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# Response to Comment on “Top-Down Versus Bottom-Up Control of Attention in the Prefrontal and Posterior Parietal Cortices”

Earl K. Miller\* and Timothy J. Buschman

We reported latencies for target selection based on the earliest neurons to show effects, which Schall *et al.* mistakenly compare to latencies based on population averages. We show that there are actually no discrepancies across studies and also discuss the relative merits of single-electrode versus multiple-electrode approaches.

We believe that Schall *et al.* (1) have misread our study (2). They compare our latency values to other studies' population averages. Instead, we reported when the first neurons first selected the target (the earlier leading edge of selectivity), not averages, so we could capture information flow between areas. The criticism that our lateral intraparietal area (LIP) target selection timing was too early is therefore unfounded. Our measurements reflect when our first LIP neurons first selected the target. Their average was later and consistent with previous work (see Fig. 1, top).

The figure presented by Schall *et al.* (1) is meant to illustrate that our results are inconsistent with multiple laboratories, but seven of the nine cited studies are from Schall's own laboratory. The revised version shown here (Fig. 1) uses the correct population average latencies from our study and indicates that our results actually align with previous work. Our target selection in LIP is earlier than in frontal cortex, consistent with a report of early target selection in LIP starting at 86 ms (in average population activity) (3), not at 130 to 140 ms as Schall *et al.* report. Their figure contains other apparent errors as well. They plotted the population latency from one study (4) at 120 ms post-array, but this is apparently the latency of their example neuron [see figure 2 in (4)]; the population latency was actually 134 ms. Furthermore, Schall *et al.* plotted our FEF target selection at 10 ms before the saccade, but we did not report this nor do the authors explain how they derived it. Figure 1 shows the correct value. The authors also appear to have plotted values that do not appear in the cited papers and thus cannot be directly verified.

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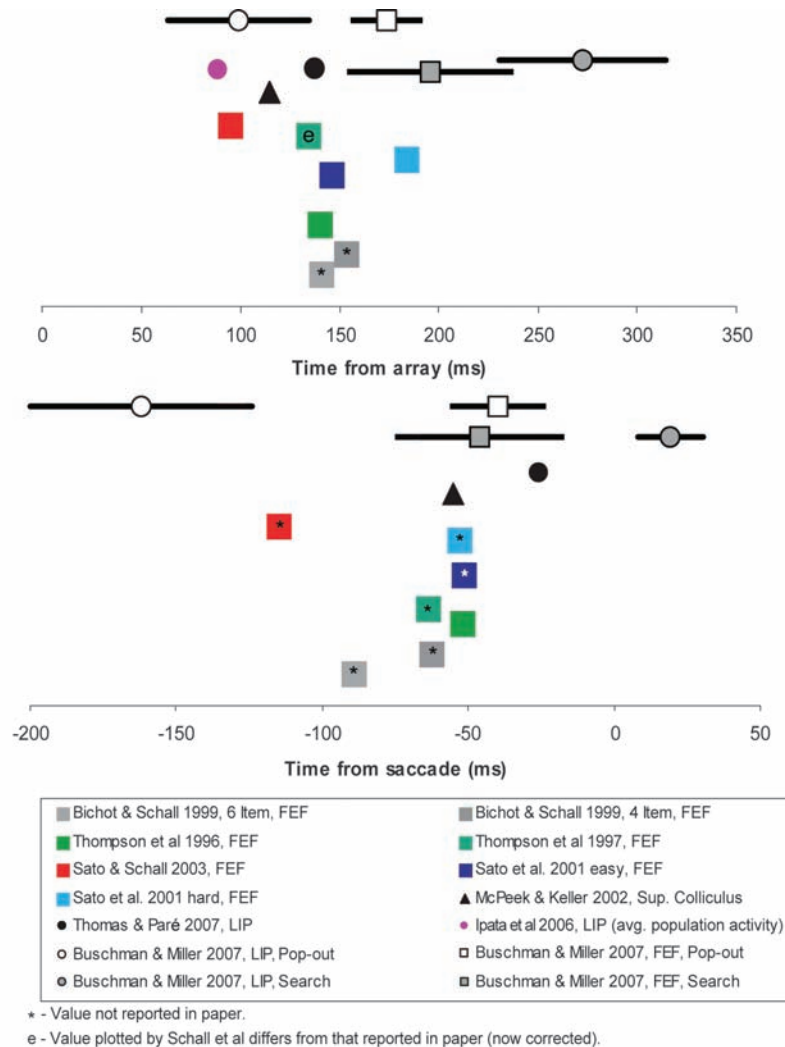
Schall *et al.* claim that our LIP target selection at 50 ms does not allow time for an initial “indiscriminate volley of activity” before target selection because 50 ms is also the average LIP activation latency. This is incorrect. Typically, half of a population shows a lower value than the average. Thus, a 50-ms average activation latency means that half of LIP neurons were activated before our first LIP neurons selected the target at 50 ms. So, our results are actually compatible with an initial indiscriminate activity volley. Their concern about including in the analyses neurons that found the target after the saccade is unfounded. If we had included these postsaccadic neurons in a population average latency, it would have skewed the results. However, our mutual information statistic was applied to individual neurons, not neural ensembles as stated in (1), and we reported when target selection reached significance in the earliest selective neurons, not the population average. Thus, postsaccadic neurons had no impact on our results. In any case, concern about different latencies across studies is surprising considering the different paradigms. Other studies used larger search arrays, mostly free-viewing (we used fixed gaze) and (notably) single tasks, whereas our monkeys switched between two. Any of this could account for differences in absolute timing. Further, there is little reason to expect that determining latency by an “arbitrary criterion” (5) should yield the same values as mutual information analysis (2). Thus, the critical question in our study was the relative, not absolute, latencies between areas and tasks studied with the same experimental paradigm and analyses.

