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SPIKE ARRIVAL TIMES : A HIGHLY EFFICIENT CODING SCHEME FOR NEURAL NETWORKS

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1. Introduction - Temporal constraints on neural coding.

The speed with which visual processing occurs in the human brain puts heavy constraints on the way in which information is processed. Indeed, we have recently argued that processing is so fast, that most visual processing must be achieved using a single feed-forward pass through the visual system (Thorpe, 1988; Thorpe & Imbert, 1989). Briefly, the argument is as follows. (1) Neurophysiological data have shown that neurons in the temporal cortex have highly selective responses (to faces for example), which start with latencies that are often in the range 100 to 140 ms (Perrett, Rolls & Caan, 1982). (2) Anatomically, it would appear that there are at least 10 synaptic stages between the photoreceptors of the retina and these visually responsive neurons in the temporal lobe (i.e., 2 in the retina, 1 in the lateral geniculate nucleus, 2 each in V1, V2, and V3, and one more in inferotemporal cortex). (3) Since the 10 synaptic layers must be crossed in 100 msec, this implies that each layer has only an average of 10 msec processing time. (4) Given that the firing rates of cortical neurones are typically in the range 0 to 100 spikes per second, it follows that a neuron in any given layer can only generate 1 or perhaps 2 spikes before neurons in the next layer have to respond.

Clearly, this puts major constraints on the way in which information is coded. For example, it is unreasonable to propose that firing rate per se can be used as an accurate code for analogue values. One possibilitity is that with two spikes, one can use the interval between them as a code - the closer the spikes, the stronger the activation. However, the evidence indicates that a large amount of information can be transferred using only 1 spike per neuron.

In this paper, I would like to suggest what I believe is a novel way of coding information in neural networks. It will be proposed that analog information can be encoded by the relative arrival times of spikes. It will also be shown how such a scheme allows very rapid resolution of the classic "Winner-takes-all" problem.

2. The spike arrival time hypothesis.

It is a well known neurophysiological fact that the time taken for a neuron to reach its threshold for generating a spike depends on the strength of the stimulus - the stronger the stimulus, the faster the neuron depolarizes, and the sooner it generates a spike. Imagine, therefore, what happens when an image is flashed onto a simple retinal array of sensory cells. If the cells in the retina are sensitive to local intensity, a wavefront of spikes will be generated in the optic nerve, with the leading spikes corresponding to the points on the retina where the intensity is highest. As a result, even if each retinal cell generated one, and only one, action potential, the complete intensity distribution of the image could be coded by the relative timing of spikes in the different fibres of the optic nerve. Obviously, the example given here is not biologically realistic - retinal ganglion cells do not simply code the local intensity level. Rather, their activity is more clearly related to local contrast. Nevertheless, the argument is just the same - whatever the parameter coded by the input array, the relative arrival time of spikes can be used to code analog values with considerable precision, and this, even if only one spike per fibre is available.

Of course, in order for relative spike arrival times to be a useful code, it is necessary for the next processing layer to be able to make use of such information. Is such a process physiologically plausible? The answer would appear to be a definite yes. Christoph Koch and Tomasio Poggio have recently proposed that synaptic veto mechanisms could exist in the retina with the property that if a spike from one input arrives before another, it could block the transmission of the second spike. Furthermore, it has been known for some time that neurons in the auditory system are sensitive to the relative arrival times of auditory stimuli in the two ears - such information is used in determining the spatial position of auditory stimuli (References). Another example concerns the processing of sensory information in electric fish. Heiligenberg and his collaborators have recently reported the some neurons are sensitive to electrical pulse arrival time differences in the microsecond range.

In all the above examples, the differences in spike arrival time are due to timing differences in the arrival times of the actual physical stimuli, be they points of light, auditory stimuli to the left and right ears, or electrical discharges to the left and right sides of a fishes body. What is being proposed here is simply that the nervous system could make use of differences in spike arrival times resulting not from temporal differences in the stimulus itself but rather the delays introduced by the coding.

