

Source localization of EEG signals generated during sequence learning and expectation monitoring



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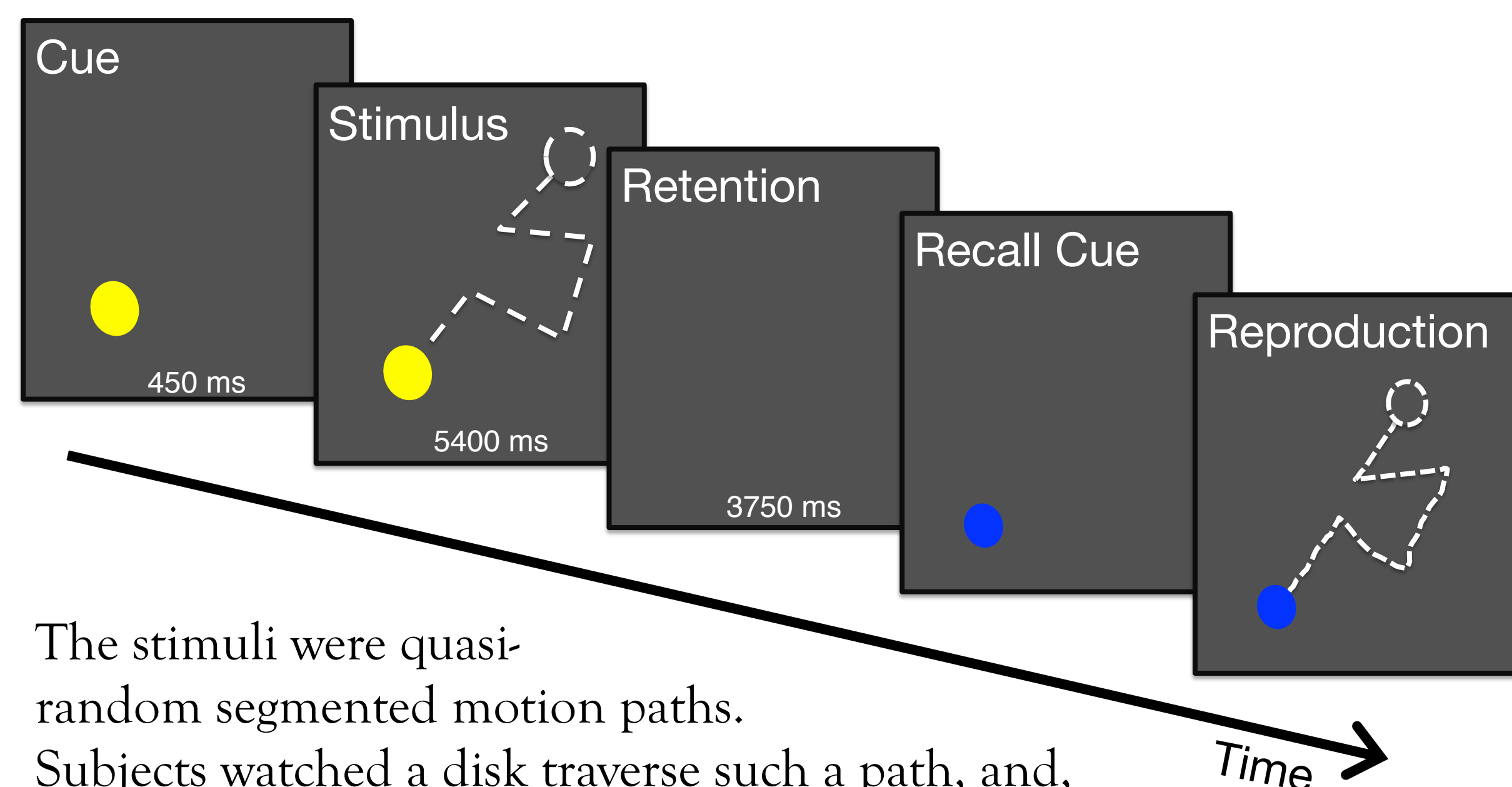


Is anticipation an important part of sequence learning?

Learning about sequential structure is a prerequisite of cognitive abilities such as multi-step motor skills, navigation, and troubleshooting. To perform these tasks, people must use their sequence knowledge to make predictions.

