ARTICLE Active Learning Exercises in Synaptic Physiology and Connectivity for the Neuroscience Lecture Hall, Laboratory Course, or Outreach Setting

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It is well-understood that active learning approaches have positive learning outcomes and improve retention. Active learning strategies for the neuroscience laboratory setting have been extensively developed. Fewer active learning approaches are available for the traditional lecture-based setting. Here we describe novel active learning exercises that teach fundamental principles of neuronal circuits and synaptic connectivity ideal for introductory neuroscience courses. Given the complexity of synaptic networks in the brain and the difficulty this material can present to students, our novel exercises can be beneficial to the neuroscience education community.

Key words: active learning; synapses; neuronal connections; connectivity matrix; introduction to neuroscience

There is now overwhelming evidence that active learning approaches promote better learning outcomes and increased student engagement in science, technology, engineering, and mathematics (STEM) coursework. A growing body of literature also supports the use of active learning strategies in neuroscience education (Quinan et al. 2023; Buffalari et al. 2022; Ng and Newpher 2020). While active learning approaches in the neuroscience laboratory setting have grown, far fewer have been developed that can also be used in the neuroscience lecture hall.

There are many topics in introductory neuroscience that students find challenging due to the complexity and multidisciplinary nature of the study of the brain. In particular, synaptic connectivity and neuronal wiring can be challenging because of the diverse types of circuits present in the brain at local (e.g., intracortical, intrahippocampal) and more long-range scales (e.g., thalamocortical, nigrostriatal). As our understanding of neural circuitry in the normal and diseased brain grows, so too has the need to effectively teach this fundamental feature of brain organization to students.

In the present report, we describe the development of active learning exercises to teach principals of synaptic connectivity which can be used in the lecture hall or laboratory setting and can be adapted for environments with limited resources. We also describe our implementation of these exercises in outreach settings and in undergraduate neuroscience coursework. Resources for implementation of these exercises are easy to construct and made freely available.

Learning Objectives

The active learning exercises were designed to achieve the following learning outcomes.

1. Students will understand the fundamental design features of neuronal circuits including reciprocal connections.

2. Students will understand the difference between excitatory and inhibitory postsynaptic potentials.

3. Students will understand electrophysiological approaches to describe neuronal synaptic circuits.

DESCRIPTION OF CLASS EXERCISES

Exercise 1: Network of 3 neurons

Resources needed:

Worksheet found in Supplement (or blank sheet of paper) and pencil/pen.

Instructor notes:

This exercise challenges students to draw as many unique 3-neuron networks with the goal of trying to determine how many possible networks might exist in nature. Three examples of acceptable 3-neuron networks are illustrated in Figure 1. It is recommended that students engaging in this exercise already be familiar with introductory concepts such as the basic parts of the neuron (soma, dendrites, spines, axon, etc.) as well as basic concepts of synaptic connectivity (presynaptic vs. postsynaptic). Instructors can first review with the students the 4 possible connections that can exist in a 2-neuron network (the 2 neurons are not connected; the 2 neurons are reciprocally connected; neuron 1 is connected to neuron 2 only; neuron 2 is connected to neuron 1 only). It is recommended that the students first be engaged to think about how many possible connections might exist in a 3-



Figure 1. Three acceptable examples of possible 3-neuron networks.



Figure 2. Example of a 3-neuron connectivity matrix (left) and acceptable wiring diagram of the same network (right). Green traces in matrix and black neurons in wiring diagram represent EPSPs from excitatory neurons (e.g., glutamatergic). Red trace in matrix and red neuron in wiring diagram represent IPSPs from an inhibitory neuron (e.g., GABAergic).

neuron network if there are 4 possible connections in a 2neuron network. After some discussion, students begin to fill out their worksheet. Instructors can allow anywhere from 10 to 30 mins for students to complete the activity. A 3-neuron network can be interconnected in 64 unique ways so even in 30 mins, it is unlikely that students will draw all 64 unique ways, especially because it gets difficult to organize which combinations remain after drawing ~10-15 networks. This will be slightly frustrating, but this actually contributes to the experience students have when recognizing the complexity of neuronal networks in the brain.

