What is a moment? "Cortical" sensory integration over a brief interval

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Recognition of complex temporal sequences is a general sensory problem that requires integration of information over time. We describe a very simple "organism" that performs this task, exemplified here by recognition of spoken monosyllables. The network's computation can be understood through the application of simple but generally unexploited principles describing neural activity. The organism is a network of very simple neurons and synapses; the experiments are simulations. The network's recognition capabilities are robust to variations across speakers, simple masking noises, and large variations in system parameters. The network principles underlying recognition of short temporal sequences are applied here to speech, but similar ideas can be applied to aspects of vision, touch, and olfaction. In this article, we describe only properties of the system that could be measured if it were a real biological organism. We delay publication of the principles behind the network's operation as an intellectual challenge: the essential principles of operation can be deduced based on the experimental results presented here alone. An interactive web site (http://neuron.princeton.edu/~moment) is available to allow readers to design and carry out their own experiments on the organism.

How does a brain integrate sensory information that is gathered over a time period on the scale of ~0.5 s, transforming the constantly changing world of stimuli into percepts of a "moment" of time? This integration is a general problem essential to our representation of the world. In audition, the perception of phonemes, syllables, or species calls are examples of such integration; in the somatosensory system, the feeling of textures involves such integration; in the visual system, object segregation from motion and structure from motion require short-time integration; in the olfactory system, sensing odors during a sniff involves temporal integration. Linking together recently acquired information into an entity present "now" is a fundamental part of how the perception of a present moment is constructed; a key issue in this regard is how such integration over time can be carried out with neural hardware.

We describe here a simple and biologically plausible network of spiking neurons that recognizes short, complex temporal patterns. In so doing, the network links together information spread over time. The network was designed by using a well-defined but previously unnoticed computational principle. It is capable of broad generalization from a single example and is robust to noise. These capabilities are demonstrated here by considering the real-world problem of recognizing a brief complex sound (a monosyllable; see Fig. 1). We chose this representative but specific task because it is a natural capability of our auditory systems. The task is well defined and conceptually easy to describe, and real-world data are available to exemplify the important problem of natural variability and noise. The object here is to understand how high selectivity for spatiotemporal patterns can be obtained in a biological system. The performance of this simple system as a word recognizer is, of course, far worse than digital computer-based commercial systems, but the comparison is not relevant.

In this article, we describe the network by presenting only observations and experiments that would have been performed on the network if it were a real biological organism. As with a real organism, we do not explicitly describe the principles underlying the network's operation but merely describe the experimental facts that one can record about it; the principles of operation must be deduced. In a few months, we will present in a second article a full and explicit description of the principle behind the design and performance of the system.

We have chosen this unusual mode of presentation based on our own experience with the system. We were surprised to find that the information described in this article was sufficient to deduce the principles on which the system works. Had this system been a real biological system, we ourselves would have been inclined to believe instead that the secret of the specificity must lie in additional cell types, cellular biophysical complexity, or other as-yet unmeasured fundamental properties. We would have glossed over subtleties that actually and clearly indicate how the system works, and we would never have found the interesting principle on which the network computation is based.

How often have we been guilty of similar behavior in looking at data from neurobiology? Probably often, from lack of practice in interpreting data instantiating a new principle in an unusual fashion. How often have others been guilty of similar behavior? We cannot know—probably less than ourselves. However, feeling that some in the community might appreciate an opportunity to interpret the behavior of a system that is guaranteed to have no hidden components, we have chosen to present in this article only conventional "experimental information"—conventional information that we know is sufficient to derive the underlying computational principle and sufficient to understand how the system computes. Someone who simply wants to be told the principle will find that information in the second article, to be published shortly after this one.

We will begin by describing the network's complex pattern-recognition behavior and the firing patterns of those neurons that are correlated with this behavior. We will then turn to the full network and describe its neuroanatomy (cell types, synapse types, and connectivity pattern), physiological properties in response to acoustic stimuli, and single-cell properties as observed *in vitro*. We will write as though the network were a real organism, as far as the experimental measurements are concerned.