Although sequence learning has been extensively studied, the precise role of expectation in observing and reproducing sequences is not yet well-defined. In order to characterize the relationship between expectation and sequence learning, we asked participants to observe and reproduce novel motion sequences. We measured how eye movements (Experiment 1; Maryott et al., 2011) and neural activity (Experiment 2) change over the course of learning. We also assessed the response to stimuli that deviate from a well-learned sequence.

Experimental task



The stimuli were quasi-random segmented motion paths. Subjects watched a disk traverse such a path, and, after a short retention interval, used a stylus and graphics tablet to reproduce the disk's trajectory from memory.

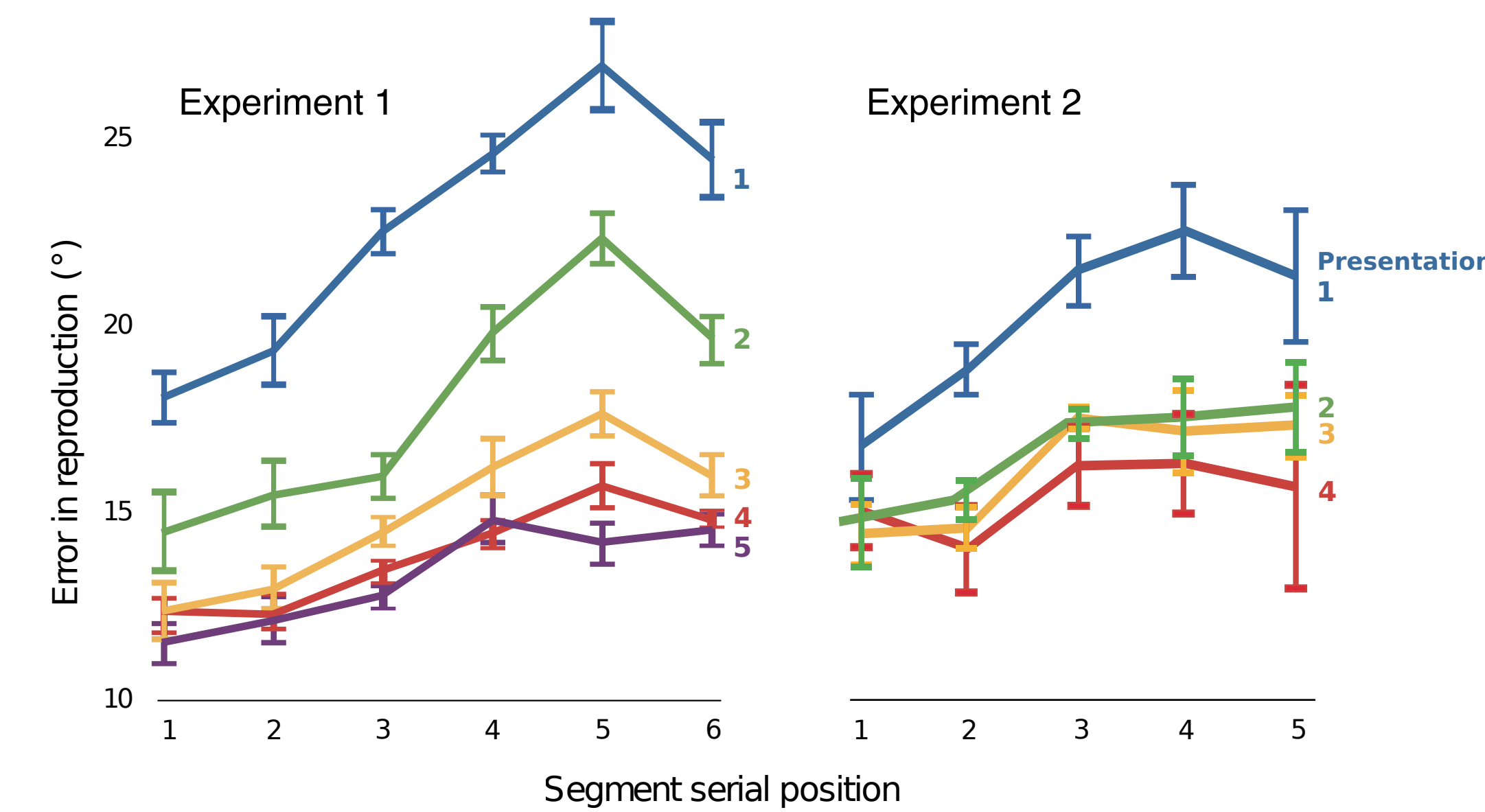
Each trial comprised several presentations of one such path; subjects reproduced the disk's movements after each presentation.

