differential response associated with the sound
change (oddball sound minus standard sound) at significant latencies, for each experiment
and duration. For each latency, electrodes associated with significant clusters are displayed
above as red stars on the scalp. * *p < 0.025.*
(B) Grand-average electrical activity of the differential response (oddball minus standard) at
three central electrodes (E54, E7, E65, in red) which were significant for both short (40) and

long (478) duration. Shaded regions show interpolated standard error of the mean (SE) at
each time point. Positive values indicate that oddball elicited greater response than standard.
Results of cluster permutation are displayed as black bars extending through significant
latencies. – *p < 0.025.*
(C) Grand-average amplitude of the differential response (oddball minus standard) across
participants at the same three significant electrodes averaged within significant latencies for
each experiment and duration. For visualization only, since no significant latencies existed for
the duration 209, an intermediate time window was used, by computing an average between
the time windows of significant latencies for duration 40 and 478. Bar plots represent average
values across participants. Individuals' values are separately displayed by each point.

Source reconstruction results

Provided results at the sensor level, we investigated Local vs. Global for the duration

40 and 478. Specifically, for duration 40 we tested in which source estimates the

activation in Local Discrimination was higher compared to Global Discrimination

(H1= Local > Global) within the time window revealing the significant effect at the

sensor level (0.192-0.224s; see Figure S2A); by contrast, for duration 478 we tested

which sources had an activity which was higher for Global Discrimination as

compared to Local (H1 = Global > Local) at latencies from 0.196 to 0.3 s (the time

window comprising the significant effect at the sensor level).

At duration 40, whole-brain analysis showed significant voxels located around

anterior superior temporal sulcus (STS) in the right hemisphere (Figure 3A, left

panel). An activity-based ROI was drawn around the peak of activation at 208ms

(Figure 3B, left panel).

At duration 478, the same procedure yielded to significant voxels around right medial

superior temporal gyrus (STG), the anterior part of left STS, and left Heschl's gyrus

corresponding to early auditory cortex (Figure 3A, right panel), with a peak of

activation at 236ms (Figure 3B, right panel).

These results provide evidence that local and global processing represent alternative

processes relying on partially different networks within the auditory system. These

networks are inversely employed as a function of sound duration and stimulus

properties.

A

Source Reconstruction

40: Local > Global   478: Global > Local

208ms   236ms

B

Grand-average time course of ROIs

40: Local > Global   478: Global > Local

Right STS   Left Early AC   Left STS

Figure 3. Results of Source Reconstruction.
(A) Group-level results of non-parametric permutation test performed within significant time
windows at the whole brain level. Results were corrected for false discovery rate (FDR).
(B) Three ROIs were identified. Grand-average time course of source activity over the entire
time window (0-0.5s) are plotted for each ROI. Shaded regions show interpolated standard
error of the mean (SE) at each point.

DISCUSSION

The auditory system operates at different timescales extracting information at high

(local) and low (global) temporal resolution. Global structure emerges at longer

timescales, as the system extracts abstract information from local features. Here we

aimed to (1) test the automaticity of sound discriminations based on local and global

computations and (2) and understand if discriminative responses driven by local and

global processes subtend to different neural correlates. We employed a

computational model to control auditory statistics and synthetically create stimuli with

the same global structure but emerging from different local features. We presented a

stream of sound triplets containing two consecutive standards followed by an
oddball; oddballs could vary from standards for its local or global structure; while
stimuli were equalized to the same RMS, local differences were more prominent at
shorter durations and global differences at longer ones. Compatibly, results showed
that when sound duration was short, changes in local properties elicited greater
neural responses than different global ones. When duration of sounds was longer,
the change in global structure elicited a higher response that was not detectable
when only their local features changed (Figure 2A, B, C). The opposite trend in the
neural response observed according to sound duration (see Figure 2C) provides
evidence that the local or global processes are alternative and, pre-attentively
selected merely based on the amount of information provided in the upcoming
stimulation. Source modeling showed different putative underlying neural correlates
distinguishing the two computational modes (local and global) and hemispheric
asymmetries. The observed neural correlates indicated not only that a change had
occurred, but also the nature of the change. Importantly, these responses could be
measured without participants being asked to pay attention to any stimulus property.
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Automaticity of Local and Global Processing
Our findings show that different subprocesses (local vs. global) exist and are
specifically tuned to detect different types of sound changes. The engagement of
one processing strategy or the other occur automatically and is driven by properties
of the change of sound. In fact, participants were engaged in an orthogonal task
while exposed to the sound stream and were not instructed to perform any related
task. Strikingly, the directionality and magnitude of the neural response was the
same as in previous psychophysical investigations (Figure 2C; McDermott,
Schemitsch, and Simoncelli, 2013; Berto et al., 2021) when participants were
attentive to the sounds and performed deliberate judgments over two alternative
forced choice (2AFC).
Attention plays a role in determining to which temporal scale the auditory system
attend to (Lange, Roesler, and Roeder, 2003; Sanders and Astheimer, 2008). For
instance, in a task involving rhythmic sound trains, listeners who were instructed to
pay attention to long-term variations showed different patterns of responses as
compared to those who paid attention to the global structure of the sound stream
(e.g., Large and Jones, 1999). The auditory system switches between time scales

