SONIFICATION AND VISUALIZATION OF NEURAL DATA

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ABSTRACT

This paper describes a method for integrating audio and visual displays to explore the activity of neurons in the brain. The motivation is twofold: to help understand how populations of neurons respond during cognitive tasks and in turn explore how signals from the brain might be used to create musical sounds. Experimental data was drawn from electrophysiological recordings of individual neurons in awake behaving monkeys, and an interface was designed to allow the user to step through a visual task as seen by the monkey along with concurrent sonification and visualization of activity from a population of recorded neurons. Data from two experimental paradigms illustrating different functional properties of neurons in the prefrontal cortex during attention and decision-making tasks are presented. The current system provides an accessible way to learn about how neural activity underlies cognitive functions and serves as a preliminary framework to explore both analytical and aesthetic dimensions of audiovisual representations of the data.

1. INTRODUCTION

Our brains are able to manage a great deal of information, from taking in sensory perceptions to forming decisions and transforming plans to actions. Current research explores how this is achieved by a network of billions of interconnected neurons, communicating through electrical impulses called action potentials, or spikes. The activity of single neurons can be recorded through electrodes placed in the brain while subjects (in this case rhesus macaques) perform experimental tasks designed to examine specific cognitive functions. Neural responses are often very diverse, and when trying to understand how a population of neurons might work together, simply averaging across all neurons results in a loss of information, while plotting the raw responses of all neurons can quickly become difficult to interpret. Sonification offers a complementary way to explore the data and in a literal sense ties in closely with the idea of listening to a dynamic conversation among neurons during cognitive tasks.

The idea of listening to the brain has been explored at both the macroscopic and microscopic levels. Electrical signals recorded from the scalp (electroencephalogram, or EEG) have long been studied as a representation of aggregate neural population activity. Sonification of EEG signals has been applied in a variety of contexts: for scientific understanding [1], as a potential diagnostic tool for detecting abnormal brain rhythms in epileptic patients [2], and as auditory feedback for human computer interaction applications [3]. Previous work has also explored sonification of neurons isolated in culture [4, 5].

For recordings from individual neurons in awake behaving subjects, audification of neural spike trains during data collection has long been used as a tool for navigating through different areas of the brain. During in vivo single electrode experiments, electrophysiologists often listen to an amplified voltage signal while lowering the electrode into the brain in order to estimate depth and cortical area as well as identify neurons. Once a neuron is isolated, listening to its spike train, which sounds like a series of pops and clicks, provides a fast and convenient way to gauge, for example, how strongly a neuron responds to a particular visual stimulus in real time. The ability to listen to the neural activity while visually paying attention to the stimulus on the screen enables the experimenter to constantly monitor both. Beyond a few neurons, it becomes difficult to hear nuances within the population activity. In the current study we concurrently sonify and visualize activity from a population of neurons along with a schematic of the behavioral task being performed both to try and provide an intuitive way to identify patterns in the data and to explore different ways in which signals from the brain can be used to create musical sounds.

2. SYSTEM

The current implementation provides a way to explore data after it has been collected. The system enables the user to load neural spike trains and trial information and then listen to and visualize the data as it relates to a behavioral task (Fig. 1). The user can interactively play through entire experimental trials or portions of trials while being presented with a constantly updating schematic of the task performed by the monkeys as well as the elicited neural responses.

2.1. Data

In a typical neurophysiological experiment, an animal is trained to repeatedly perform many trials of a carefully controlled task so that
multiple instances of neural responses to a particular experimental condition can be analyzed. Three representations of data were explored: single trials, condition averages, and condition average differences. Single trials consist of spike times for each neuron with millisecond precision, whereas condition averages represent the smoothed instantaneous spike rate averaged across multiple trials of the same experimental condition for each neuron. Average differences summarize the difference in spike rate between two conditions for each neuron across time. The user can load different combinations of single trials, average trials, or average difference trials for a particular task.

2.2. Interface

The data are visualized as rasters, which are labeled and stacked as blocks on the left side of the screen. Example screenshots are shown in Fig. 3 and 5. Within a raster, each row represents one neuron’s response across time. For individual trials, dots represent a spike at that particular time, whereas for the average and difference plots, spike rate is indicated by the color of the heat map. The average spike rate across all neurons over time for each raster is shown below the raster blocks and highlighted for the current raster.