After the time to work on the worksheet has elapsed, instructors are encouraged to engage students for discussion and feedback. First, instructors can ask students to reveal how many unique networks they drew, recognizing that each student's network number might vary substantially. Next, instructors can invite students to share one example of a network they drew (such as in Figure 1). If there is a black/white board, students could be invited to draw the example on the board, or the instructor could draw the example on the board as the student describes the network (ex. "neuron 1 is connected to neuron 2, neuron 2 is connected to neuron 1 and 3..."). Once a few different examples are described, the instructor can invite students to describe what they believe is the maximum number of possible networks that can be made with 3 neurons. With the caveat that a neuron is not connected to itself (autapse) the number of possible connections in a 3 neuron network is described by the following equation: 2^{n^2-n} (where n = the number of neurons in the network). Thus, there are 64 unique types of networks possible with 3 neurons.

Exercise 2: Circuit diagram of neuron networks Resources needed:

Blank sheet of paper and pencil/pen. Worksheet found in Supplement or Mobile device, PC, or laptop with internet connection.

https://comresearchapp.nyit.edu/neurosim/ Instructor notes: This exercise challenges students to draw the circuit diagram (Figure 2, right) of a network of n neurons when the synaptic physiology of the network is presented (Figure 2, left). We created a graphical user interface (GUI: https://comresearchapp.nvit.edu/neurosim) which presents data from hypothetical whole-cell patch clamp experiments where 2-10 neurons were simultaneously recorded to determine synaptic connectivity (Figure 2, left panel). Our motivation to create the GUI in this way was inspired by a growing number of published papers using this approach to graphically present data from multi-neuron recordings (see Figure 6 of Peng et al. 2019). The GUI creates random combinations networks for 2-10 neurons according to the equation described above; therefore, the 64 different networks can be generated in a 3-neuron network by the GUI. As shown in Figure 2, presynaptic action potentials (shaded boxes) and synaptic potentials (open boxes) are displayed in a matrix inspired by similar matrices found in primary research articles (Peng et al. 2019; Steiner et al. 2019). Both excitatory and inhibitory neurons are present in most GUI generated networks but at a ratio of 10:1 (respectively) to approximate what is observed in the neocortex. Excitatory post-synaptic potentials (EPSPs) are displayed as green, depolarizing signals and inhibitory postsynaptic potentials (IPSPs) are displayed as red, hyperpolarizing signals.

The major emphasis of this exercise is to engage students in a cognitive process that reveals the architecture of the neural circuit that produced the data depicted in the connectivity matrix. Thus, the students draw the correct circuit of neurons. Before engaging in this exercise, students must first understand basic and intermediate concepts of action potentials, neurotransmitters, receptors, and synaptic transmission. It is important that instructors first use the GUI to create several matrices of several 3-neuron networks to guide the students in interpreting the data. By using 3-neuron networks, the instructor is able to connect this exercise with concepts addressed in exercise 1. Therefore, it is important to demonstrate how the GUI produces 3-neuron networks identical to some of the examples students created on their own during exercise 1.

It is likely that students will experience some difficulty in learning how to interpret the connectivity matrix without significant guidance from the instructor. It is important to first emphasize that these data represent results obtained from a hypothetical experiment where n number of neurons were simultaneously recorded with whole-cell patch clamp methods such that membrane potential and PSPs could be recorded. In addition, using these recording methods, each neuron could be intracellularly stimulated in order to evoke action potentials in any given neuron. Thus, the matrix contains data from an experiment where one neuron in the network was stimulated to evoke action potentials while PSPs were recorded from all other neurons in the network. Using the example 3-neuron matrix in Figure 2, when neuron#1 was made to fire 3 action potentials (gray shaded box in cell), we see that EPSPs were recorded in both neurons #2 and #3. These data indicate that neuron 1 is an excitatory neuron that is synaptically connected to both neurons #2 and #3. However, when neuron #2 was made to

fire action potentials, no PSPs were recorded in neuron #1 nor #3. Finally, when neuron #3 was made to fire action potentials, we observe IPSPs only in neuron #2, indicating that neuron #3 is an inhibitory neuron and only connected to neuron #2. Thus, understanding how to interpret the data in this example connectivity matrix should result in students being capable of drawing a circuit diagram like that shown in Figure 2 (right panel). Once the instructor is confident that the students understand how to interpret connectivity matrices, are comfortable using the GUI, and fully understand the nature of the activity, instructors can implement the final part of exercise 2.