and what the listeners are paying attention to influences sound discrimination and

sensory processing. (Hink and Hillyard, 1976; Schwent et al., 1976; Hansen and

Hillyard, 1983; Lange, Roesler, and Roeder, 2003; Sanders and Astheimer, 2006).

Attention over selective features also engages different hemispheres, according to

the timescale at which participants are expecting sound changes to occur

(Brechmann and Scheich, 2005).

Nonetheless, in our experiment, we showed that the properties implicit in the sound

are sufficient to automatically elicit separate discriminative responses (Figure 1B, C,

D; Figure 2). Noticeably, the present results emerged despite triplets were

continuously changing (the only fixed parameter was either the local or the global

change) and thus can be generalized to multiple sound textures (Figure 1; see also

Supplementary Information, Table S1). These results suggest that the auditory

system is capable to automatically attune to specific type of sound changes, to

detect stimuli variances in the most efficient way and proved that this effect emerges

independently from attentional control. This expands seminal studies disclosing the

MisMatch Negativity response (MMN; Näätänen et al., 1978; Tiitinen et al., 1994), a

neural marker revealing automatic auditory change-detections. MMN is the outcome

of a process by which the system "scans" for regularities in the entering sounds and

uses them as reference to detect variations within the auditory scene (for reviews

see Näätänen et al., 2001, 2010).

MMN response to a deviant sound is not affected by prior expectations that the

oddball will occur (Rinne et al., 2001). In our study, expectations that a change would

occur in the third element of the triplet had a probability of 1 in each experiment

(Local and Global Discrimination; Figure 1D). Thus, our results cannot be simply

explained by spurious attentional effects. Differences between oddball responses,

compared to the previous standard, in our study can only be due to pre-attentive

discriminative responses to the properties of the deviant sound.

These results add up to the auditory MMN, which set the basis for the existence of a

primitive intelligence in the auditory system (for review see Näätänen et al., 2001).

Here, we showed that the auditory system not only orients the attention towards

relevant, deviant events in the environment but is also capable to automatically

categorize such acoustic difference according to the level of change and the

timescales at which deviation occurred.

Local and Global Discrimination subtend to alternative processes

Electrophysiological signatures of local and global sound representations automatically emerged from our protocol as a function of sound duration, advocating for the -at least partial- independence of the two computations (Figure 2). As global representations are built upon local features (McDermott and Simoncelli, 2011; McDermott, Schemitsch, and Simoncelli, 2013), we could have expected that the two computations were cumulative processes, with global representation adding on top of local one and pertaining to similar neural activations. However, the processing of information at local or global timescale might differ not only quantitatively but also qualitatively (e.g., the response to small changes of pitch at global timescales -tend to be faster and more accurate as compared to the detection of a large pitch change occurring at a fast rate; Sanders and Poeppel, 2007). When the sensory information load is prohibitive, high temporal resolution information tends to get lost in the averaging process. Thus, since local features are not retained after averaging (McDermott, Schemitsch, and Simoncelli, 2013), it checks out that the two computations represent alternative processes, and that the system switches from one to the other depending on the intrinsic sound properties (e.g., statistical variability) and the amount of available information in the auditory stream (e.g., increased stimulation length). Recent evidence in the animal model showed that auditory statistics ensembles are represented by distinct responses at the level of the midbrain (Zhai et al., 2020). These neural representations to auditory statistics occur at dissociable time scales, permitting the discrimination and recognition of natural sounds, with local information supporting sounds differentiation while the emergence of global structure their recognition (Zhai et al., 2020). In our study, whole brain results in the source domain (Figure 3) support this suggestion of dissociable neural responses to local and global statistical properties. By comparing local and global discrimination at short duration we showed that discrimination based on local features entrained more the anterior part of the STS in the right hemisphere. Conversely, the same contrast at long durations linked the emergence of global discrimination predominantly to the left hemisphere; precisely response peaked both around Heschl's gyrus, corresponding to early auditory cortex, and in the STS and STG; Figure 3A). The hemispheric asymmetry emerging from source reconstruction falls into place with previous observations about the existence of an asymmetric