Behavior and Electrophysiological Correlates. In the particular network described here, a previously unused principle of computation that enables the network to recognize the spoken monosyllable "one," as well as nine other different patterns, has been instantiated through a particular choice of network parameters. The method used to determine the parameters that enable

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Abbreviation: PSTH, peristimulus time histograms.

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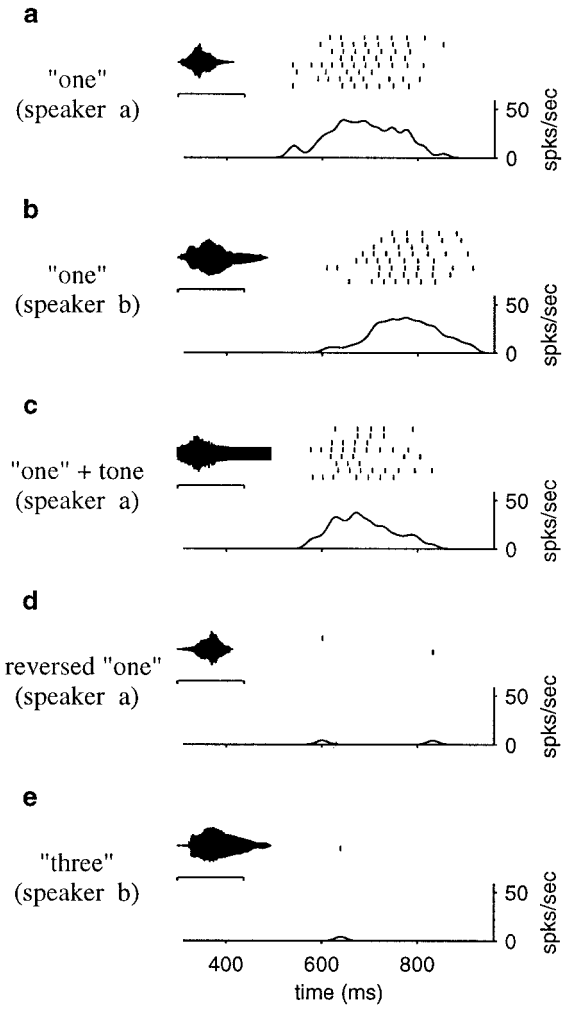

Fig. 1. Extracellularly recorded responses of a single γ-type neuron to five different acoustic waveforms. A noisy membrane current was added to every neuron in the simulation of the neuronal mathematics for the organism, to simulate the noise caused by other inputs that would always be present in a real biological system. Before the experiment, the network parameters were set by using only a single exemplar of ''one'' spoken by speaker a, plus single examples of nine other different patterns (each recognized by one of nine other γ-neurons, not shown here). (*a*) Spike rasters, aligned in time to the start of the acoustic waveform shown in the Inset, in response to eight different trials using an utterance of ''one'' from speaker a (not the training exemplar). Below the rasters is their corresponding peristimulus time histogram (PSTH), smoothed by a Gaussian with a standard deviation of 12 ms. The γ-cell begins spiking near the end of the word. Tick marks in the Inset correspond to 0 and 500 ms. (*b*) Same format as *a*, for an utterance of the word ''one'' from a different speaker (speaker b). (*c*) Same format as *a* for a ''one'' spoken by speaker a in the presence of a loud tone at 800 Hz. The waveforms are markedly different in *a*, *b*, and *c*, but the γ-cell responds to all. (*d*) Same format and utterance as in *a*, but the acoustic waveform has been reversed in time. (*e*) Same format as *a*, for an utterance by speaker b of the word ''three.'' Few or no spikes occurred in response to the waveforms of *d* and *e*. Other, similar-sounding words (for example, ''wonder'') occasionally cause the cell to fire as well, indicating that these output cells are not completely specific but merely encode utterances quite sparsely.