There is substantial flexibility embedded in exercise 2 for instructors. In one approach, instructors can print out a matrix of a specific number of neurons (e.g. 6 or 10 neurons, Figure 3) and ask all students to each draw the circuit diagram of this same network on their own on a sheet of paper. Once completed, the students can pair up and exchange circuit diagrams for review. In this approach, since all students got the same matrix, the instructors could ask one student to draw their circuit on the black/white board for review, if one is available. An alternative approach could be for the instructor to give the students more freedom to use the GUI to generate their own matrix with whatever number of neurons they wish and to complete the circuit diagram. Then the students can pair up and share the matrix and circuit diagram for review.

Exercise 3: Physiology of neuron networks in Exercise 1 & 2

Resources needed:

Mobile device or laptop/PC with internet access. Neuronify GUI found at <u>https://ovilab.net</u>.

Instructor notes:

This exercise extends on the previous two exercises and is best delivered immediately after the first two. The main objective of this exercise is to demonstrate how different types of neuronal networks shape the physiology of the network including the firing properties of individual neurons embedded in the network. For this exercise students will be



Figure 3. Example of a 6-neuron (left) and 10-neuron connectivity matrix (right). Green and red traces in matrices denote excitatory and inhibitory postsynaptic potentials, respectively.

using a mobile device or PC/laptop and running the Neuronify neuronal network simulator previously described (Dragly et al. 2017).

A critical element of this exercise involves the instructor demonstrating the functionality of the simulator. Ideally, the instructor is best suited to demonstrate how to use the GUI in front of the class if a projection system is available, Otherwise, step-by-step printed instructions can be provided to students. Although there are diverse ways to use the Neuronify GUI to teach principles of neuronal network physiology (Dragly et al. 2017; Northcutt, 2021), only 3 major features of the GUI are required for exercise 3. First, students must understand how to use the excitatory and inhibitory neuron buttons to drag and drop neurons onto the whiteboard to build a network. Next, students must know how to use the "Measurement" button to drag and drop one or more voltmeter/oscilloscope to measure the firing of neurons in the network. Finally, the students must know how to use the building the neuronal network, implementing a stimulation to one or more of the neurons in the network, and using an oscilloscope to monitor the output of individual neurons in the network. It is recommended that the instructor guide all students in building the same 2 or 3 neuron network and having students check their work in pairs.

Figure 4 displays a simple 3 neuron network built using the Neuronify GUI modeled after the same network that was drawn in exercise 2 and shown in Figure 2, which is made up of 2 excitatory neurons (blue) and 1 inhibitory neuron (red). Thus, an important element in the execution of exercise 3 is to purposefully refer back to the networks discussed in exercise 1 and 2. In the exemplar network in Figure 3, all 3 neurons are connected to an oscilloscope to monitor firing, but only neuron 1 is attached to a DC-type source of stimulation (orange box). Comparing the 3 different oscilloscopes, it is now visibly evident how inhibitory input from neuron 3 reduces the excitatory influence that neuron 1 has on neuron 2 which results in a decrease in firing rate.

Once instructors are confident that students understand how to use the Neuronify GUI, exercise 3 involves building a network that they encountered in exercise 2. The time it will take to build this network will depend on the number of neurons in the network used in exercise 2. Instructors have the flexibility to provide more or less structure to exercise 3 by requiring students to try different stimulation parameters in the network and/or requiring the output (firing rate) of one



Figure 4. Example of a 3-neuron network created in Neuronify where all neurons are being recorded from with an oscilloscope and Neuron 1 is electrically stimulated. Note Neuron 2 is an inhibitory neuron.

or more neurons to be recorded with the oscilloscope function. Firing rate can be calculated by counting the number of spikes per unit time in the oscilloscope window as one simple option for quantitative measurements of neuron output. There are also other options for firing rate measurement in the Measurement tabs.