sampling of acoustic temporal information in right and left auditory cortices (Flinker et
al., 2019).
The right STG has been identified as a potential generator for auditory MMN (Optiz
et al., 2002; Doeller et al., 2003; Molhom et al., 2005). Here, the entrainment of right
STS for the short stimuli is in line with a recent model suggesting a right hemisphere
dominance for the processing of spectral content presented at a slow rate (Flinker et.
al., 2019) and could account for higher sensitivity to local-acoustic-features-change
detection in deviant sounds.
Previously, right hemisphere was found to be more sensible to global structure
changes (Brechmann, Baumgart, & Scheich, 2002; Poeppel et al., 2004). This
apparent discrepancy with the present results could be explained by considering that
other studies addressed global processing by presenting variations of acoustic
features at longer timescales (e.g., tracking slow rate modulation changes).
By contrast, for long durations, a change in global structure elicited greater neural
response in the left hemisphere. This result may be surprising, as the left
hemisphere has often been associated to the processing of fine-grained temporal
details (Fiez et al., 1995; Johnsrude et al., 1997; Belin et al., 1998; Celsis et al.,
1999) which perhaps underly its specialization in processing linguistic features
(Tallal, Miller, & Fitch, 1993). However, a response in the left STS is in line with
evidence appointing left STS as an area involved in sound object categorization (i.e.,
Liebenthal et al., 2010). Strikingly, we reported a peak of activity over the anterior
and lateral parts of left Heschl gyrus and the anterior part of left STG (see Figure
3A). These areas have been previously referred to as the "what" auditory pathway, a
network involved in sound identity (see Ahveninen et al., 2006; Bizley et al., 2013).
Consequently, their involvement in global processing further supports that, as sound
duration increases, auditory statistics emerge allowing for a different sound-object to
be automatically detected (McDermott and Simoncelli, 2011). Interestingly, previous
evidence showed that left STG can be compartmentalized into sub-regions partaking
to different levels of processing, with the anterior part being associated with the
integration of phonemes into more complex temporal patterns, such as words
(DeWitt and Rauschecker, 2012). This specialization could extend to naturalistic
sounds processing, beyond speech, and could represent a general abstraction
mechanism to derive global abstract structure from local acoustic elements
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CONCLUSION

Seminal studies on the auditory mismatch negativity (MMN) provided the basis for the notion of a primitive intelligence in the auditory system, dedicated to alerting and orienting towards changes of regularities in the environment. By combining electrophysiology with a computational approach, we revealed the cortical representations of the auditory system's ability to automatically differentiate changing sounds, depending on their statistical variability and amount of available information in the auditory stream (e.g., sound duration). Different cortical responses emerged as a function of specific stimulus-driven auditory representations, revealing different networks that represent discriminative responses to local vs. global changes. These responses appeared to occur pre-attentively and to be alternative to one another. These results open the possibility to use neural markers associated with local and global discriminations for further studying specific auditory computations in both basic and applied research.

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CONFLICT OF INTEREST

The authors declare no competing interest.

FIGURES TITLES AND LEGENDS

Figure 1. Synthetic stimuli and Experimental Protocol.

(A) Example of sound synthesis. Sound waveform of 7s original recording of a fire cracking sound (left panel) and of 5s synthetic excerpt originated from the same recording by extracting the set of auditory statistics with an Auditory Texture model (McDermott and Simoncelli, 2011). Spectrograms of each sound are displayed below

for comparison. (B) Auditory statistics extracted from two original recordings (in this

example, waterfall and bulldozer) are imposed to two white noise samples (their

spectrograms are represented on the left). The outcomes of the imposition are

displayed as spectrograms on the right. The two synthetic sound excerpts containing

the *same set of statistics* have the same global structure but differ for their local

properties as they are derived from different white noise samples. On the other hand,

when *different statistics* are imposed on the same white noise both local and global

structures vary. Stimuli with the same auditory statistics will be perceptually very

similar and identified as the same sound object (i.e., both are instances of a

bulldozer sound); different set of auditory statistics will generate a different sound

object (i.e., bulldozer in one case, waterfall in the other). (C) Average standard

deviation of auditory statistics between oddball and standard for each experiment at

each sound duration. Variability increases with duration in Global Discrimination, as

global structure emerges, and decreases in Local. (D) Experimental protocol. Triplets

of sounds were presented at a fast rate (one sound every 500ms). Two sounds were

identical (standard), while the third was different (oddball) and could vary for its local

or its global properties, depending on the experiment (Local or Global

Discrimination). Since statistical variability changes as a function of sound length,

three sound durations equally spaced logarithmically (40, 209, and 478ms) were

employed to tap into each auditory mode separately (local vs. global processing).