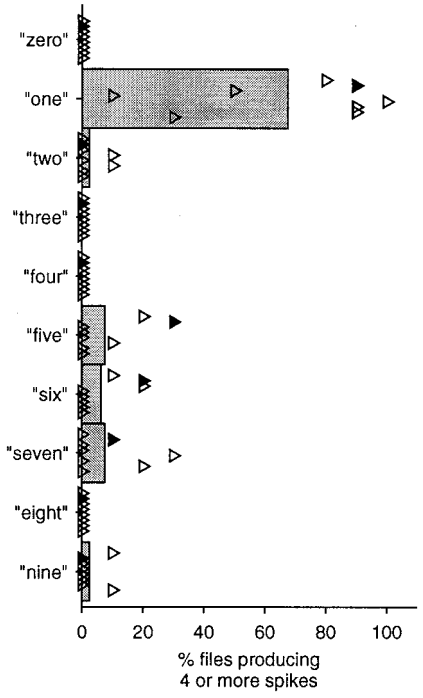

Fig. 2. Summary of responses of a single γ-cell to 10 spoken digits, ''zero'' through ''nine'' (speech data taken from the TI46 database, available from the National Institute of Standards and Technology). Each digit was spoken 10 times by eight different female speakers while the responses of the γ-cell were recorded. For the purpose of evaluating the cell's selectivity, each trial was classified as ''responding'' if the γ-cell fired four or more spikes and as ''not responding'' otherwise. Triangles indicate averages over different utterances by individual speakers, whereas the gray bars indicate data averaged over all utterances of all speakers. For five of the eight speakers, the cell's response is highly selective for the word ''one.'' The filled symbol indicates the speaker from which the single training utterance was taken.

recognition of each pattern is noniterative and requires information based on only a single example of the pattern to be recognized. Although the method is straightforward, it is not the focus of our study, and we will not describe it further, only noting that we believe the parameters could also be set by biologically plausible synaptic learning rules. "Recognition" of each of the 10 patterns is signaled by the firing of a corresponding pattern-selective neuron. We have labeled such neurons γ-neurons (see *Neuroanatomy* section below) and will focus on the behavior of the particular γ-neuron that is selective for "one". The neuron fires in response to this word, whether it is spoken rapidly or slowly, or when spoken by a variety of speakers. When a loud sound at 800 Hz is played simultaneously with "one," the network's ability to recognize the word is only slightly degraded. In contrast, the γ-neuron does not respond to "one" played backward or to most monosyllabic utterances, although on occasion it does respond to words which are similar to "one." In short, the system contends with the kind of natural variations and context with which humans can contend and has a good ability to reject simple masking sounds.

Data from one γ-neuron are shown in Fig. 1 and illustrate the selectivity of the neuron's response to simple sound stimuli. Fig. 1 *a–c* illustrates the response to the word "one," spoken by two different speakers and in two very different acoustic contexts. The neuron responds robustly in all three cases. In contrast, as illustrated in Fig. 1 *d–e*, the neuron responds weakly or not at all to other utterances, despite their superficial similarity to the word "one." γ-Neurons do not respond to pure sine wave tones (data not shown).

Fig. 2 illustrates the result of stimulating the system with a variety of spoken digits. For most speakers, the neuron was highly selective for the word "one." Most of the failures to respond to "one" were on utterances of three speakers for whom the system had not been trained (lower three triangle symbols in column marked "one" in Fig. 2). This failure is perhaps not

surprising in view of the fact that the parameters for this pattern had been set based on a single example from another speaker. More surprising is the fact that the γ-neuron generalized from a single utterance of the training speaker to most utterances of four other speakers.

As we will show, the system's complex word-recognition calculation, which in this case involves integrating information spread out over ~0.5 s, is carried out by cells that have remarkably simple biophysical and physiological properties. The network's neurons can be well described as a straightforward collection of classical integrate-and-fire neurons with elementary synaptic connections between them.

Neuroanatomy. We describe the architecture of the network as if it were arranged in a biological-like layout. γ-neurons are found grouped into the superficial layers of what we call here "area W." Auditory information reaches area W via another area, area A, which may be thought of as a cortical sensory area. Neurons in area A are frequency tuned (see *Electrophysiology* section below) and are arranged in groups having similar preferred frequencies; that is, frequency is tonotopically mapped. Output neurons of area A project to what we have called "layer 4" of area W. Word selectivity arises in area W, and we will therefore focus our anatomical description on area W.

The axons of area A output cells arborize narrowly in layer 4 of area W and preserve the tonotopic mapping found in area A. Layer 4 of area W contains two types of cells, both of which receive direct excitatory synaptic input from area A afferents. α-type cells are excitatory, and β-type cells are inhibitory. Both of these types of layer 4 cells are found in similar quantities. All cells are electrically compact.

