Lateral interactions in the superior colliculus, not an extended fixation zone, can account for the remote distractor effect

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Abstract: Recordings of neuronal activity in the monkey superior colliculus (SC) suggest that the two apparently independent effects of a visual distractor on both temporal (latency) and spatial (metrics) saccade parameters may be the result of lateral interactions between subpopulations of saccade-related neurons located at different sites on the motor map of the superior colliculus. One subpopulation is activated during the planing and initiation of a saccade; the other is activated by the appearance of a distractor. The inhibitory or facilitative nature of this interaction depends on the distance between the distractor and the target and is consistent with the complex pattern of intrinsic and commissural collicular connections.

Presenting a visual cue (a "distractor") simultaneously with a target affects either the timing (increased reaction time) or the metrics ("averaged saccades") of visually guided saccades, depending on the position of the distractor relative to the actual target (Walker et al. 1997). Findlay & Walker (F&W) regarded this finding as evidence for the existence of two independent processes separately controlling the metrics ("Where") and the timing ("When") of saccades. Furthermore, because this increase in saccade reaction time (SRT) persisted even when the distractor was presented at a rather eccentric position (up to 10°), Walker et al. (1997) concluded that the collicular fixation zone is probably much larger than originally inferred from monkey experiments (Munoz & Wurtz 1993a; 1995b). F&W then conclude in section 2.2.5 and elsewhere that "visual onsets, even in the periphery, act to enhance fixation centre activity." They suggest that the main effect of a remote distractor is activation of the fixate system, which would slow the triggering process (sect. 4.1.2). The "fixate system is accessed by stimulation from an extended central region of the visual field." Their conclusion suggests that a delay in saccade initiation is caused by a delay in the drop-off of SC fixation cell activity known to precede any saccade (Munoz & Wurtz 1992). F&W therefore envisage an increase in fixation activity following visual onsets in the periphery that manifest themselves at level 2 in their scheme. The results of recent physiological studies have demonstrated that this mechanism must be modified. The visual receptive fields of collicular fixation neurons are small and encompass only foveal and parafoveal regions of the contralateral visual field (Krauzlis et al. 1997; Munoz & Wurtz 1993a). Only a small percentage of fixation neurons have visual receptive fields that extend out to 10° of visual angle in the contralateral hemifield (Everling et al. 1998).

A more plausible mechanism that could account for the increase in SRT following the presentation of a remote distractor is the lateral inhibitory network within the intermediate layers of the SC itself. Anatomical studies have shown that there are many GABAergic inhibitory interconnections that are both intra- and intercollicular (Behan & Kime 1996; Mize et al. 1991; Olivier et al. 1998). In addition, electrophysiological recordings in slices of ferret SC (Meredith & Ramoa 1998) and the SC of awake monkeys (Munoz & Istvan 1998) have also revealed strong intrinsic and commissural inhibitory interactions following electrical stimulation at remote locations on the SC motor map. Therefore, in the scheme of F&W, it is likely that the presentation of a remote distractor would serve to activate a second population of saccade-related neurons in the salience map, rather than lead to direct activation of neurons comprising the fixate system. Then, via lateral inhibitory interactions within the salience map at level 2, the generation of the motor command to initiate a saccade would be delayed.

Another interesting result obtained with the presentation of a simultaneous distractor is that presentation of a distractor in close proximity to the target can produce the global effect in which the saccade actually goes to an intermediate position between the target and the distractor (sect. 4.2.2). In this situation, the visually evoked activity induced by the distractor is close to the location, within the salience map, of the visually evoked activity induced by the target, resulting in two overlapping regions of activity. There is evidence for excitatory lateral interactions between near sites within the SC (McIlwain 1982; Munoz & Istvan 1998) that could facilitate the generation of these averaging saccades. As a consequence, presentation of a near distractor could produce a shift of the center of gravity of active cells within the salience map and, consistent with the "population-averaging" hypothesis (Lee et al. 1988), change the amplitude and direction of the saccade. This could explain the "global effect" (averaged saccades) observed when the distractor is presented in the vicinity of the actual target.