An automated algorithm (Agam et al., 2005) segmented each reproduced trajectory, and recorded the absolute difference in direction between each segment in the original stimulus and its equivalent in the reproduction.

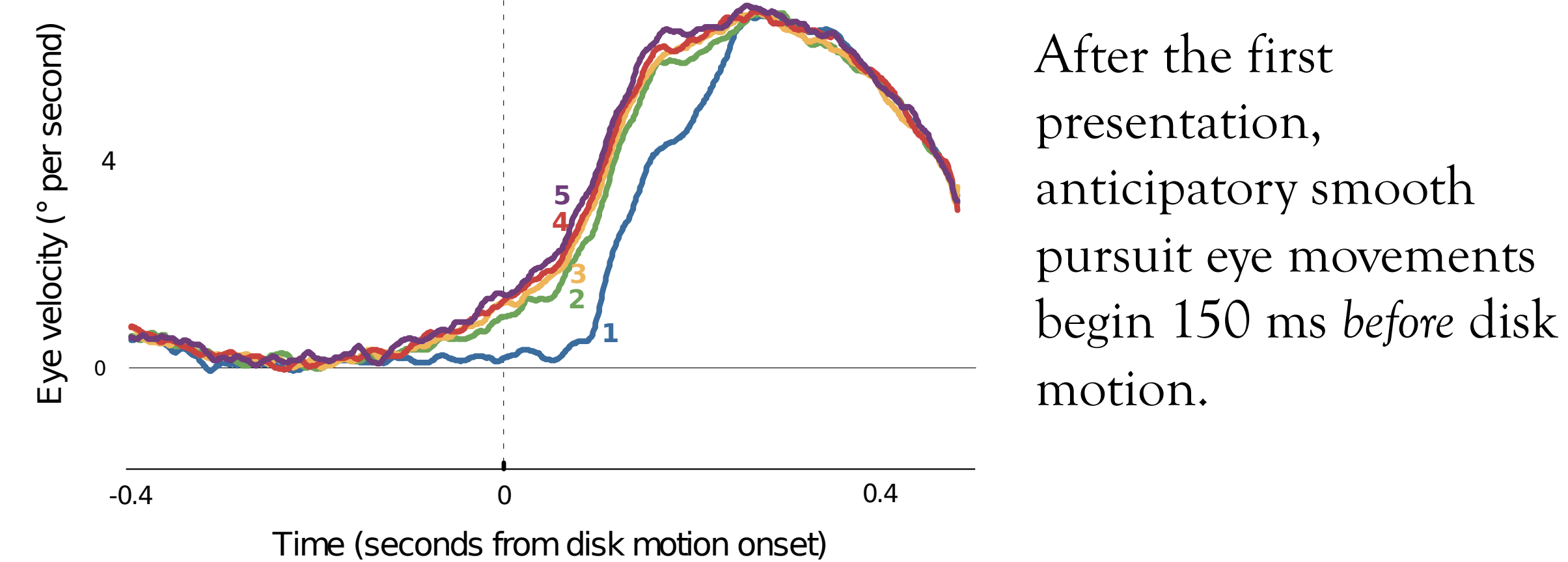
Agam, Y., Bullock, D., & Sekuler, R. (2005). Imitating unfamiliar sequences of connected linear motions. *Journal of Neurophysiology*, 94, 2832-43.
 Maryott, J., Noyce, A., & Sekuler, R. (2011). Eye movements and imitation learning: Intentional disruption of expectation. *Journal of Vision*, 11(1-7).
 Pascual-Marquis, R-D. (2002). Standardized low resolution brain electromagnetic tomography (sLORETA): technical details. *Methods & Findings in Experimental and Clinical Pharmacology*, 24 (suppl D), 5-12.
 Ridderinkhof, K. R., Ullsperger, M., Crone, E. A., & Nieuwenhuis, S. (2004). The role of the medial frontal cortex in cognitive control. *Science*, 306, 443.
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Successful sequence learning

The figure below shows behavioral data from Experiments 1 and 2. Over repeated presentations, overall error decreases and serial position curves flatten.