The axons of both α- and β-neurons arborize widely within area W, each making a total of approximately 75–200 synaptic connections with other neurons, across all tonotopic frequency groups. Approximately half of the connections from each cell are onto α-cells, the other half are onto β-cells. Axons of α- and β-cells also arborize in layers 2 and 3, where they contact γ-cells.

The number of γ cells is about 3% of the number of α- or β-cells. Each γ-cell receives approximately 30–80 synapses from cells of type α and of type β; these inputs are drawn from cells in all frequency groups. γ-cells are the output cells of this system; their axons project to other cortical areas, where they make excitatory synapses. They do not feed back to α- or β-cells.

Distances within area W are short, and the diameters of axons of all cell types are relatively large. Thus, propagation delays within area W seem to be unimportant. Latencies from area A to area W are the same for all cells.

Electrophysiology *in Vivo*. *Area A.* As described above and shown in Fig. 3, the projection neurons of area A provide the input to area W. We continue our description in the language of neurobiological experiments but note that the neural interactions important for word selectivity are found in area W; the mechanisms that give rise to the properties of area A neurons are not relevant. The detailed (nonbiological) source code for area A in the simulations can be found on the main web site associated with this article (http://neuron.princeton.edu/~moment).

The properties of area A neurons can be summarized by saying (*i*) that area A neurons are frequency tuned and (*ii*) that the neurons respond to transient changes in acoustic signals with a train of action potentials of slowly decaying firing rate. Cells in area A responded transiently to three types of features: "onsets" (≈35% of cells), "offsets" (≈35%), and "peaks" (≈30%) of power in modulated sine wave tones. The cells exhibited no tonic response to continuing steady sounds of any frequency. Every response produced a slowly decaying train of action potentials after initiation (see Fig. 4*a*). Different cells had different response decay rates. Fig. 4*b* illustrates two onset cells with

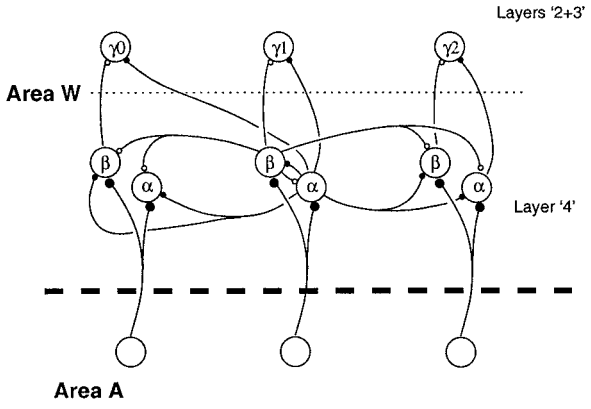

Fig. 3. Schematic neuroanatomy for area W and its input. The thick dashed line separates area A from area W; the thin dotted line separates layers 2 + 3 from layer 4 in area W. Small filled circles indicate excitatory connections, whereas small open circles indicate inhibitory connections. The connections of a typical α-cell and a typical β-cell, both shown in the center, are sketched. In the simulations, area W is small, containing 325 neurons of each α- and β-type, and a given cell makes synapses on 15–30% of these cells. Our simulation contains 10 different γ-cells, each selective for a different temporal pattern. Each γ-cell receives inputs from 30–80 cells of each type, α and β.

different decay times. Over the population of recorded neurons, a wide variety of decay times was found, ranging uniformly from 0.3 s to 1.1 s. Once a cell initiated a response, subsequent features in the sound stimulus that occurred during the decay had no effect on the spike train. After the end of the decay, newly occurring features can reinitiate the response. (Nevertheless, for simplicity, the particular simulations shown on the web site associated with this article were restricted to using only the first feature detected, without the possibility of reinitiation.)

