Comment on "Top-Down Versus Bottom-Up Control of Attention in the Prefrontal and Posterior Parietal Cortices"

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Buschman and Miller (Reports, 30 March 2007, p. 1860) described the activity of ensembles of neurons in parietal and frontal cortex of monkeys performing visual search for targets that were easy or hard to distinguish from distractors. However, their conclusions are called into question by discrepancies between their results and publications from other laboratories measuring the same neural process.

This comment addresses discrepancies between a recently published study by Buschman and Miller (*1*) and a 14-year-old literature, which has built on the accumulated knowledge about a neural circuit over the past 40 years. The study in question compared when the spatial location of a visual target for an eye movement was signaled by neurons recorded in prefrontal areas, including the frontal eye field (FEF), lateral prefrontal cortex (LPFC), and the lateral intraparietal area (LIP), of macaque monkeys performing visual search for targets that were either easy or difficult to distinguish from distractor stimuli. Buschman and Miller reported that when the search target was easy to find, neurons in parietal cortex signaled its location before neurons in prefrontal cortex. When the search was more difficult, prefrontal cortex signaled the target location before parietal cortex. However, these data and conclusions are inconsistent with results from multiple laboratories.

The authors reported that during their pop-out search, "LIP showed selectivity for the target location approximately 50 ms after array onset, followed by LPFC and then FEF after 120 and 220 ms, respectively." [See supporting online material and figure S4 in (*1*)]. However, when the target was easy to find, many neurons in all areas located it after the saccade, and when the target was harder to find, nearly all neurons reported by the authors located it after the saccade. In contrast, several studies in monkeys performing a conventional pop-out search task have found that the target is located ~130 to 140 ms after the array appears by neurons across the brain regions known to be involved in visual search,

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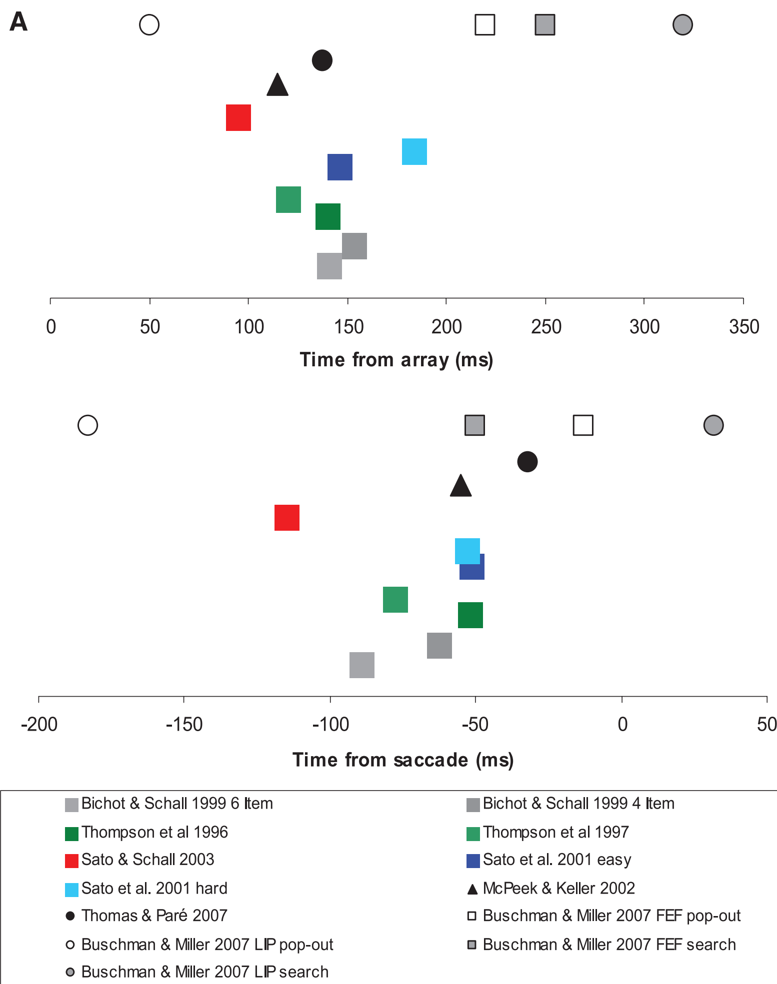