Many additional elements of the neuronal network circuitry can be manipulated with the GUI to increase the level of engagement and difficulty experienced by the students during exercise 3. What we describe above is the simplest exercise format that best follows the work performed in exercises 1 and 2. Additional changes made to the exercise design may require additional demonstration of the functionality of the GUI and may require background knowledge not specifically covered as suggested above. For example, the GUI allows students to manipulate neuronal membrane properties of individual neurons in the network including resting membrane potential, action potential resistance, threshold. membrane and membrane capacitance. Manipulating these variables in one or more neurons will have profound effects on the neuronal output that can be used to enrich the learning objectives of exercise 3. Students will, however, need to have the prerequisite conceptual background on these concepts as well as understand how to use these features of the GUI.

RESULTS

Implementation of Exercise 1 & 2 in an In-Person STEM Outreach Setting

We implemented exercises 1 and 2 in STEM and medicine outreach events (in-person) at New York Institute of Technology on two separate occasions with ~100 high school students from across the United States. These students were in a summer program for students interested in careers in medicine. We did not have any information about their academic backgrounds or completed coursework. We did not have permission to collect any information about the students and did not have an opportunity to collect quantitative feedback data from these students. Both occasions were held in a large auditorium equipped with a document camera system as well as a computer and large screen projection system. Students were given pencils, blank white sheets of paper, and a copy of the exercise 1 activity worksheet (Supplement 1). A brief (10-min) lecture (Powerpoint) was given to introduce the students to the concepts of neurons, functions of dendrites and axons, and the basic concept of neuronal connections at the synapse using an example of a 2-neuron network. The 4 possible connections that can exist in a 2-neuron network (the 2 neurons are not connected; the 2 neurons are reciprocally connected; neuron 1 is connected to neuron 2 only; neuron 2 is connected to neuron 1 only) were illustrated.

Students were then given instructions to think about and draw as many 3-neuron networks they could imagine using the exercise 1 activity sheet. After ~10 mins, the presenter asked for volunteers to share 1 example of the network circuit they had drawn and this was redrawn by the presenter using a blank Powerpoint slide and drawing pen tool. After drawing circuits from about 10 volunteers, the presenter

asked students to count how many circuits they had drawn and how many possible connections exist. The presenter then explained some of the computational features that emerge with an increasing number of possible connections as each additional neuron is added to the network.

In preparation for exercise 2, another brief (10min) lecture introduced the concept of the action potential and synaptic excitation and inhibition via neurotransmitters without going into specific neurochemistry or ion channel physiology. The technique of recording membrane voltage as a tool to understand synaptic communication was also discussed at a very basic level. Next, the students were introduced to the synaptic connectivity matrix GUI we developed using a 3-neuron network on a printed sheet of paper displayed on the document camera. The presenter carefully went over how to read the matrix including postsynaptic responses that were excitatory versus inhibitory. Next, the students were slowly walked through what that circuit diagram would look like as the presenter drew the circuit on the sheet of paper displayed on the document camera. The students were encouraged to see if they had drawn a similar circuit earlier on their activity sheet as part of exercise 1.

Next, the presenters displayed the GUI via the computer projection system and selected a 5-neuron network matrix to display. The students were then asked to draw the companion circuit diagram for that matrix and given about 3 min to complete the task. The presenter picked a volunteer to display their drawing of the circuit diagram appropriate for the 5-neuron matrix using the document camera. The audience was asked to check their work against what was displayed. Next, a 7- and 10-neuron network matrix was presented, and students asked to draw the corresponding circuit diagram. A volunteer for each matrix was asked to come up and show their drawing on the overhead camera.

As part of a wrap up to this exercise and outreach event, examples of the complexity of neural circuits responsible for emotions and cognitive functions was briefly discussed in the context of how difficult it has been to understand brain diseases and to find cures. The total time of this portion of the outreach event that included exercises 1 and 2 was approximately 45 minutes. A 15 minute question and answer period took place after the exercises. For both events, student questions were overwhelmingly focused on the neuronal circuitry of a normal brain and changes in connectivity and function in brain diseases such as ADHD, autism, narcolepsy, Parkinson's disease, etc.

Implementation of Exercise 2 in the Virtual/Remote Classroom Setting

We incorporated exercise 2 into a learning activity in an upper-division neurobiology course called Diseases of the Nervous System at the University of California, Irvine (UCI). The course had a total of 90 students. Students met virtually and worked in breakout rooms in groups of 8-10, overseen by learning assistants (LAs). Most enrolled students were 3rd or 4th year Human Biology majors who had successfully completed (3.0 GPA) all lower-division Biology and Chemistry core courses, including a lower-division neurobiology course.