Cells in area A were found to be frequency tuned. Fig. 4*c* shows the response of a typical onset cell as the power and frequency are varied. The cell responds to a small range of frequencies, the width of which grows with the power of the signal. All cells were found to be frequency tuned in this sense. Within each cell's range of response-producing frequencies, the cells displayed an almost all-or-none response; provided the signal intensity was above a minimum threshold, each cell fired almost the same number of spikes regardless of the frequency or intensity of the signal. Fig. 4*d* illustrates the frequency tuning of seven different cells over a range of signal powers. Different signals that were successful in driving area A neurons did not seem to produce significantly different responses. Fig. 4 *e–f* shows that the stereotyped response of a typical onset cell in area A was essentially identical for three very different acoustic stimuli that drove it.

For each type of area A cell (onset, peak, or offset), different cells with preferred frequencies spanning the entire frequency spectrum were found. For each type and for each preferred frequency, cells with a broad range of decay rates were found.

Area W. We now turn to the electrophysiology of neurons in area W, where word selectivity arises. As in area A, cells of both type α and β in layer 4 of area W are arranged in groups with similar preferred frequencies. The responses of both α- and β-cells were found to be similar to the output cells of area A which drive them: the three types of onset, offset, and peak cells were all found in layer 4 of area W. As in area A, for each type of α- or β-neuron (onset, peak, or offset), different cells, with preferred frequencies spanning the entire frequency spectrum, were found. For each type and for each preferred frequency, cells with a broad range of decay rates were found. The responses of one onset and one offset cell are illustrated in Fig. 5*a*.