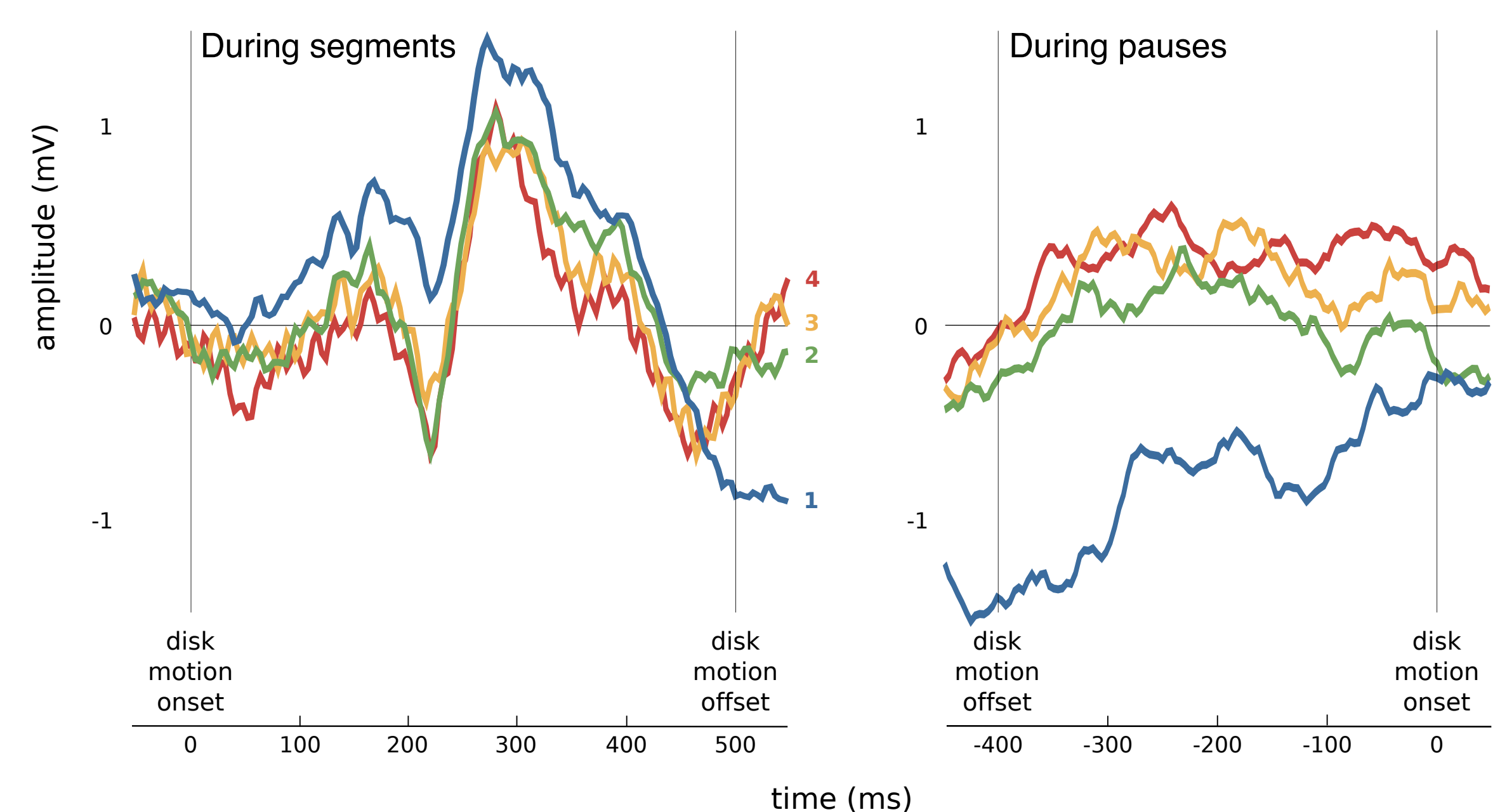
Successful anticipation



After the first presentation, anticipatory smooth pursuit eye movements begin 150 ms before disk motion.