To test these hypotheses directly, we recorded the activity of SC neurons in monkeys performing a gap paradigm in which the fixation point disappears 300 msec before a target appears in the center of the neuron's response field and a distractor is presented somewhere else in the visual field. To separate the neural response elicited by the distractor from the phasic saccade-related activity of SC neurons, distractors were presented at various locations in the visual field 100 msec prior to target appearance. Figure 1 shows the activity of a single saccade-related neuron with buildup activity when only a target (T) was presented (Fig. 1A – control)

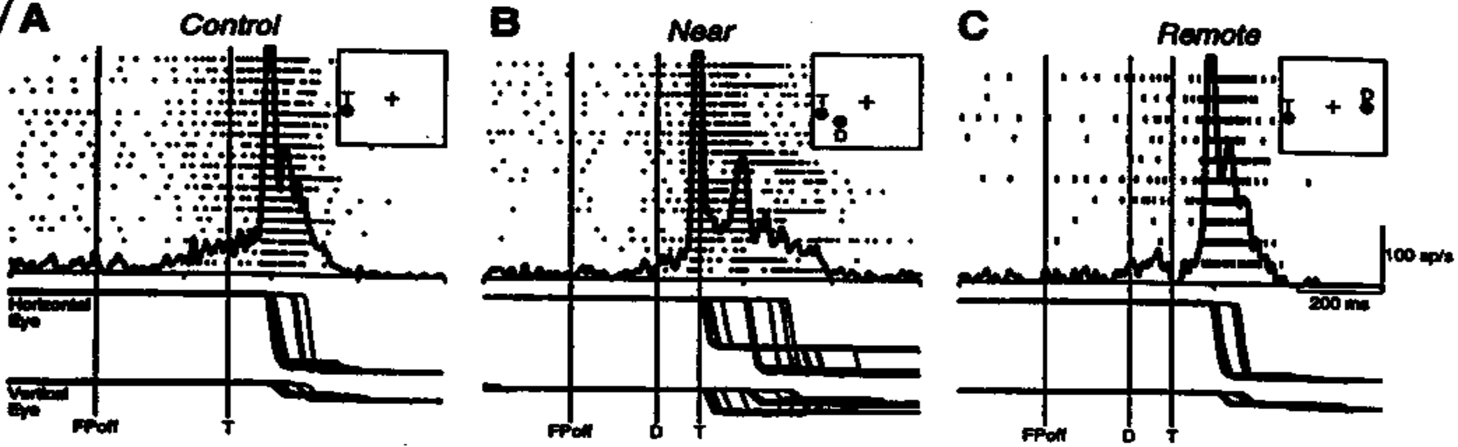

Figure 1 (Olivier et al.). The effect of distractors on the discharge rate of a SC neuron with buildup activity. (A) The neuronal discharge during visually guided saccades is shown when there was no distractor, (B) the distractor was presented near the center of the neuron's response field, and (C) when the distractor was presented at a remote location relative to the neuron's response field, as depicted by the schematic in each inset. Each line of rasters represents the neuronal activity from one trial and the average activity of the cell for all trials in a given condition is illustrated by the spike density function. The accompanying horizontal and vertical eye position traces are shown at the bottom of each panel.

and when a distractor (D) was presented at either a near (Fig. 1B) or remote (Fig. 1C) location. In all trials the monkey was rewarded only if it made a visually triggered saccade to the target, which was always presented in the center of the neuron's response field. In the control condition, the neuron displayed low-frequency motor preparation activity during the gap period and both visual and motor bursts associated with target appearance and saccade generation, respectively. The influence of the distractor depended on its position with respect to the target. When the distractor was presented near the target location (Fig. 1B), the neuron showed a transient visual burst that, because of the already elevated level of motor preparation near that location, sometimes triggered short-latency saccades to the distractor itself. When the distractor was presented far from the target location (Fig. 1C), there was a transient inhibitory pause in discharge and no saccades were triggered to the distractor. Therefore, we can speculate that, when the remote distractor is presented simultaneously with the target, as in the original experiment of Walker et al. (1997), inhibition delays the saccade-related neurons from reaching the level of discharge required to initiate a saccade and therefore delays its initiation.

We suggest that the two distinct effects of a remote distractor on both the temporal and spatial saccade parameters can be explained by a single mechanism: the interaction between two zones of active, saccade-related neurons within the salience map at level 2 in the F&W scheme. One population of saccade-related neurons is activated by the target and the other one is activated by the distractor. The nature of this interaction will depend on the relative location of these two active cell populations within the salience map and is consistent with the complex pattern of inhibitory and excitatory intrinsic and commissural connections within the SC (Meredith & Ramoa 1998; Munoz & Istvan 1998; Olivier et al. 1997; 1998).