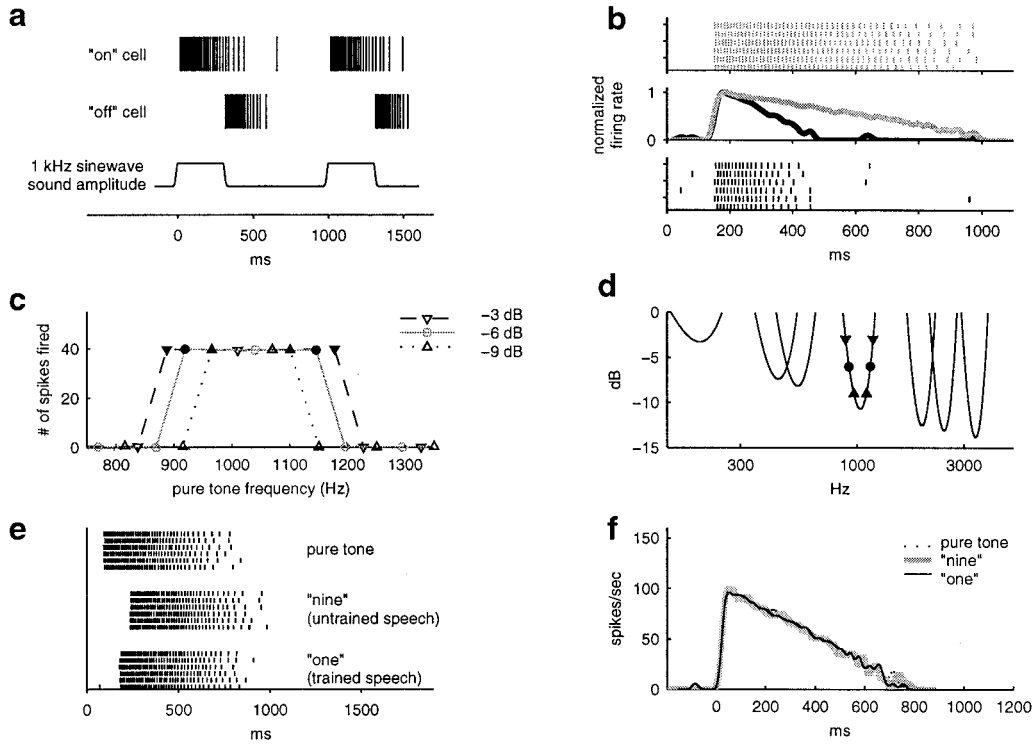

Fig. 4. (*a*) Spike rasters for a typical onset cell and a typical offset cell in response to two pure sine wave tone stimuli, as indicated at the bottom of *a*. The beginning and end of each tone are slightly smoothed as shown to minimize the generation of spurious frequencies by the sharp transient. (*b*) Responses of two different onset cells to six different trials of a pure tone onset. One cell is shown in gray, the other in black (top and bottom of *b*). *Middle* shows PSTHs of the responses of the two cells. (*c*) The number of spikes generated in response to ''step'' sine wave inputs (as shown in *a*) as a function of sine wave frequency, plotted for three different sine wave amplitudes. Signal power is measured in decibels relative to an arbitrary reference power. As long as the frequency is within a range that depends on signal power (larger range for larger signal powers), the number of spikes generated varies little. Filled symbols indicate the boundary between presence and absence of a robust spiking response. (*d*) Parabolic fits to measurements of threshold power vs. frequency, for seven different onset cells. Each parabola represents a single cell. Filled symbols correspond to filled symbols in *c*. (*e*) The response of an onset cell to three different stimuli, a pure tone onset, the word ''one'', and the word ''nine.'' (*f*) Histograms of the responses of *e* time-shifted into best alignment. When shifted into alignment, there is no apparent difference between these histograms or between the spike rasters of the three sounds.

Amplitude steps of pure sine wave tones were used to drive two onset cells with different decay rates, illustrated in Fig. 5*b*.

In sum, when studied with pure tones, the decay rates and frequency tuning properties of α- and β-cells were very similar to those described for area A (see Fig. 4). In contrast, small but reliable differences were found when the cells were stimulated

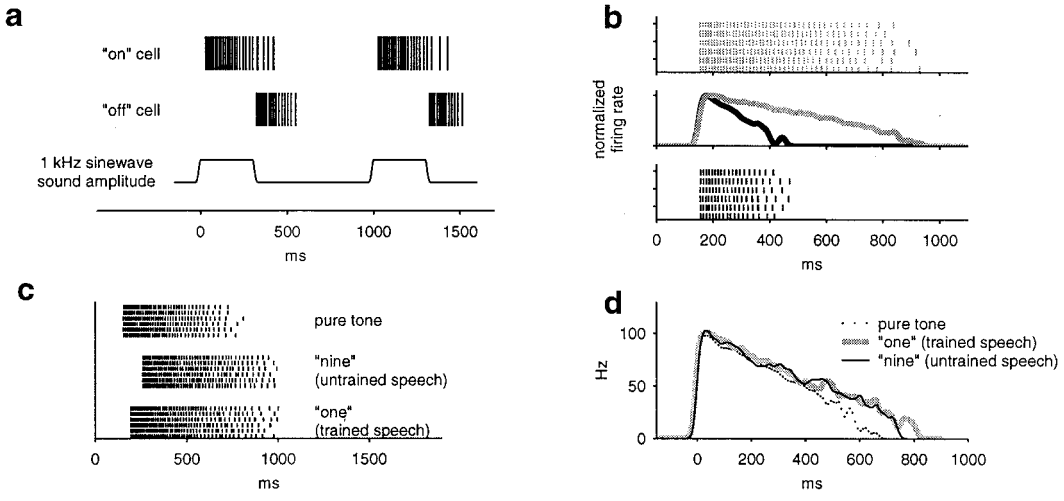

Fig. 5. Responses of layer 4 area W cells. (*a*) The spike rasters for a typical onset cell and a typical offset cell in response to sine wave pulses (format as in Fig. 4*a*). (*b*) Responses of two different onset cells to six different trials with the same pure tone onset (format as in Fig. 4*b*). (*c*) The response of an onset cell to three different stimuli, a pure-tone step, the word ''one,'' and the word ''nine'' (format as in Fig. 4e). (*d*) Histograms of the responses of *e* shifted into a common response onset time (format as in Fig. 4*f*).

with speech signals. Fig. 5*c* illustrates the responses of an onset cell to three different stimuli: a pure tone step, an utterance of "nine" (on which the organism had not been trained), and an utterance of "one" (a word on which the organism had been trained). Fig. 5*d* shows the PSTHs of these responses, aligned to a common response onset time. Although in area A the responses to pure tones and speech are indistinguishable from each other, in area W the PSTHs of the responses to speech are subtly but consistently different from the PSTH of the response to the pure tone. After approximately 400 ms, the response to speech signals is consistently stronger and more persistent than the response to pure tone steps. Thus, layer 4 of area W is the first level of the pathway leading to the word-selective γ-cells of layers 2 + 3 that shows a response component specific to speech. We do not know the precise role that this late-sustained component may play in word selectivity. Firing patterns and response properties of α- and β-cells seem essentially identical.

