Unit Responses and Interactions at Superior Colliculus First Stage of Input Reception

Retinal and cortical projections to the superior colliculus (SC) have been anatomically demonstrated[1-4]. Recently some of their functions were defined[5-9]. It was revealed that the cortical visual areas project to the same SC regions as the optic tract[10,11]. Consequently response characteristics of the cat SC neurones to optical stimuli were found to depend on the integrity of the cortical visual areas [3,12-17]. A study was, therefore, undertaken on the responses to and on the interactions of inputs originating in the visual cortical areas 17 and 18, and in the optic tract at SC first stages of reception. Because of its two way connectivity with SC[18], the pulvinar nucleus was included for comparison.

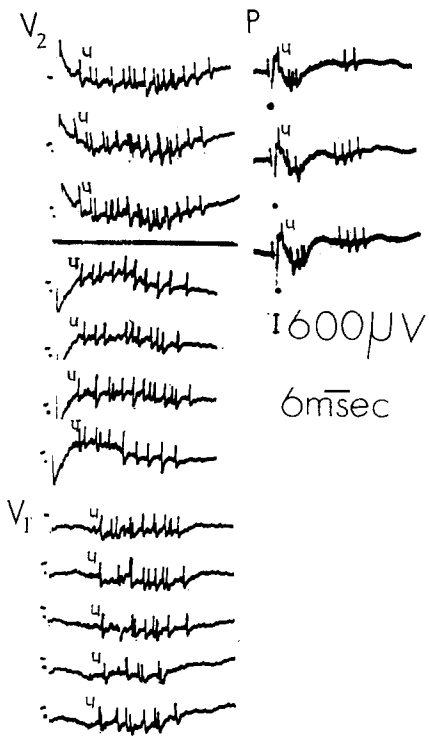

Fig. 1. Extracellularily recorded unitary responses (U) of neurones located at the superficial layers of SC evoked by single pulse stimulation of the cortical visual areas 18 (V_2), 17 (V_1) and of the pulvinar nucleus (P). The response of the same unit to each of the three illustrates the convergence of their inputs to the same SC cells. Note differences in response pattern of the visual areas as compared to the pulvinar nucleus. Stimulation parameters: 25 volt intensity, 0.15 msec pulse duration; 1 pulse per 2 sec.

Methods. The studies were conducted on 11 adult female and male cats, anesthetized with pentobarbital sodium (25–30 mg/kg, i.v.), and paralized with Gallamine, under artificial respiration. The methods used in microelectrode recordings, in stimulation, and in the determination of actual electrode placements were previously reported[19]. Stimulation sites included the cortical visual areas 17 and 18[20], the optic tract and the pulvinar nucleus. Extracellular unitary responses were recorded from SC by means of tungsten microelectrodes. A physiological solution of dextrose was injected into the animals every few hours for nourishment. The stability of the unitary records was achieved by performing a pneumothorax and by keeping the exposed brain under a 3–5% agar gel.

Results. Numerous neurones in the superficial layers of SC were evoked by stimulation of the cortical visual areas 17 and 18. These were characteristically composed of long bursts (Figure 1). The same units were sometimes driven also by the pulvinar nucleus but with a response composed of a few short bursts (Figure 1). The latencies for driving such units were usually longer and more variable in the case of area 17. However, units driven by either one of these sites, showed properties of monosynaptic driving: constancy of the unit response and of its latency and constancy of phase relationships of unitary responses to local field potentials. While some divergence of inputs from these sites to different SC layers[18] has been observed, convergence of these to neurones of SC superficial layers is illustrated in Figure 1.

Monosynaptic driving of units was obtained in the superficial SC layers also following stimulation of the optic tract (Figure 2). Some of these consisted of a single spike response which repeated itself at relatively long intervals. This occurred possibly due to the convergence of optic tract fibers which varied greatly in their thickness. Other such responses consisted of bursts of 2 or 3 spikes. Similarily to the response illustrated in Figure 3A often these responses showed an outstanding constancy of pattern: each burst response consisting of the same number of spikes. These were presumably obtained at the first stage of SC reception of the optic tract inputs since they showed properties of monosynaptic driving. Their invariable pattern, consisting in the sample illustrated of a 3 spike burst, suggested an encoding process. A preconditioning train stimulus which was delivered to the cortical visual area 18 was shown to modify the response. As is shown in the figure it curtailed the last spike in most of the burst responses of the unit illustrated (Figure 3B). On the other hand, the pre-conditioning stimulus delivered by itself caused nothing but an increase in firing rate (Figure 3C). This effect was not manifested by a similar stimulation of either area 17 or the pulvinar nucleus.

