Letter to the Editor

Reply to Balan and Gottlieb

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REPLY: Several important questions are raised in the recent comparison by Balan and Gottlieb (2009) between the description by Balan et al. (2008) of lateral intraparietal (LIP) neuron activity in monkeys performing visual search with manual responses and our recent report of frontal eye field (FEF) neuron activity in monkeys performing visual search with saccade responses (Cohen et al. 2009). Both studies manipulated the number of distractors in the search display. Balan et al. 2008 reported decreased firing rate with increasing set size, but they reported no delay in the time at which activity for the target exceeded activity for the distractors, referred to as *target selection time*. Cohen and colleagues (2009) also reported decreased firing rate with increasing set size, but also observed delayed target selection time with increasing set size. How should we interpret the different observations across laboratories, effectors, cortical areas, and task designs? First, we emphasize that this is not a case of one observation being correct and the other incorrect. The results of both studies are valid within their respective contexts. However, the question remains: which difference between studies explains the different outcomes? We argue that task demands are the major factors. In other words, measured under the same task demands, we predict that the same pattern of results would be obtained across effector (manual response vs. saccade) and cortical area (LIP vs. FEF).

The first step of the argument is to appreciate that categorical statements about the relationship between target selection time and response time are not possible because these times vary for at least three reasons. First, *neuron type matters*. Multiple studies have found that the timing relationship between target selection time and response time varies across neurons that can be distinguished by other properties (e.g., McPeek and Keller 2002; Sato and Schall 2003). Second, *the visual properties of the stimuli matter*. If the target is easy to locate among nontarget items, then target selection occurs earlier with less variability in time; however, if the target is difficult to locate among nontarget items, then target selection occurs later with more variability in time (Sato et al. 2001). Third, *task demands matter*. Studies with an easy, pop-out color search, requiring monkeys to produce one accurate saccade to the target to earn reward, have found that for many neurons target selection time does not account for much of the variability of saccade response time (e.g., McPeek and Keller 2002; Sato et al. 2001; Thompson et al. 1996). The variation in response time arises from the delay introduced by time taken by presaccadic movement neurons to trigger the saccade (Hanes and Schall 1996; Woodman et al. 2008). In contrast, studies with an easy, pop-out color search, allowing monkeys to produce multiple saccades to ultimately fixate the target, have found that target

selection time accounts for more of the variability of saccade response time (Ipata et al. 2006; Thomas and Paré 2007). In their response, Balan and Gottlieb cite the study of Bichot and Schall (2002) as evidence that the target selection time of FEF neurons responding to color or shape pop-out stimuli increases with response time. However, this relationship was the result of the stimulus feature repetition priming that was the object of the study—this just amplifies our conclusion that the relationship between target selection time and response time is not fixed, but instead depends strongly on trial history and task demands.

The second step of the argument is to appreciate that the differences between the studies are more subtle than they may appear. For instance, both studies found significant variation of firing rate with set size. We believe that Balan et al. (2008) and Cohen et al. (2009) observed decreased peak firing rate with increasing set size, attributed simply to the number of stimuli appearing due to suppression from the surrounds of receptive fields (Schall et al. 2004). Importantly, Balan et al. (2008) observed that firing rates of LIP neurons were higher for set sizes two than four and four than six, even before the search array was presented. This was due to the nature of their task, in which two, four, or six stimuli were presented on the screen before they changed shape to become targets and distractors. An experiment to resolve this issue is a simple extension of the tasks, to include catch trials in which there is no target. In this case, the target-selecting neurons will not select the target (because it is absent) and there will be no response time because the appropriate response would be to maintain gaze at the center of the display. We predict that FEF and LIP neurons would still display reduced firing rate with increased set size. Whatever the result, though, a mechanistic link between the time of modulation of visually responsive neurons to select the target and the response preparation process is not hard to conceptualize and even operationalize (Purcell et al. 2009). Such a link between discharge rate and time of response preparation is less clear, especially given earlier observations that the firing rate also varies with saccade production (Goldberg and Bushnell 1981; Robinson et al. 1978; Thompson et al. 1997) and target–distractor similarity (Sato et al. 2001).

Balan and Gottlieb (2009) stated that Cohen et al. (2009) did not report a positive correlation between target selection time and response time. In fact, the main finding of our study was that target selection time increases with set size, which follows increased response time with increased set size (see Fig. 4 and Table 1 in Cohen et al. 2009); for set size eight, across monkeys, this correlation was 0.54. To be sure, target selection time in FEF does not account for all the variance in response time. As noted earlier, the activity of the movement neurons necessary to produce the saccade (or the manual movement) introduces additional systematic (Woodman et al. 2008) and random (Hanes and Schall 1996) delays of response time. Thus

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it is necessary to appreciate the contributions of successive stages of processing to the mean and variance of response time (Sternberg 2001).

In addition, Balan and Gottlieb (2009) now report a correlation between target selection time and response time measured within each set size. This agrees with findings reported by Cohen et al. (2009). The major difference in observation between the two studies is that, whereas Balan et al. (2008) reported a consistent increase in response time but not in target selection time of LIP neurons when compared across set sizes, Cohen et al. (2009) found a significant increase in both response time and target selection time of FEF neurons. It should be noted that a significant variation of target selection time and response time with set size was found earlier in a study of FEF using color–shape conjunction search displays (Bichot and Schall 1999). Given the functional similarity of visually responsive neurons in LIP and FEF, we believe the most parsimonious explanation of this particular difference between the reports is due to task-demand differences such as the following.

First, Balan et al. (2008) presented monkeys with the same two targets during each recording session. In humans, this has the effect of making visual search automatic and decreases the strength of set-size effects (Schneider and Shiffrin 1977). This consistent target mapping means that the absence of a selection time difference in LIP across set sizes could have been due to attention automatically selecting the targets among the distractor objects that never had any behavioral relevance. In monkeys, this causes FEF neurons to develop feature selectivity for simple colored targets (Bichot et al. 1996). To avoid this confound, Cohen et al. (2009) used a different target (among eight possibilities) for each successive recording session. Second, Balan et al. (2008) presented monkeys with different set sizes in blocks of trials in each session. This approach can complicate the interpretation for at least two reasons. First, many studies find that response times become shorter during a block of set size two versus four or six that can lead to less accurate performance when exposed to larger set size (see Fig. 2 in Balan et al. 2008). Second, by sampling different set sizes across blocks of trials, variation in the state of the monkey such as reward satiation, fatigue, or attentiveness can create incidental variation of response time that is unrelated to variation of target selection time. Such variability in performance was evident in the fact that Balan et al. (2008) observed an increase in response time with set size in about 70% of experimental sessions. In contrast, Cohen et al. (2009) presented different set sizes in randomly interleaved trials and observed a significant variation of response time with set size and relatively low and constant error rates in 100% of sessions. We wonder whether a correlation between target selection time and response time across set sizes exists for the subset of 70% of sessions that showed a significant behavioral effect in Balan et al. (2008).

In summary, Balan et al. (2008) and Cohen et al. (2009) both represent valuable contributions to the literature on visual search, attention, and decision making, and the issues raised in this exchange highlight the need for a disciplined approach to experimental design across laboratories so that reliable interpretations across studies can be obtained. For example, the basic differences between the two studies can be resolved by collecting data from FEF, LIP, and related structures during visual search tasks that manipulate the presence of catch trials, the contingency of reward on single versus multiple saccades to the target, and interleaved versus blocked exposure to different trial types. Neuroscience cannot progress unless empirical bridges connect the islands of knowledge obtained in different laboratories.

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