The characteristics of the layer 2–3 "one"-selective γ-cell shown in Fig. 1 have already been described. The simulation contains nine additional γ-cells, each tuned to detect a different pattern composed of a randomly chosen arrangement of onsets, peaks, and offsets. The selectivity properties of each of these γ-cells, with respect to their target pattern and variants around it, are similar to that of the "one"-selective γ-cell, and we do not describe them further here. When γ-cells respond, they generally do so with a pattern containing four to eight spikes with a typical frequency of 30–60 Hz.

Intracellular Recording in a Slice Preparation. Finally, we turn to *in vitro* studies of the biophysical properties of the α-, β-, and γ-neuron types in area W. The three cell types are qualitatively similar, and seem to be well described by simple integrate-and-fire cell models.

Synapse properties were studied by using conventional two-electrode methods. Excitatory postsynaptic currents (illustrated in Fig. 6*a*) have an extremely fast rise time and decay exponentially with a time constant of 2 ms. Inhibitory postsynaptic currents (illustrated in Fig. 6*b*), in contrast, have a slower rise time. Inhibitory postsynaptic current waveforms were well fit by alpha functions (fits not shown), with a peak amplitude time of 6 ms. The recordings shown in Fig. 6 *a–b* were made with cells held at −65 mV (millivolts), but waveform amplitudes and time constants changed little when the holding potential was varied within the range −75 mV to −55 mV. Paired-pulse experiments (data not shown) have demonstrated that both excitatory and inhibitory synapses in area W neither adapt nor facilitate, and that synaptic currents caused by closely timed action potentials add linearly. The excitatory postsynaptic potentials and inhibitory postsynaptic potentials obtained in the same cells as shown in Fig. 6 *a* and *b* when the voltage clamp was removed are shown in Fig. 6 *c* and *d*.

α-Cells and β-cells were found to be electrotonically compact, with membrane time constants of approximately 20 ms. We applied a series of constant current steps of different amplitude to these cells. One such application is illustrated in Fig. 6*e*, and the result of the entire series of steps is summarized by the data points shown in Fig. 6*f*. By all studies we have made, both α and β-cells have properties that can be duplicated by leaky integrate-and-fire neurons with a short absolute refractory time period. The solid line in Fig. 6*f* is the result of fitting such a model to the data points shown in the same panel. The parameters of the fit were absolute refractory time period, 2 ms; membrane time constant, 20 ms; resting potential, −65 mV; firing threshold, −55 mV; reset potential after spiking −75 mV; and membrane capacitance, 250 pF. Although *in vivo* firing rates greater than 150 Hz are seldom seen, the maximum firing rate of all three cell types is around 500 spikes per s when driven by steady currents.

