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Simultaneous Recording of Input and Output of Lateral Geniculate Neurones

To understand the way in which the cat dorsal lateral geniculate nucleus (LGN) processes visual information it would be useful to know the number and type of retinal inputs to individual LGN neurones. Using electrical stimulation of the optic nerve Bishop *et al.*[1] concluded that an impulse in a single optic nerve fibre is sufficient to excite a single LGN neurone. From the appearance of excitatory postsynaptic potentials (EPSPs) recorded essentially intracellularly, Creutzfeldt suggested that LGN neurones are driven by perhaps one[2] or a few[3] retinal ganglion cells. Hubel and Wiesel[4] proposed models of convergence of several retinal inputs on single LGN neurones based on analyses of receptive fields. Guillery[5] produced anatomical evidence that some types of LGN neurones receive inputs from several different retinal fibres. Now we report direct observations which were made by recording simultaneously from single LGN neurones and from individual retinal ganglion cells which provided excitatory input to them. We shall not consider inhibitory influences, which are currently under study.

A cat was held in a stereotaxic apparatus under nitrous oxide–oxygen–carbon dioxide (67%–31.5%–1.5%) anaesthesia, paralysed by a continuously infused mixture of 'Flaxedil' and *d*-tubocurarine. The left eye was sutured to a ring which formed part of the apparatus used for introduction of a recording microelectrode into the eye through a cannula penetrating near the ora serrata. The cannula pivoted on a ball-joint at the sclera; the remote end of the electrode-advancer was supported by an orthogonal pair of hydraulic drives at some distance from the pivot, so that the retinal location of the electrode tip was under precise control. Neosynephrine and atropine were used to retract the nictitating membrane and dilate the pupil. A craniotomy sealed with 3% saline-agar was made to allow extracellular recording from the right LGN with glass-insulated, tungsten microelectrodes. Cell waveforms were identified by the criteria of Bishop *et al.*[6]. The cat faced a grey tangent screen with a uniform luminance of 10 cd m^{-2}. Neural activity was elicited by movement of hand-held targets of different shapes, sizes and contrast or by spots of light from a projector. A 3 mm artificial pupil and appropriate spectacle lenses were used. Retinal recordings were obtained from ganglion cells in the left visual hemifield, within 20° of the area centralis. Recording from layers A and B of the LGN was confirmed in a number of cases by the histological identification of electrolytic lesions.

The upper half of Fig. 1 summarizes the recording situation schematically. The visual field position of the receptive field of an isolated LGN neurone was determined on the tangent screen. The retinal electrode was next manipulated approximately to the conjugate retinal locus. When a ganglion cell was found, the position of its receptive field was used to indicate any correction that was necessary in the next placement of the retinal electrode. This search was continued until we recorded from a ganglion cell which was an excitatory input to the LGN neurone under study. This report is based on retinal inputs to sixty-two LGN neurones in twenty-seven cats.

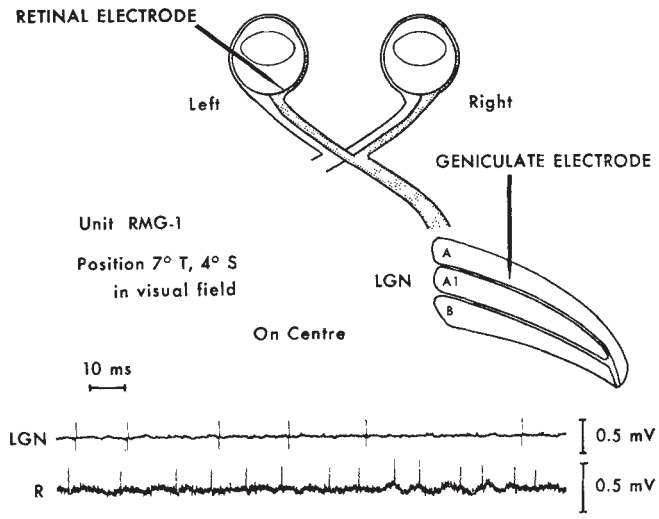

Fig. 1 The upper portion shows the recording situation schematically. The two oscilloscope traces below the diagram were photographed simultaneously on the same paper. The lower trace shows the recording of a retinal ganglion cell, the upper the recording of an LGN neurone driven solely by the ganglion cell. Note that every LGN neurone spike follows a ganglion cell spike by about 2 ms. Negativity up, on spike records.

For five LGN neurones (8%) every spike was found to be driven by a single retinal ganglion cell. The lower half of Fig. 1 illustrates this for an on-centre LGN neurone and retinal ganglion cell. The two spike traces shown were photographed simultaneously on the same screen. Every spike in the LGN trace is preceded by a retinal ganglion cell spike occurring approximately 2 ms earlier. The sharpness of this timing is in strong contrast with the irregularity of intervals between successive impulses in the individual traces. The magnitude of the delay was always in the range expected on the basis of conduction velocity of extra-retinal optic nerve fibres[7] and the relatively slower intra-retinal conduction velocity of the unmyelinated segment. For the particular pair of recordings in Fig. 1, 18 s of film showed 208 LGN spikes, each of which was related to the retinal spike in the manner shown in Fig. 1; that is, all LGN spikes could be accounted for. Furthermore, the film showed 290 ganglion cell spikes elicited by various types of stimuli; thus 72% of the ganglion cell spikes caused LGN neurone spikes. Similar film records of the unstimulated maintained discharge also showed that this LGN neurone had no truly spontaneous activity. Of the five single-input LGN neurones four had receptive fields more than 5° from the centre of the area centralis.

