Journal Club

Editor's Note: These short, critical reviews of recent papers in the *Journal*, written exclusively by graduate students or postdoctoral fellows, are intended to summarize the important findings of the paper and provide additional insight and commentary. For more information on the format and purpose of the Journal Club, please see http://www.jneurosci.org/misc/ifa_features.shtml.

Probing Perceptual Performance after Microsaccades

Xiaoguang Tian[1,2] and **Chih-Yang Chen**[1,2]

[1]Graduate School of Neural and Behavioural Sciences, International Max Planck Research School, Tuebingen, 72074 Germany, and [2]Werner Reichardt Centre for Integrative Neuroscience, Tuebingen, 72076 Germany

Review of Yuval-Greenberg et al.

Microsaccades are small saccadic eye movements that occur during gaze fixation. Although these eye movements have been known to exist for a long time (Barlow, 1952), their possible roles have remained elusive. In more recent years, it has become recognized that these microscopic eye movements have similar kinematics to larger saccades that we normally generate when scanning our visual environment (Zuber et al., 1965). They are also generated by the same brainstem neural circuitry that generate larger saccades (Van Gisbergen et al., 1981; Hafed et al., 2009; Van Horn and Cullen, 2012).

Out of such brainstem circuitry, involvement of the superior colliculus (SC) in microsaccade generation is important because it provides insight into these movements' possible functional roles. For example, the SC plays an important role not only in eye movement generation, but also in cognitive processes related to selective visual attention (Lovejoy and Krauzlis, 2010). Thus, involvement of the SC in microsaccade generation (Hafed et al., 2009) suggests that microsaccades may

likewise be related to perception and cognition. Indeed, previous work has shown that microsaccades could be a readout of covert visual attention (Hafed and Clark, 2002; Engbert and Kliegl, 2003). Microsaccades were shown in these and other studies to be strongly modulated by attentional cues: microsaccade rate first decreases at ~100–150 ms after cue onset and then rebounds before returning to baseline. Microsaccade direction is also influenced by cue location, and in a manner that is correlated with changes in attentional performance: immediately after cue onset, microsaccades tend to be in the same direction of the cue; shortly afterward, they shift away from the cue. Even though neurophysiological investigations of the links between microsaccades and covert visual attention have begun to appear (Hafed et al., 2013), such links (and their neural mechanisms) still warrant investigation.

In a recent publication in *The Journal of Neuroscience*, Yuval-Greenberg et al. (2014) have made steps to further clarify such a relationship. These authors' starting point was appealing: most studies of the relationship between microsaccades and attention investigate cue-triggered microsaccades, whereas microsaccades can also occur seemingly spontaneously during fixation even without a specific task. The authors therefore designed an experiment in which subjects simply fixated and only generated so-called spontaneous microsaccades that were not evoked by cues. The authors' question was whether spatial attentional state was

correlated with the direction of such spontaneous microsaccades.

In their study, Yuval-Greenberg et al. (2014) detected microsaccades in real time. Immediately after a microsaccade was detected, eight peripheral grating patches were presented for 100 ms, and they were placed equidistant from either the fixation cross (Experiment 1) or from the instantaneous eye position at stimulus onset (Experiment 2). When the gratings disappeared, a central arrow pointing away from the fixation spot was presented, and the arrow either pointed to the grating closest to the detected microsaccade direction (congruent) or the diametrically opposite direction (incongruent). Subjects had to discriminate the orientation of the grating pointed to by the arrow, independent of all other gratings. Grating orientation was slightly rightward or leftward of pure vertical, and the task was made challenging enough that subjects' perceptual performance was near threshold. The experimental question was, then, whether perceptual performance was different if the grating appeared in the same (congruent) direction or opposite (incongruent) direction relative to a microsaccade. Yuval-Greenberg et al. (2014) found that performance was better for congruent targets than for incongruent ones. In Experiment 1, performance was 72.6% on incongruent trials and 75.1% on congruent trials (a difference of 2.5%), and the results were similar in Experiment 2 (66.96% vs 71.07%; a difference of 4.11%). Yuval-Greenberg et al. (2014) thus concluded that attention was allo-

cated at the congruent targets when a microsaccade toward their direction had just occurred.

Exploring spontaneous microsaccades is particularly useful because it allows us to increase our understanding of mechanisms that are specific to microsaccades and independent of other potential sources. For example, consider a simple countermanding task; subjects prepare a large saccade, and then a subsequent "stop cue" instructs them to cancel this saccade. Theoretically, it could be the case that cue onsets in covert attention tasks elicit a large saccade plan, which is somehow canceled because of the requirement to fixate. Such cancelation might result in generating a smaller, miniature eye movement on the scale of microsaccades. Because of this possibility, exploring microsaccade-related changes in perceptual performance, independent of prior cueing, is indeed important (Hafed, 2013). However, although we share the excitement for the approach of Yuval-Greenberg et al. (2014), we would like to raise some important points that we feel should not be overlooked when interpreting their results, especially in light of the previous literature.