As a vertical bar moves across time for a given trial, the task screen on the right updates with a schematic of the stimulus that the monkey is viewing at that particular time in the trial. For single trial rasters, the dots representing spikes are dynamically enlarged for the current time. The user can click anywhere on any raster to change the current time and use computer keyboard shortcuts to change certain parameters of the sound, such as the data to sound mapping, musical scale, speed of playback, and data integration time. To change the instrumentation, the user can manually change properties of the sound engine.

2.3. Data to sound mappings

Out of the large space of possible data to sound mappings, three were implemented for the current system, termed avgRatePitch, neuronPitch, and eachRatePitch. The avgRatePitch mapping provides the most basic summary of average population activity, where a range of spike rates is mapped to a range of pitches such that higher spike rates correspond to higher pitches. The average firing rate across all neurons is sampled every specified number of samples, and the corresponding note is played, creating a steady stream of single notes. This mapping can be used both for single trials and condition averaged trials. For the neuronPitch mapping, which applies to single trials, each neuron is assigned a unique pitch, and a note is played at that pitch each time the neuron spikes. If specified, the neurons can be split into two sets, each set with its own instrument. The eachRatePitch mapping focuses on the average spike rate of each neuron over time. Neurons are grouped into 2-4 groups, and each group is assigned an instrument. After a specified number of samples, every fifth neuron within each group is selected, and a pitch corresponding to its spike rate is played, again with higher spike rates corresponding to higher pitches. The neurons within each group are continuously cycled at every sampled time interval.

2.4. Implementation

A software system was designed consisting of a data engine that handles loading, processing, and graphical display of experimental data as well as a sound engine that handles the synthesis of sound parameters mapped from the data. Networked communication sent from the data engine to the sound engine allows for a separation of the extraction of data parameters for sonification from the actual mapping of data to sound.

Initial preprocessing of the data, which included sorting the neurons, creating matrices of spike times, and computing trial-averaged instantaneous spike rates, was done in MATLAB and output as text files. Images of the behavioral task, average activity plots, and labels were generated and saved as .raw image files. The interface was developed in C++ and uses OpenGL / GLUT for the graphical display. Timing of the playback is controlled using RtAudio [6] such that every time a specified number of samples has passed, the appropriate sound parameters are calculated and then sent via Open Sound Control (OSC) [7] to a sound engine. In the current implementation, a ChucK [8] script runs concurrently and handles synthesis. For each OSC message received, ChucK plays a single note with the specified instrument and frequency. Due to the constraints of pitch, the sonified output is stretched in time compared to the actual timing of the data such that the sonification is slowed by a minimum factor of 10.

3. RESULTS

Data from two separate experiments were used to explore how aud iovisual displays of neural data might aid in understanding how behavior correlates with neural activity and in achieving different musical aesthetics. Within the context of the two experiments presented, the three different data to sound mappings highlight different aspects of the main effects in the data.

On single trials and average trials, the avgRatePitch mapping reflects the average envelope of activity across all neurons such that sharp onsets and offsets of overall neural activity create salient rising and falling of pitch. The amount of sustained neural activity present across a certain span of time can be estimated by the absolute pitch played, but since there is a steady string of notes, the relative intensity of activity as compared to baseline is perhaps less apparent. The constant tempo, single string of notes, and temporally smoothed profile create a steady melody that is easy to follow.

On the other hand, the neuronPitch mapping for single trials reflects the amount of participation from the population of neurons since spikes from each neuron have a unique and independent representation (a note played at each spike). While it is not possible to simultaneously track the activity of all individual neurons at all points in time, a sparse sound corresponds to low neural activity while a dense concentration of notes reflects the simultaneous activation of multiple neurons. A persistent sounding of particular notes indicates the elevated activity of specific neurons. For this mapping, there is no rhythmic structure imposed on the sounds. This leads to sporadic bursts of sound triggered by events that drive the activity of the neurons. Since the neurons are represented as independent notes, this mapping showcases the complexity of activity in the population on a millisecond by millisecond basis and creates a more chaotic sound.

For average and difference trials, the eachRatePitch mapping provides a blend of average rate and individual neuron information since the discrete sampling of individual neuron spike rates within each assigned group means that a changing subset of neurons in every group is represented at a given time. The regular sampling of activity imposes a steady rhythm on the notes, and the assignment
During the same number of notes plays at every fixed interval, creating a structured and continuously flowing progression of chords. An example set of eye traces from microstimulation-evoked saccades are shown. The array of gratings was positioned such that one grating was centered at the average evoked saccade endpoint. C. Trials in which the monkey was cued to attend to the response field are labeled "Cue RF" whereas trials in which the monkey was cued to attend to the opposite array location are labeled "Cue away."

of instruments to each group can make the activity of some groups of neurons sound more prominent than others. In this mapping, the same number of notes plays at every fixed interval, creating a structured and continuously flowing progression of chords.