The remaining fifty-seven LGN neurones yielded a different picture. In each, only a proportion of the LGN spikes could be accounted for by a preceding impulse in one simultaneously recorded ganglion cell. In eleven of these instances recording stability was such that we were able to go on and find more than one of the ganglion cell excitatory inputs. Fig. 2 shows an example in which two inputs were found. Both were of the off-centre type as was the LGN neurone. Plots of the receptive

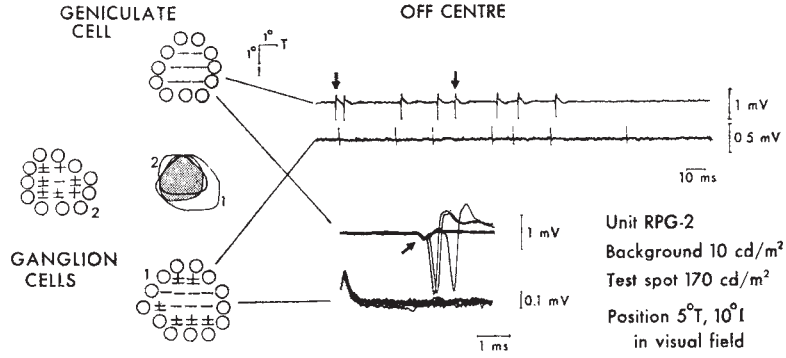

Fig. 2 The receptive field plots at left are of an LGN neurone and two ganglion cells which directly excited it. (+) indicates response at "on", (−) indicates response at "off", (0) indicates no response. The size of the circles indicates the size of the test spot used, 0.7°. The receptive field outlines of the three units are also shown superimposed in their relative positions in the visual field, the LGN receptive field being stippled. The spike traces correspond to the LGN neurone and ganglion cell 1 as shown by connecting lines. The upper pair of traces show LGN spikes related, with a latency of about 2.5 ms, to spikes of ganglion cell 1. The arrows show two spikes that are not so related. In the lower set of traces, which are the superposition of a number of sweeps, both beams of the oscilloscope were triggered by the occurrence of a ganglion cell spike (lower beam). An S-potential (arrowed) is observed at the LGN neurone (upper beam), 2.5 ms after every retinal spike. Three S-potentials are seen to lead to spikes.

fields of all three are shown separately and superimposed in outline. We commonly found the centres of such ganglion cells' fields to be somewhat offset from each other, as in Fig. 2. The relatively smaller size of the LGN field is presumably caused by inhibitory effects.

The top two spike traces of Fig. 2 are analogous to those of Fig. 1. Some of the LGN spikes can be seen to follow the ganglion cell spikes about 2.5 ms later, but two of them (arrowed) are clearly not related to this ganglion cell. The bottom two oscilloscope traces illustrate the relation between ganglion cell 1 and the LGN neurone in another way. Both traces are synchronized by the occurrence of a ganglion cell spike, a number of which are shown superimposed in the lower trace. The upper trace, the recording of the LGN neurone, shows that every ganglion cell spike was followed 2.5 ms later, with almost no latency jitter, by a pre-potential (arrow), three of which led to the firing of spikes. These pre-potentials have been called S-potentials[8] (for synaptic) or optic-tract synaptic potentials[4]. They are generally thought to be extracellularly recorded EPSPs.

Detailed analysis of the unit in Fig. 2 showed that for various stimulating situations an average of 53% of the LGN spikes were driven by ganglion cell 1. When ganglion cell 2 was later recorded similar stimulation yielded an average of 43% of the LGN spikes driven. When the time-base was synchronized with this ganglion cell a different S-potential could be detected, although it was too small to be detected in base line noise with non-synchronized records. Ganglion cells 1 and 2 accounted for less than 100% of the LGN neurone spikes, suggesting that at least one more input to the neurone existed. In other cases where we have found more than one input to an LGN neurone the sum of the percentages of the LGN neurone spikes driven by each input has amounted to more than 100%. This suggests coincidence in time of retinal spikes from different inputs leading to some of the spike output of the LGN neurone.

Of the fifty-seven neurones which had multiple inputs there were twenty-two in which just one of the inputs accounted for 80% or more of the LGN spikes. In the remaining cases the major part of the excitatory drive was provided by only two or three retinal inputs.

The following picture emerges. An LGN neurone receives excitatory input from one or a few retinal ganglion cells, which is sufficient to account for most of its output. That is, the convergence of major excitatory input on an LGN neurone is small. Nonetheless, there is clearly spatial and temporal integration of inputs. For those LGN neurones with multiple retinal inputs, the excitatory receptive field (that is, all those regions which can be stimulated, at "on" or "off", to yield discharge) is a weighted sum of a number of retinal fields. It is not equivalent to the receptive field of any one of the retinal inputs, because these fields themselves are not coincident in space. Temporally, multiple inputs may coincide in their relationship to a particular spike at the LGN neurone, a result which is indicated by those multiple input cases in which the percentages of the spikes driven by the individual inputs add up to more than 100%. Another point with regard to multiple input fields is that in no case did an off-centre ganglion cell trigger an on-centre LGN neurone, nor an on-centre ganglion cell trigger an off-centre LGN neurone. Finally, for the majority of LGN neurones it is likely that most, if not all, of their output is closely synchronized with respect to individual impulses in their retinal inputs.

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