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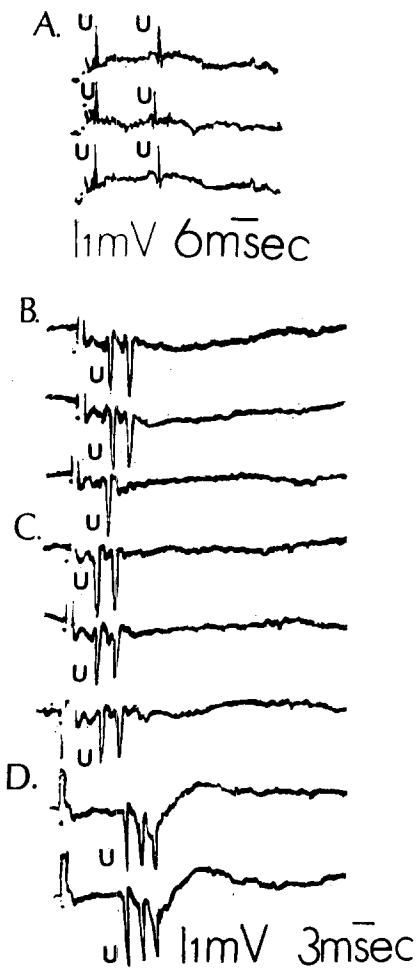

Fig. 2. Samples of unitary responses (A, B, C and D) recorded from SC superficial layers following single pulse stimulation of the optic tract, and which show properties of monosynaptic driving. Parameters of stimulation: 9v (0.15 mAmp) intensity, 1.0 msec pulse duration; 1 pulse per 2 sec.

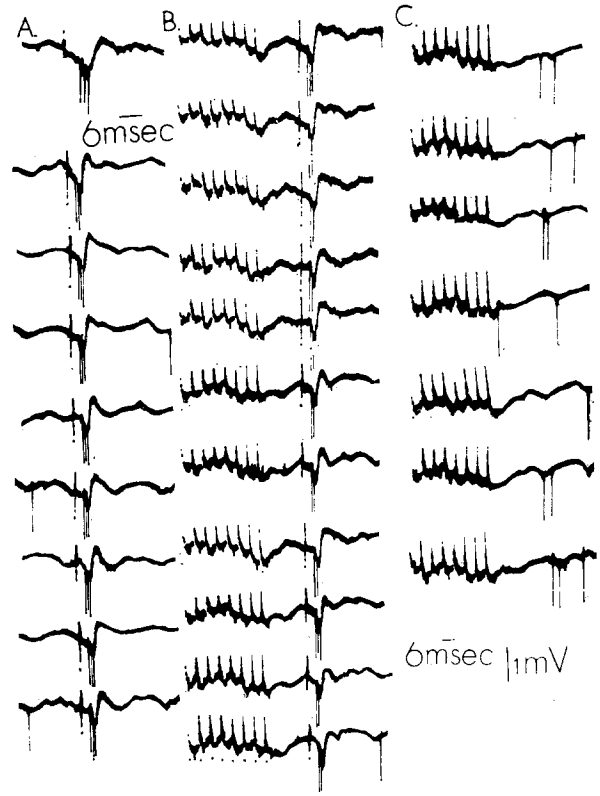

Fig. 3. Extracellularily-recorded SC units evoked by stimulation of the optic tract – its modification by preconditioning stimuli delivered to V_2. A) An invariable three-spike response of an SC unit to a single pulse stimulation of the optic tract. B) The curtailment of the 3rd spike in 11 out of 13 burst responses to optical tract stimulation under the influence of a train stimulus pre-conditioning delivered to V_2. C) Control responses obtained with the pre-conditioning stimulation delivered by itself. Stimulation parameters: Test stimulus to the optic tract – 15 volts (0.25 mAmp) intensity, 0.2 msec pulse duration, 1 pulse per 2 sec. Pre-conditioning stimulus – a train of 40 msec duration of pulses at 200/sec rate, 0.2 msec pulse duration, and 20 volts intensity. Interval between test and pre-conditioning stimuli: 20 msec.

Discussion. In SC superficial layers unitary responses were obtained from common neurones following stimulation of cortical visual areas 17 and 18 and of the pulvinar nucleus. These responses varied, in pattern. Some of them showed characteristics of monosynaptic driving. The latter type of response was also obtained from neurones of the same region following stimulation of the optic tract. The latter often showed great constancy of the number of spikes per burst response, suggesting an encoding process. Preconditioning stimuli delivered to area 18 at 10–15 msec intervals prior to the test stimuli modified such responses to the optic tract: each burst was shortened in a constant manner. This observation supported the contention of an encoding process for visual signals at SC level and for the potentiality of visual area 18 to control such processes. Evidence was thus provided that SC, besides its function in visuomotor action, might also play a role in the corticopetal forewarding of visual signals. This action is perhaps performed by SC in parallel to and in conjunction with the lateral geniculate nuclei.

Zusammenfassung. Durch Stimulation der visuellen corticalen Zone 17 und 18 des Pulvinarnukleus und des tractus opticus wurden Reiz-Potentiale von SC-Neuronen abgeleitet. Die präkonditionierte Stimulation des visuellen corticalen Zone 18 ergab ein konstantes Reiz-Muster.

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