The γ-cells of layer 2 + 3 are qualitatively similar to α-cells and

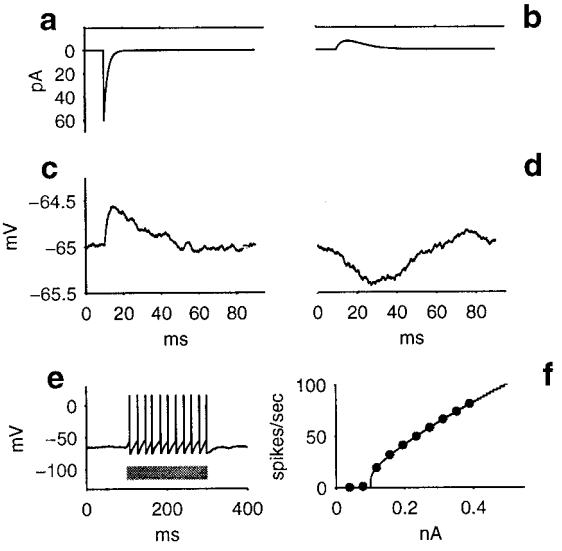

Fig. 6. Whole-cell recordings from α- and β-cells in layer 4. (*a–d*): A minimal stimulation protocol was used to observe synaptic responses caused by the activation of a single axon afferent to the recorded cell. (*a*) Excitatory postsynaptic current measured in a β-cell under voltage-clamp conditions. (*b*) Inhibitory postsynaptic current measured in an α-cell. (*c*) Excitatory postsynaptic potentials measured in the same cell as in *a*. Resting state here corresponds to the cell's resting membrane potential, −65 mV. (Because noise is present in all real biological systems, here and in all other simulations, independent white Gaussian noise with SD = 0.2 mV was added to the neuron's membrane potential at each 0.1-ms timestep.) The trace shown is the average of 1,000 repeats. (*d*) Inhibitory postsynaptic potentials measured in the same cell as in *b*. (*e*) Spiking response to an above-threshold current step, showing no spike-frequency adaptation. Gray bar indicates the time during which current was injected. (*f*) Firing rate of an α-cell as a function of input current. Points are the experimental measurements, and the solid line is a calculated fit to these points, based on a leaky integrate-and-fire model of the cell.

β-cells in every way, but quantitatively, γ-cells have a smaller membrane resistance and a shorter membrane time constant of 6 ms. Inhibitory postsynaptic currents and excitatory postsynaptic currents seen in γ-cells have time courses very similar to those seen in α-cells and β-cells (Fig. 6), but the typical peak currents are about three times as large.

Conclusions This system carries out a difficult computation in a manner that results in significant robustness to variability and noise. It recognizes whole-sound sequences in a way that is not sensitive to the kinds of variability that are present in natural vocalizations—variations in voice quality, in speed of speaking a syllable, and in sound intensity. The computation integrates a short epoch of the past into a present decision about the category to which a recent sound belongs. Despite the complexity and robustness of the computation, the elements that compose the system, and the inputs to it, are remarkably simple. Most importantly, they are similar to the elements found in real neurobiology, and our goal is to understand how neurobiology might integrate and recognize spatiotemporal patterns. The biophysics of individual neurons and synapses is that of classical integrate-and-fire neurons with nonadapting synapses. The projection neurons of area A respond to stimuli in a fashion not unlike some responses available in processing regions of a variety of sensory modalities. In short, given apparently ordinary input and computing elements, the system robustly carries out the complex task of recognizing spoken words.

The principle behind the algorithm effectively carried out by this network of simple biologically plausible neurons will be described in the subsequent article and is applicable to a wide

variety of inputs and situations. Here we only remark that consideration of the details given will convince a reader that we have not clothed a backprop-trained network in biologically plausible camouflage, and that the network is using neurons collectively and not using them as logic elements.

Any neurobiological computation should be robust to cellular variations. For example, high accuracy in individual synapse properties is biologically unrealistic, and a computational neurobiologist will not take seriously schemes requiring great accuracy of individual synapses. The present system itself is "biological" in this regard—simultaneously varying each synaptic connection strength between neurons in area W by a different random factor of $\pm 50\%$ has no appreciable effect on the response of the α-, β-, or γ-cells.

The article with an explicit description of the principles of operation of the system will be presented in 3 months. Our surprise in finding that the network principles could be fully deduced, based on the straightforward experimental results presented here, leads us to ask whether long chains of logical deduction similar to the one appropriate in this case could be usefully applied in neurobiology. We do not claim to know the answer to this question, but we believe it is useful to raise it.

We assure the reader that knowledge of any additional features of neurobiology is not required beyond that herein described, either explicitly or implicitly. However, some readers may wish to learn more details or may wish to carry out experiments of their own design. We have constructed an interactive web site, http://neuron.princeton.edu/~moment, where these experiments can be done. The web site contains speech files with numerous examples of spoken utterances, sine wave pulses, and the corresponding recordings that would be available from single-electrode extracellular studies of the output cells of area A and the α-, β-, and γ-cells of area W. The sound files can be heard, and the sound files and spike rasters can be downloaded. A user can also upload new sound files to the website and study the electrophysiology of responses to those files.

The second article will contain references to the relevant artificial and biological neural literature. The challenge presented in this article has involved describing a computational network as if it were a biological one. In this spirit, references to relevant material that led the creators of the network to the principles underlying it are not appropriate, and we have chosen to include none in this article.

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