Figure 2. Results of time-domain analysis at sensor level.

(A) Grand-average topographies of the differential response associated with the

sound change (oddball sound minus standard sound) at significant latencies, for

each experiment and duration. For each latency, electrodes associated with

significant clusters are displayed above as red stars on the scalp. *$p < 0.025$.*

(B) Grand-average electrical activity of the differential response (oddball minus

standard) at three central electrodes (E54, E7, E65, in red) which were significant for

both short (40) and long (478) duration. Shaded regions show interpolated standard

error of the mean (SE) at each time point. Results of cluster permutation are

displayed as black bars extending through significant latencies. *– $p < 0.025$.*

(C) Grand-average amplitude of the differential response (oddball minus standard)

across participants at the same three significant electrodes averaged within

significant latencies for each experiment and duration. For visualization only, since

no significant latencies existed for the duration 209, an intermediate time window
was used, by computing an average between the time windows of significant
latencies for duration 40 and 478. Bar plots represent average values across
participants. Individuals' values are separately displayed by each point.
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Figure 3. Results of Source Reconstruction.
(A) Group-level results of non-parametric permutation test performed within
significant time windows at the whole brain level. Results were corrected for false
discovery rate (FDR).
(B) Three ROIs were identified. Grand-average time course of source activity over
the entire time window (0-0.5s) are plotted for each ROI. Shaded regions show
interpolated standard error of the mean (SE) at each point.
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697 **SUPPLEMENTARY EXPANDED METHODS (Appendix 1)**
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Sample size
The number of participants was estimated through simulations. We used the
procedure described in Wang and Zhang (2021) and simulated a dataset with two
conditions (Local and Global) of ERP data. First, we selected a group of electrodes
of interest at central locations (E7, E65, E54; see Figure 2B and S2B in red) which
typically capture auditory responses. For the simulation, we selected a time window
between 0.1 and 0.3s, based on previous MMN studies (see Näätänen et al., 2007
for review). The amplitude values at the electrodes of interest for the two conditions
were sampled from a bivariate normal distribution (within-subject design), which
mean and standard deviation were chosen based on results of four pilot datasets
(mean Local= 0.16; mean Global= 0.56; sd Local= 0.52; sd Global= 0.54).
We then ran cluster-based permutation on simulated datasets, to test whether any
statistical cluster (t-values) exhibited significant difference between the two
conditions with an alpha level of 0.05. The procedure starts with a sample size of 10
and increases in steps of 1 until it reaches a power of 0.80. We run 1000 simulations
for each sample size and calculated the power as the proportion of the number of
times finding significant clusters in these 1000 simulations. The simulation results

showed that in order to obtain a power above 0.8, a sample size of N= 24 was

required (see Figure S1).

The algorithm to perform such analyses can be downloaded from this link:

https://osf.io/rmqhc/.

Behavioral Results

For each condition, percentage of correct beep detections was above 90% (Local 40:

mean= 0.99, std= 0.03; Local 209: mean= 0.99, std= 0.05; Local 478: mean= 1, std=

0; Global 40: mean=0.99, std= 0.05; Global 209: mean= 0.97, std=0.08; Global 478:

mean= 0.97, std= 0.11; Figure S2). We run a two-way ANOVA for repeated

measures with factors Experiment (2 levels, Local vs. Global) and Duration (3 levels,

40, 209, and 478) to address whether experiment type and stimulus length impact on

beep detection and participants' attention to the task. No significant main effects

were observed (Experiment, $F_{(1,23)}$= 3.62, p =0.07, n^2= 0.14; Duration, $F_{(2,46)}$= 0.58,

p= 0.56, n^2= 0.3), nor their interaction (Experiment*Duration, $F_{(2,46)}$= 0.45, p= 0.64,

n^2= 0.2).

These behavioral results provide evidence that participants were attentive and

responsive during sound presentation throughout the experiment and that attention

to this orthogonal task was not influenced by experiment and sound duration.

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A

Grand-average topographies (oddball − standard)

B

Response to sound change at central electrodes (oddball − standard)

C

Average over time of response at central electrodes (oddball − standard)

A

Source Reconstruction

40: Local > Global

478: Global > Local

208ms

236ms

B

Grand-average time course of ROIs

40: Local > Global

478: Global > Local

Right STS

Left Early AC

Left STS