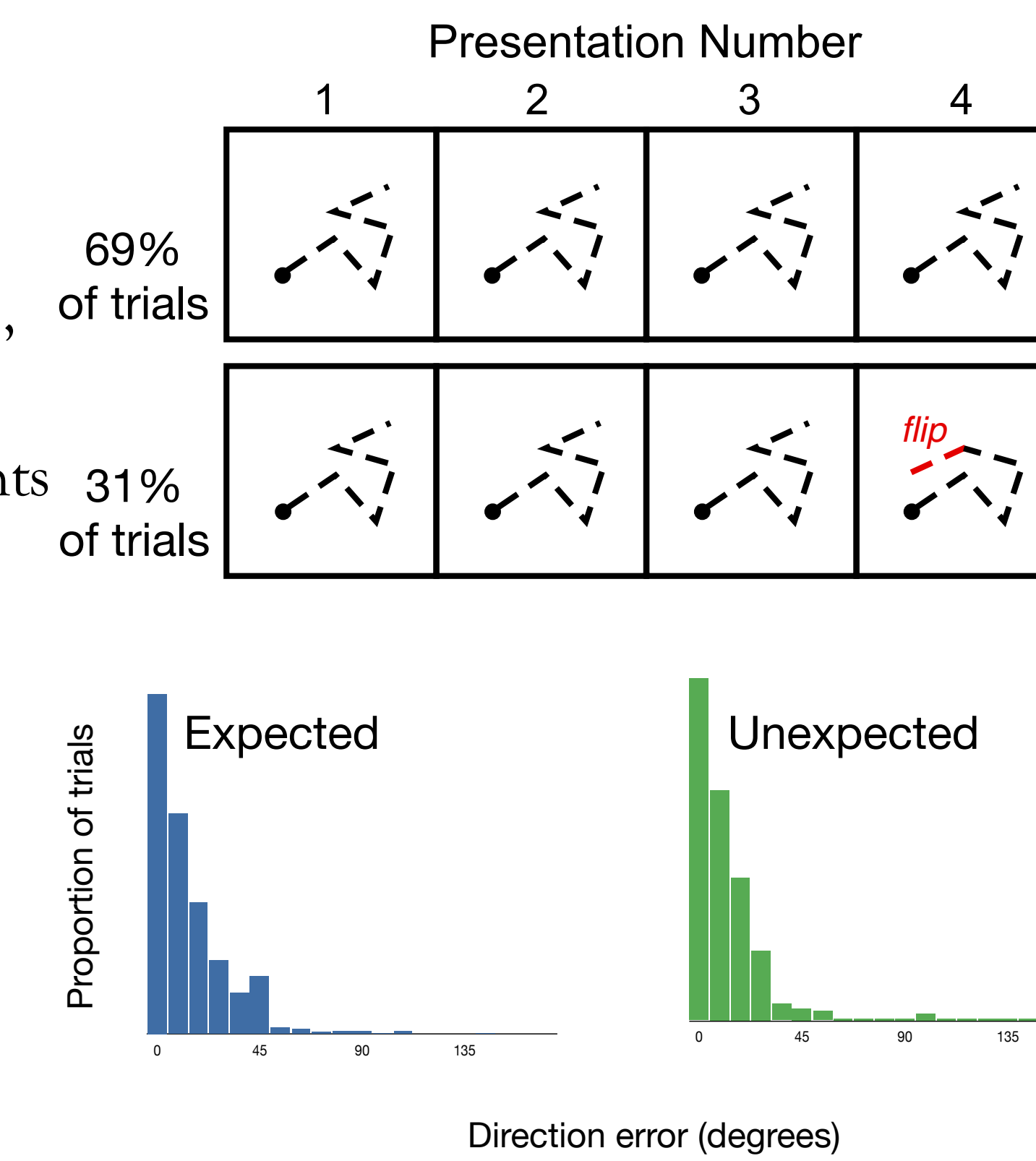
Both behavior and eye movements show a dramatic change from the first presentation to the second, followed by smaller changes across later presentations.

This pattern is also seen in evoked response potentials (ERPs) recorded during each segment, and during the pauses between them.