3. The problem of continuous input.

While it is relatively easy to see how an image flashed on the retina could lead to a information-rich wavefront of spikes in the optic nerve, it may be less obvious how the visual system could cope with continuously changing information. However, one important factor that may well reduce this problem are eye-movements. It has recently been reported that transmission in the visual pathways in inhibited during eye movements, and that this inhibition is relaxed as soon as the eye movement has terminated (Ref.). It could be that this could provide the synchronization necessary to allow relative spike arrival times to be used later in the system.

Another possibility for providing the synchronization may be found in the oscillatory activity found in many parts of the nervous system. In particular, it is possible that the 50 Hz oscillations recently reported in the visual cortex by Gray and Singer (1988, 1989) and Eckhorn and coworkers (1988) could be used to this effect. They have reported that neurons tend to fire during the negative going part of the local field potential oscillations. More strongly activated neurons would tend to fire earlier in the cycle, and this information could be used during processing by subsequent stages.

4. An application : The "Winner-Takes-All" problem.

One standard problem in connectionist models is the so-called "Winner-takes-all" problem. Consider an array of units, with varying levels of activity. We want to select only the most active one. One commonly used method is to introduce inhibition between all the units. Since the most active unit inhibits the others the most strongly, after a number of iterations the activity in all units except the most active will decrease until in the end, only one unit remains active. The problem is that the number of iterations can be quite large. Although it is possible to optimise such parameters as the amount of lateral inhibition, it is clear that at least 3 iterations are required (Feldman & Ballard 1982; personal communication).

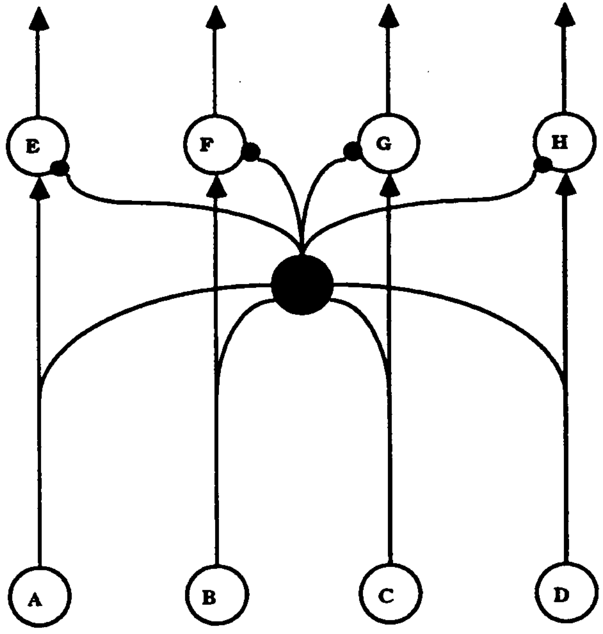

Figure 1. A network using relative spike arrival time to solve the Winner-Takes-All problem.

The figure illustrates how, if spike arrival times are used as an analog code, solving the Winner-takes-all problem is almost trivial. The four input units (A-D) have direct connections to four output units (E-H), but they also have collateral connections to an inhibitory interneuron. Imagine that all four input units generate spikes, but that the spike in unit B is initiated a few milliseconds before the others. Unit F will respond to its input as usual, but because B's spike also activates the inhibitory interneuron, the other three units will either fail to respond, or respond with longer latencies to their respective inputs. As a result, the output pattern will correspond to a Winner-Take-All function of the input, but unlike conventional neural algorithms the time taken is just determined by the conduction delay and the synaptic integration time of the output layer (i.e. a few milliseconds).

5. Perspectives.

The coding scheme proposed here would appear to provide a powerful way of increasing the processing speed of neural networks, and may provide an important insight into how the visual system can process highly complex visual inputs with only 100-150 msec of processing time. It may also be the case that such a coding scheme could be used in artificial neural network systems. An analog retina in which the individual pixel elements generate impulses with a delay that depended on local image intensity would be relatively easy to construct. Subsequently, circuits of the type described in the preceding section could be used to "pick off" the most active inputs as well as performing other more complicated operations.

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