Additionally, the playback speed affects the granularity with which changes in activity across time can be perceived in that slower speeds highlight local changes while higher speeds provide more of an overview of single trial dynamics. The choice of instruments and musical scale also directly affect the overall aesthetic of the sound.

4. EXAMPLES

The following two experiments explore the different response properties of neurons in an area of the brain involved in planning and executing eye movements. Our eyes are constantly receiving sensory input, and visual attention plays a crucial role in how we experience the world. Even though it may seem like we can see everything around us, only a limited amount of information is actually selected for detailed processing. Since we have the highest visual acuity at the center of gaze, our eyes are constantly scanning to bring different visual information into focus. We can also attend to peripheral locations while keeping our eyes fixed, for example while driving and keeping an eye on the road but constantly monitoring the surroundings. A working model for how the brain might resolve these different means of selecting visual information centers on shared neural mechanisms underlying both the control of eye movements and the voluntary allocation of attention.

4.1. Spatial attention task

In order to study neural mechanisms underlying visual attention, monkeys were trained to direct and sustain attention at a peripheral location without the use of eye movements (Fig. 2) [9]. During each trial, the monkey maintains fixation at the center of the screen and uses a lever to indicate whether one grating embedded among five distractors changes orientation across two flashes. A spatial cue is given early in the trial, and in order to correctly detect the grating change, the monkey needs to direct attention to the cued location. All six locations are equally likely to be cued, and the cue is always valid.

Single electrode recordings were made in the frontal eye field (FEF), which is an oculomotor area known to play a role in controlling eye movements. The FEF contains a spectrum of visual to (eye) movement responsive cells, which form a map of visual space. For a given neuron, the particular region of space that it represents is called its response field (RF). The RF’s of individual neurons are found by electrically stimulating at the recording site, which causes the monkeys to make a stereotyped eye movement (saccade) towards a particular area of visual space. The comparison of interest is the neural responses when the monkey is attending to the RF of the recorded neurons vs. when the monkey is attending elsewhere. Within this task, individual neurons show vastly different response profiles even though the monkey does not make any eye movements. As a population, the spike rates of these neurons encode whether the monkey is paying attention to a particular area in visual space throughout the duration of each trial.

Fig. 3 shows an example screenshot with two single trials, two condition averages, and one average difference plot comparing neural responses when the monkey is cued to attend the RF vs. cued to attend away. Neurons from independent recordings were combined into example trials and aligned so that their RFs are located at what is schematically diagrammed as the lower left corner of the screen. The trials span four seconds. Vertical lines on the rasters indicate different epochs of the trial, and shading on single trials marks the periods during which a visual stimulus other than the fixation spot is presented. The neurons are sorted such that the more visually responsive neurons are at the top of each raster.

The corresponding video capture, which demonstrates the
three different data to sound mappings, can be viewed at the link given at the end of the discussion section. A feature that stands out both in the rasters and the sonified output is the increased activity in response to visual stimuli presented in the response field. Furthermore, the neurons sustain an enhanced level of activity when the monkey is attending to the RF location even when the screen is blank without a visual stimulus to drive the cells. During the presentation of the gratings, the neurons also show enhanced visual responses to the grating in the RF when attended vs. not attended even though the visual stimulus is the same in both conditions. At the end of each trial, the level of neural activity quickly falls off.

4.2. Sensory-guided decision and eye movement task

A separate experiment explored the role of neurons from a similar area of the brain during a task that involved perceptual judgments and planning of eye movements (Fig. 4) [10]. In this task, the monkey is shown two targets in the periphery, and a random moving dot pattern appears in the center of the screen for 800 ms. The monkey must determine the direction of motion of the dots and later report its decision in the form of an eye movement to one of the two targets. On different trials, the strength of the motion signal towards one target or the other is varied from 0 to 40%. Once the fixation spot turns off, the monkey can move its eyes to the chosen target. Neurons were recorded from prearcuate cortex, a region of the brain near (and potentially overlapping with) the FEF, using an electrode array.