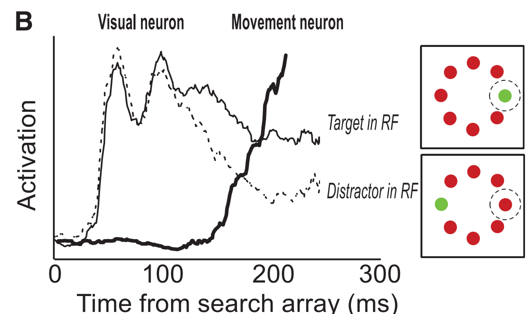

Fig. 1. (**A**) Comparison of average time of target selection across indicated data sets within indicated studies. The values reported in (*1*) do not correspond to the values reported in previous studies. (**B**) Two major types of neurons in the FEF. Visual selection neuron (thin) responds briskly but initially not selectively to stimuli in the receptive field. After >100 ms the activity is higher when the target (solid) as opposed to distractor (dotted) is in the receptive field. Saccade-related neuron (thick) has no visual response but begins to discharge after the target is selected. Saccades are initiated when the activity of these neurons reaches a threshold after a stochastic rate of growth.

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namely the FEF (*2*–*7*), LPFC (*8*), and LIP (*9*, *10*) [also see (*11*)] and superior colliculus (SC) (*12*) (Fig. 1A). Besides differing substantially from previous measurements, the time values reported by Buschman and Miller are curious in three other respects.

First, the very short delay needed by several LIP neurons to locate the target corresponds to the average visual response latency for this cortical area (*9*). All previous studies found that visually evoked responses in the FEF, LIP, and SC produce an initial indiscriminate volley of activity followed by modulation manifesting target localization. The only exception to this pattern is when FEF neurons undergo plastic changes to become selective for one visual feature after monkeys are trained exclusively on targets of that feature (*13*). There is, however, no evidence that the monkeys in (*1*) received similar training and no apparent reason why only LIP neurons should have such unusual responses.

Second, the analyses of (*1*) curiously included about two-thirds of the LIP and FEF neurons that located the target after the saccade had been produced and clearly could not contribute to guiding the saccade. Furthermore, the fact that in the more difficult search trials so few of the FEF (32%) and LIP (14%) neurons located the target before the saccade stands in stark contrast with previous results obtained in the FEF and LIP during difficult search tasks (*4*, *5*, *10*). These discrepancies between the spike data and previous work suggest that either very different neuronal samples or suboptimal modulation of neurons were measured in (*1*).

Third, contrary to what (*1*) suggests, the differences between the neural latency to find the target during pop-out ("between 50 and 100 ms after array onset") and search ("approximately 250 ms after array onset") does not correspond to the difference in reaction time for the two conditions: 233 versus 272 ms. These discrepancies between the time values of unit modulation and previous work also raise concerns about the informativeness of the field potential analyses in (*1*).

The discrepancies between (*1*) and previous reports are due to several important methodological issues. First, whereas previous studies sampled neurons one at a time, Buschman and Miller report data from many neurons sampled simultaneously. However, the analysis of target selection timing actually did not compare the signals produced by groups of neurons recorded within and across data sessions. A mutual information statistic was used to measure when the ensemble of neurons located the target in the search display. In contrast, all previous work compared directly the discharge rates when the target versus a distractor fell in the responsive center of the receptive field. If these two analysis techniques are measuring the same neural event, then the resulting measurements should be shown to coincide or large differences in timing results must be reconciled. This was not done in (*1*). Second, neurons in the FEF and LIP, and to some extent the LPFC, have bounded receptive fields with zones of peak sensitivity. Responses to stimuli presented near the border of receptive fields are weaker and more variable. While recording simultaneously from multiple neurons with bounded receptive fields, Buschman and Miller did not position stimuli in the sensitive zone of each receptive field but instead placed stimuli at constant locations. No maps of receptive fields were presented for evaluation. Thus, the responses of some unknown fraction of neurons reported in (*1*) may have been suboptimal, thus making the measurement of modulation times unreliable. Third, cortical areas like the FEF, LIP, and LPFC contain qualitatively different types of neurons. In particular, some neurons select targets, some control gaze (Fig. 1B), and others discharge only after saccades or exhibit no clear modulation at all (*14*, *15*). The absence of data showing the characteristics of the neurons sampled in (*1*) raises the possibility that many were not modulated at all, thereby calling into question the reliability of the time values reported and making it impossible to relate the new findings to previous work.

In conclusion, recording from many neurons simultaneously is certainly a powerful approach that can yield new insights into neural coding, but the findings reported in (*1*) exemplify the challenges inherent in this approach. The failure to distinguish functional neuron types or to optimize conditions for each neuron isolates this paper from a rapidly advancing literature.

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