Erratum to: Secondary adaptation of memory-guided saccades

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The original html version of this article was missing the last paragraph under the section “Secondary adaptation during memory-guided saccades with delayed feedback.” Below find the missing paragraph.

Within the same framework of motor control theory, we propose that the accuracy of saccades can benefit from two types of teaching signals. One teaching signal is the difference between the primary saccade endpoint and the visual feedback (i.e., visual or retinal error). When feedback is available at the time of the saccade, learning depends on this teaching signal. When feedback is delayed, its temporal mismatch with the forthcoming primary saccade command weakens this learning process. In the context of adaptation during the MGSA task with delayed feedback, we observed a second, compensatory learning mechanism that must rely on another teaching signal. What might be the nature of this other teaching signal? First, we propose that it minimally involves a stored or maintained representation of the visual error. Second, this working memory representation, however, is likely to be distinct

from the working memory representation of the position of the past visual cue. Third, since the majority of the learning took the form of secondary corrections to the primary memory-guided saccade, learning did not primarily result from an adjustment in the gain of the memory-guided saccade or the stored representation of the cued location. Instead, the representation of visual errors on past trials is primarily used for planning the small corrections made after the saccade is generated toward the memorized location. The first of these secondary corrections were generated at long latencies after the primary saccade (i.e., ~300 ms) and fall in the range of volitional or internally guided saccades (Deubel 1995; Hopp and Fuchs 2004). It is unlikely that they were preprogrammed in conjunction with the primary saccade since corrective saccades that are preprogrammed have latencies as short as 100 ms (Becker 1989). Subjects reported becoming aware that their performance worsened during the adaptation block, but importantly ascribed it to their fallible memory. Moreover, they reported using strategies to improve their performance and although self-reported strategies may not be reliable descriptors of actual behavior, they do indicate that, at the very minimum, subjects made an effort to compensate for their errors. These factors suggest that the secondary corrections may be voluntary and perhaps even strategic in nature where subjects become aware of their systematic errors and attempt to remedy them. However, we also found that the secondary saccades adapted gradually toward the back-stepped target and then adapted gradually toward the original target in the postadapt phase at rates comparable to those during visually guided saccade adaptation. While these gradual adaptation and de-adaptation rates may be due to learning in a noisy environment such as those present in memory-guided saccade tasks, they may also reflect a learning mechanism similar in nature to

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visually guided saccade adaptation. Therefore, while more study is required to conclusively establish whether the secondary teaching signal is strategic in nature, our data establishes that two mechanisms are occurring in parallel to control saccade metrics and maintain accuracy during our memory-guided saccade task. One mechanism utilizes information about the original target location to generate primary saccades, while the other accesses predictive information about the back-stepped target location to generate secondary saccades. We can only speculate about the neural circuitry underlying this secondary teaching signal, but the frontal eye field (FEF), the posterior parietal

cortex (PPC), and dorsolateral prefrontal cortex (DLPFC) are good candidate sites (Murthy et al. 2007; Curtis 2006). Extensive research has shown that FEF and the PPC are crucial for the generation of memory-guided saccades and the DLPFC is engaged in a wide variety of control- and decision-based tasks, including spatial and mnemonic memory tasks (Curtis 2006; Curtis and D'Esposito 2004). Moreover, if lesioned, the FEF/PPC and DLPFC are known to cause systematic and variable errors, respectively, in memory-guided saccades (Dias and Segraves 1999; Li et al. 1999; Ploner et al. 1999).