Fig. 5 shows two average spike rate responses when the monkey is shown a 40% coherence dot pattern and chooses target one (left) vs. target two (right). Although the RFs of individual neurons were not determined prior to the experiment, the neurons generally respond more strongly to what is schematically diagrammed as the left side of visual space. The average spike rate rasters are followed by three average difference rasters, showing the average spike rate when the monkey chooses target two (on the right) subtracted from the average spike rate when the monkey chooses target one (on the left) for 0%, 10%, and 40% motion coherence trials. Each trial shown is event-aligned and spans two seconds, where the first half is centered around the 800 ms presentation of moving dots, and the last half is centered around the time of the saccade. Trials are grouped according to the motion signal strength and the monkey’s target choice. The neurons are sorted by motion selectivity during the presentation of the moving dots such that neurons that show the strongest difference in activity between the two directions of motion presented are placed at the top of each raster.

The greater the motion coherence of dots, the more information is available to the monkey (and neurons) for deciding on and planning the upcoming eye movement, and this is apparent in both the rasters and sonified output (see the link at the end of the discussion section for the corresponding video capture). In the average spike rate trials, activity builds up during the dot presentation period as the monkey decides on T1 (in or near the RFs of the neurons on the left side of the task schematic screen) and prepares to move its eyes there. Conversely, activity becomes suppressed as the monkey decides on T2 (away from the neurons’ RFs). The diverging response profiles are further illustrated in the difference plots. The neurons show earlier and stronger difference signals when the monkey is presented with increasing motion signals.

5. DISCUSSION

The current system provides a preliminary framework for exploring both data analysis and the creation of biologically inspired musical elements using an integrated audio and visual interface. In the examples provided, the visual display of data rasters and rate traces in isolation already effectively convey spike timing and spike rate information. The addition of sonified output and a dynamically updating task schematic changes the user’s interaction with the data such that instead of viewing a static image, the user can step through an experimental trial. While the aim is not necessarily to discover information in the auditory displays that cannot be perceived in the visualizations, the system provides an engaging and accessible means to explore neural data and extract the main effects in each experiment. The sonified output enhances and complements the visualization, providing a multi-sensory means of experiencing and exploring the data.

To date, three types of data to sound mappings have been implemented, and in each case the mapping has been to musical pitch. In order to ensure a relatively constant level of musical consonance, the pitch mappings were scaled to highly consonant pitch
collections such as the pentatonic scale. Scaling and filtering pitch mappings, while maintaining a pleasing sonic environment, limits the resolution of the sonified data. Future work will explore how other auditory dimensions such as timbre, spatial location, rhythm, and volume may provide alternative expressive representations of neural activity. Exploration of the space of possible mappings could be directed towards extracting information from the data in an intuitively perceptible manner or towards purely aesthetic goals.

One challenge in sonifying and visualizing neural data for information content is balancing the tradeoff between accurately representing the raw signal and producing a meaningful interpretation of the information contained within the signal. The amount of information contained in a single spike, for example, remains an open question, but as observers we may not be able to easily discern the magnitude of its impact in the context of brain dynamics. Spike rates provide a good estimate of the relative activity level at a given point in time but do not take into account the possible role of temporal patterns in the data. Other potential parameters to extract from the data could include measures of synchrony, trial-by-trial variability, or correlations between neurons. The evolution of neural population activity over the course of individual trials could also be transformed into dimensionality-reduced trajectory representations and sonified to highlight behavior of the network as a whole.

Within each experiment, the network is loosely defined since current technology allows experimenters to sample only a subset of neurons, and it is not necessarily straightforward to determine the number of neurons sufficient to represent the population. Sorting neurons based on properties of the individual neurons (such as visual responsiveness, as used above) imposes particular constraints that may or may not be explicitly utilized in the brain but could help the user in functionally grouping the neurons when viewing and listening to the activity of the population.

Furthermore, brain dynamics on a single trial are rapid and complex in comparison to our ability to perceive and process visual and auditory signals. Depending on the goal of the user, it may be ideal to observe each detail or quickly gauge the neural population response. The ability to listen to neural population data in realtime would potentially be useful during the course of an experiment to monitor neural activity on a trial-by-trial basis and evaluate the quality of the data as it is being collected. A more interactive interface would also allow the user to choose data to sound mappings best suited to feature different aspects of the data.

Sonification and visualization offer tools to relate the activity of neural populations to cognitive tasks by decoding neural signals into features that can be grasped perceptually. As data sets become increasingly complex with more neurons and more simultaneously recorded brain areas, new methods for extracting information from the high-dimensional data may play an instrumental role in conveying insights about how the brain works to neuroscientists and non-neuroscientists alike.

Video captures of the examples described above are available online at: https://ccrma.stanford.edu/~mindyc/sound/demos/

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7. REFERENCES