The objective of this activity was to improve overall understanding of neuron circuitry by analyzing matrix diagrams. The activity consisted of 3 parts: A) reviewing a neural circuit based on a 3-neuron matrix, B) drawing a neural circuit based on a 5-neuron matrix, and C) developing a hypothetical matrix diagram from descriptive instructions about a circuit. For each part, students were given approximately 20-30 minutes per section to work in groups in Zoom breakout rooms, within which they were provided links to a virtual whiteboard to collaborate in real-time. Neuron matrix diagrams were provided to students in a worksheet and copied into the virtual whiteboard. At the conclusion of the activity, both groups came together and discussed their work with LAs. The entire activity took 50 minutes to complete.

The effectiveness of the activity was assessed by analyzing qualitative written reflections students submitted following completion of the exercises. We received approval from the UCI Institutional Review Board to share student responses to the following prompts in our assessment:

For today's activity, please answer the following questions:

1. Did this assignment help you to better understand neural connectivity and action potentials? If so, in what way?

2. What were some misconceptions that your group members voiced about neurons and neural firing? Were these misconceptions resolved?

Analysis of written responses revealed that 90% of students indicated that the activity improved their understanding of neuron circuitry with 84% of them noting that they were able to apply physiological concepts using the neuron matrix. 32% of students encountered misconceptions while working on the activity, but 69% of that subgroup of students were able to overcome those difficulties following additional follow-up instruction from their LAs and instructor.

Many students found the matrix diagram activity informative and an engaging way to apply their neuroscience knowledge from previous courses. They described the activity as "solving a puzzle," which helped them to "visualize and quantify the complex wirings in the neural system." Some students reported initial confusion and difficulty understanding the neuron matrix and drawing the circuitry, citing the allotted 50-minute activity time as too restrictive for the activity. Thus, this may have worked better as a homework assignment or two-day activity.

This exercise helped to reveal a common misconception students have regarding the neuron structure and directionality of action potentials. Although this was an upper-division neurobiology course, students did not seem to understand that neurons have only one axon but may have multiple collaterals. In addition, and perhaps because of simplified textbook illustrations, students believed that each neuron communicates linearly with only one downstream neuron, thus missing the concept of circuits and summation from multiple terminal inputs.

Overall, the students found the activity valuable, expressing that the "neuron matrix diagrams helped them learn about neuronal wiring within the brain by understanding how neurons interacted with one another," further enhancing student comprehension of neural circuitry and its physiological application. Our findings suggest that even advanced students in upper-division neuroscience courses would benefit from neural matrix activities to develop a better understanding of neural communication.

Below we share some of the written student feedback we received after this class:

"Working with the neuron matrix diagrams helped me learn about neuronal wiring within the brain by understanding how the various neurons interacted with one another. At first, the diagrams resembled ancient Egyptian hieroglyphics but once their usage was explained, it quickly became apparent that this was an extremely concise and efficient way to explain neuron inhibition and excitation of other nearby neurons. Transposing the information from the matrix diagrams onto an actual image of the neurons further helped to solidify my understanding of the matrix diagrams themselves as well as the interplay between the neurons inside the brain."

"Working with neuron matrix diagrams helped me to visualize and quantify the complex wirings in the neural system. Instead of only focusing on what happens between individual synapses, now I can expand my perspective to assess how multiple neurons influence each other, while at the same time keeping in mind that neurons cannot fire signals bidirectionally and that neurons have to directly synapse onto another neuron for excitation or inhibition."

"I'd never before thought of neuron connections as being anything other than linear, where connections were primarily made with other neurons in a linear direction going "forward" in one direction. The circuit drawings made me realize that neuron connections are more complicated than that."

"I'd previously thought about excitatory and inhibitory signals as being from the same type of neuron that just signaled for opposite reactions, but I now realize that the different signals can be given by different types of neurons that summate in a single neuron."

"The assignment did help me understand more about neural connectivity and action potential especially the third part. Neural connectivity is complex since one neuron can affect many other neurons."

"This assignment didn't help me understand action potential more but it did help me visualize what effect an action potential can have on other neurons. What I will say is that the complicated manner and connectiveness was clearly displayed in this assignment as it showed how multiple neurons can interact with one another."