Our first point is related to the question of what happens to perception after microsaccades, which is the time at which Yuval-Greenberg et al. (2014) probed attentional state. Saccadic suppression of perception is a powerful phenomenon, which is believed to be an important mechanism contributing to the maintenance of visual stability across saccades. This phenomenon is characterized by a substantial drop in perceptual performance as well as neuronal sensitivity around the time of saccades. Moreover, this phenomenon is also known to happen for microsaccades, both at the behavioral (Zuber and Stark, 1966) and neuronal (Hafed and Krauzlis, 2010) levels. Importantly, the suppression lasts for ~100 ms after saccade/microsaccade end. Thus, when Yuval-Greenberg et al. (2014) probed attentional state, they were, in reality, very likely measuring a much worse performance level than in baseline without any microsaccades. Unfortunately, Yuval-Greenberg et al. (2014) did not characterize baseline performance without microsaccades. They did indeed collect and analyze no-microsaccade trials. However, their analysis of these trials was not sufficient to reveal the strong impacts of microsaccadic suppression. In their analysis, they only compared congruent to incongruent locations in the no-microsaccade trials. This analysis expectedly revealed similar performance between congruent and incongruent locations on no-microsaccade trials. However, we predict that if the authors had additionally compared no-microsaccade to microsaccade trials, then they would have found that performance in the microsaccade trials was significantly worse than in the no-microsaccade trials, even for congruent microsaccades. In other words, they would have observed an attentional decrease immediately after microsaccades rather than an attentional allocation. Thus, we argue that Yuval-Greenberg et al. (2014) did not necessarily reveal an attentional shift in the direction of a recently completed microsaccade; instead, they measured a period in which perception would be strongly suppressed rather than improved, and their congruent/incongruent results suggest that the suppression was slightly weaker on congruent than incongruent trials.

An improvement in attentional performance relative to a no-microsaccade baseline has indeed recently been observed, but it happened immediately before rather than immediately after microsaccades (Hafed, 2013). This premovement observation seems to be in line with the classic "premotor theory of attention," which posits that neural circuitry for covert and overt orienting are shared (Sheliga et al., 1994). In fact, even though the task of Hafed (2013) was different from that in Yuval-Greenberg et al.'s (2014) study, the improvement in attentional performance observed in that earlier study (from ~70% for no-microsaccade baseline to ~85% if a target was presented before a congruent microsaccade) was dramatic compared with the effects of Yuval-Greenberg et al. (2014). In their paper, Yuval-Greenberg et al. (2014) clarified that, based on their experimental design, it was impossible to look at visual performance before a microsaccade. However, we think that they could still have performed pre-microsaccadic analyses if they had abandoned the online microsaccade detection approach for these analyses. They could have collected normal trials and then performed *post hoc* analyses to select trials in which the gratings appeared right before, rather than right after, a microsaccade. There would have been no need to redesign the fundamental property of their original experiment, which was to present gratings and ask how subjects perceived them around microsaccades. In fact, data for this analysis may already be available from the no-microsaccade trials described in their manuscript. Thus, we feel that the conclusions of the study can be more strongly supported if comparisons to baseline no-microsaccade performance levels and comparisons to pre-microsaccadic performance levels had been made.

Another point that we would like to raise concerns the use of the label "spontaneous" to describe some microsaccades. Given the similarity of microsaccades to larger saccades at the behavioral and neurophysiological levels, we are somewhat uncertain about why some movements need to be labeled as "spontaneous" and others not. Yuval-Greenberg et al. (2014) used this label to describe microsaccades occurring during simple fixation of a fixation cross with no other task. However, fixation itself is an active oculomotor task, and the microsaccades they observed are not necessarily "spontaneous," as they may be involved in actively optimizing eye position at the fixation cross.

To summarize, Yuval-Greenberg et al. (2014) designed a task to investigate the possible links between microsaccade directions and covert attention. They investigated the case of microsaccades occurring during steady fixation with no prior cueing, and they concluded that the direction of so-called spontaneous microsaccades is inherently linked to shifts in spatial attention. Although they proposed an appealing starting point, the important controls of comparing to baseline performance without microsaccades (as an absolute performance measure, not a relative one) and of exploring pre-movement epochs are unfortunately missing. These analyses would have added interesting observations and strong support to an amazing idea that tiny, seemingly irrelevant microsaccades can have a substantial impact on perception.

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