We fail to understand the concern that our neural latencies for target selection do not exactly correspond to the monkeys' reaction time. The PFC and LIP are not the only brain areas involved in target selection and eye movements, so there is no reason to expect an exact correspondence.

With multiple electrodes, one cannot simultaneously optimize stimuli for every neuron. Schall *et al.* (1) suggest that because stimuli were not in each neuron's “sensitive zone,” activity levels were submaximal and measurements were unreliable. However, there is nothing inherently unreliable in submaximal activity. Statistics test reliability, and ours were significant. Further, the same stimuli were in the same locations across both tasks, so stimulus placement cannot explain our finding latency differences across areas and tasks. More generally, we disagree that neurons should be studied only under “optimal” stimulation. This traditional approach has yielded insights into single neurons but does not reflect how the brain normally operates. A typical visual scene activates many neurons, only a fraction within their most sensitive zone. Thus, sampling neurons operating under more realistic conditions may be better for comparisons of functions across brain areas. Further, optimizing stimuli for each neuron precludes multiple-electrode approaches. It would limit comparisons across brain areas to individual neurons studied under different levels of experience, in different animals, etc., introducing confounding factors that could obscure real differences and/or produce spurious ones. Multiple-electrode recording minimizes such factors and thus is needed to compare different brain areas, especially the precise timing of activity that can provide clues into how they interact. Curiously, Schall has previously advocated this approach, stating that “[T]o understand whether target selection is localized temporally and anatomically, it is necessary to collect data across multiple brain areas simultaneously” (6). This is what we have done.

Recognizing methodological differences could further alleviate Schall *et al.*'s concern about large proportions of postsaccadic neurons. Neurons are sampled differently in single-versus multiple-electrode studies. With a single electrode, the investigator typically hunts for activated neurons. An interest in activity before the saccade, for example, might even unconsciously bias sampling toward that property. There was no preselection of neurons with our multiple electrodes. We may have found a large number of postsaccadic neurons in an unbiased screen because that is what is there.

Finally, we agree that new findings must be reconciled with old. It is also important to pay careful attention to details, recognize that different approaches can yield different results, and be open to new methods that can lead to advances. Newer multiple-electrode techniques limit sampling bias and allow unconfounded comparisons and precise timing relationships across neurons operating under more realistic, often nonoptimal, conditions. This does not isolate their results from previous work and single-electrode techniques; it complements them.



**Fig. 1.** Reproduction of figure 1 in (1). Contrary to (1), we reported earliest neurons, not average latencies, and here plot our actual averages. Other erroneous values have also been corrected (see text). Horizontal bars indicate 95% confidence intervals (CIs) of our values. Schall *et al.* were concerned that our LIP pop-out target selection was too early after array onset (top, white circle) and our FEF target selection before the saccade was too late (bottom, white/gray squares), but our averages actually align with previous work. Ours was the only study of LIP target selection during search (gray circles), and the only other study of LIP presaccadic target selection (bottom) during pop-out used their own arbitrary latency criterion, whereas we (white circle, bottom) used mutual information analysis, so there is no relevant comparison to our values.

References

1. J. D. Schall, M. Paré, G. F. Woodman, *Science* **318**, 44 (2007); [www.sciencemag.org/cgi/content/full/318/5847/44b](http://www.sciencemag.org/cgi/content/full/318/5847/44b).
2. T. J. Buschman, E. K. Miller, *Science* **315**, 1860 (2007).
3. A. E. Ipata, A. L. Gee, M. E. Goldberg, J. W. Bisley, *J. Neurosci.* **26**, 3656 (2006).
4. K. G. Thompson, N. P. Bichot, J. D. Schall, *J. Neurophysiol.* **77**, 1046 (1997).
5. N. W. D. Thomas, M. Paré, *J. Neurophysiol.* **97**, 942 (2007).
6. T. Sato, A. Murthy, K. G. Thompson, J. D. Schall, *Neuron* **30**, 583 (2001).

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