"The biggest misconception my group had before we did the assignment was that a neuron was only ever acted upon by one other neuron at a time. These misconceptions were resolved! To fully understand the assignment, we had to understand how they all connected."

Implementation of Exercise 2 & 3 in the In-Person Classroom Setting

We also delivered exercises 2 and 3 in two sections of a non-majors, in-person, neuroscience course at UCI (combined n=71 students). We directed students to use the GUI from exercise 2 to generate a 3, 4, and 5 neuron networks, guided students through the interpretation of the excitatory and inhibitory synaptic potentials, and directed the students to draw the network as described above. Students were then directed to launch the Neuronifv (https://dragly.org/projects/neuronify/) GUI, and the instructor provided a demonstration of how to use basic components of the software to build a neural network. Students were next asked to build an active neural network based on one of the connectivity matrices they had generated earlier (exercise 2). The students were instructed to take turns stimulating one of each of the neurons in the network while watching the evoked responses of the postsynaptic neurons on each of the connected oscilloscopes. The instructor moved around the room during the activity assisting students and answering guestions. We observed that students independently also actively helped each other and discussed their networks with each other, demonstrating their engagement. We did not experience any issues with students understanding and working with either the matrix generator or neuronify online software. An overwhelming majority of students answered "Yes" to the following feedback questions: "Did this assignment help you to better understand neural connectivity and action potential?" (98%), and "Did building the neural network from your matrix help you to better understand spatial and temporal summation?" (90%).

We received approval from the UCI Institutional Review Board to share the following of the written student feedback we received after this class:

"It helped me better understand neural connectivity & action potential because I could see a visual on how the action potentials are sent out and the rate of it. It also allowed me to play around with the different voltages and connections which gave me a better understanding of how the neurons communicate."

"One of the misconceptions about neural firing was that they could not affect more than one neuron, and that more than one neuron could not affect a single neuron causing different responses depending on whether or not the neuron was inhibitory or excitatory."

"It was very helpful to see the overall summation of neurons on Neuronify using the voltmeter feature and to see how the voltages change when different connections are modified. The changes in spacing rather than changes in amplitude were also interesting and unexpected and I can understand why those differences are there."

"I got to understand the difference between how spatial and temporal summation worked by recognizing how spatial summation has multiple presynaptic neurons connected with a single postsynaptic and how all different inputs are coming in from different neurons while a temporal summation actively fires from two single presynaptic and postsynapic neurons."

"We learned about temporal and spatial summation in class but I'm a visual learner so it was a little hard to understand what was going on simultaneously (aside from the examples of nagging friends which was helpful). But this activity made these processes more clear to me, highlighting the differences between the two."

DISCUSSION

In the present report, we describe the development of three exercises that build on one another and introduce fundamental properties of synaptic networks present in the brain. The exercises can be delivered together at once or separately across different sessions. The exercises have elements of active learning embedded in each and make use of relatively few supplies/resources, which we believe will allow for many educators to use these exercises with diverse populations of students. We have built and posted online, a new synaptic connectivity matrix GUI capable of displaying up to a 10-neuron network with both excitatory and inhibitory neurons in the network. Finally, we demonstrate two examples where we use one or more exercises to expose students to the material at different educational levels. Our first-hand experiences confirm that the exercises evoke engagement and participation, require minimal resources, and are easily implemented even in a large lecture-hall setting.

In contrast to a rapidly growing number of exercises and resources for the neuroscience teaching laboratory, far fewer have been developed that can be used in the classroom setting. Our exercises make use of GUIs that can be used on any smartphone/tablet/laptop. Thus, our exercises can be used in a traditional classroom setting as an approach to incorporate more active learning. An additional feature of our exercises is that they can be easily designed for virtual/remote courses. We hope that our exercises will inspire other new approaches for active learning of diverse topics in neuroscience education. Moreover, we hope that our work will inspire the creation of future GUIs that are capable of incorporating more advanced biophysical properties such as synaptic plasticity. active and passive dendrites, manipulation of ion channels and neurotransmitter receptors, etc.

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SUPPLEMENTAL WORKSHEET

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19.	0		20.	0		21.	0		22.	0		23.	0		24.	0	
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25.	0		26.	0		27.	0		28.	0		29.	0		30.	0	
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