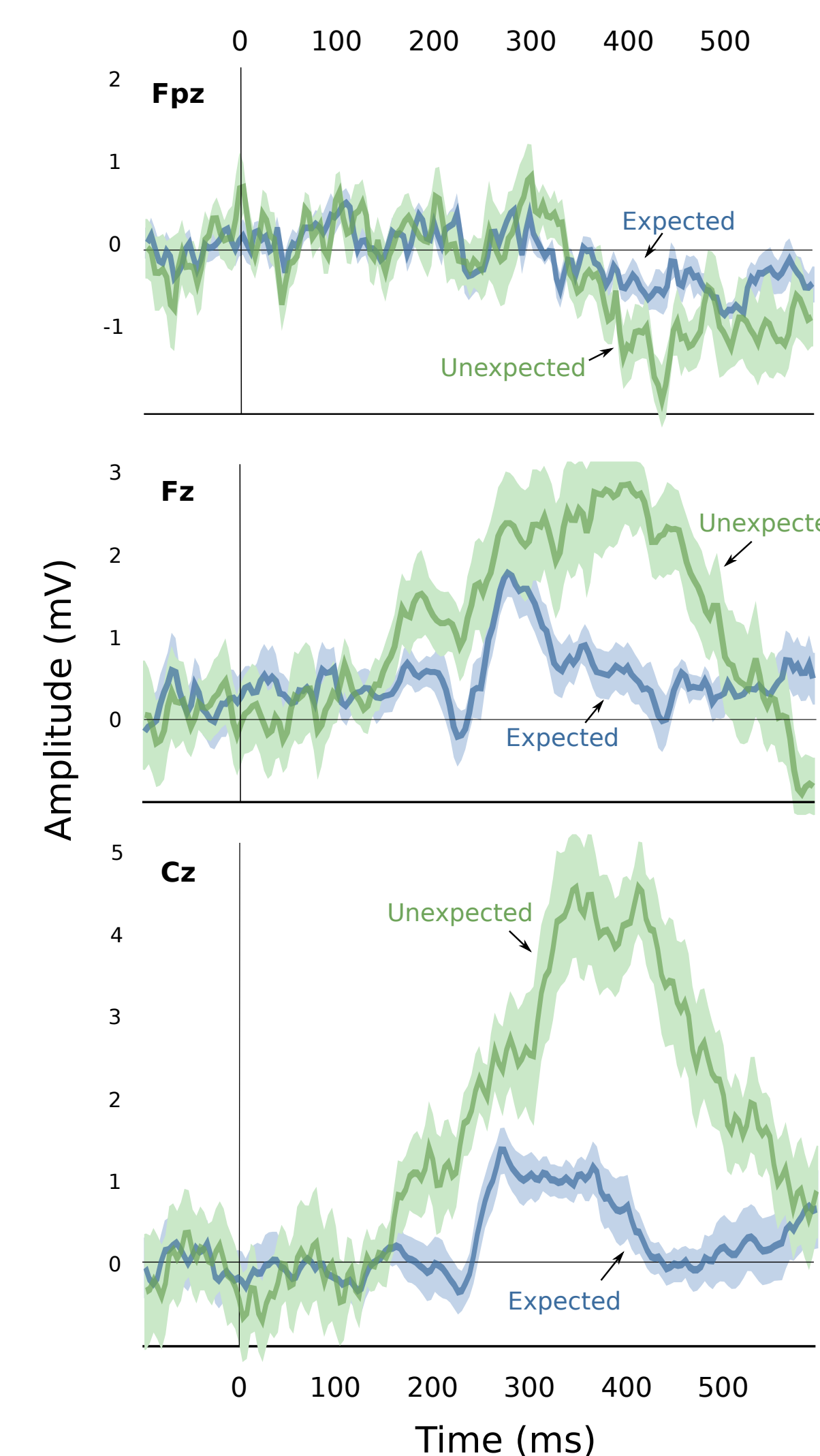
Manipulating expectations

Occasional "flips" on the final presentation of a sequence violated subjects' expectations (Maryott et al., 2011). We compared these unexpected motion segments to the equivalent well-predicted ones.



The distributions of reproduction errors were similar between expected and unexpected segments.

Distinctive ERPs to prediction errors



We recorded 129 channels of EEG data (Electrical Geodesics). The figure at left shows ERPs at midline electrodes during expected and unexpected segments.

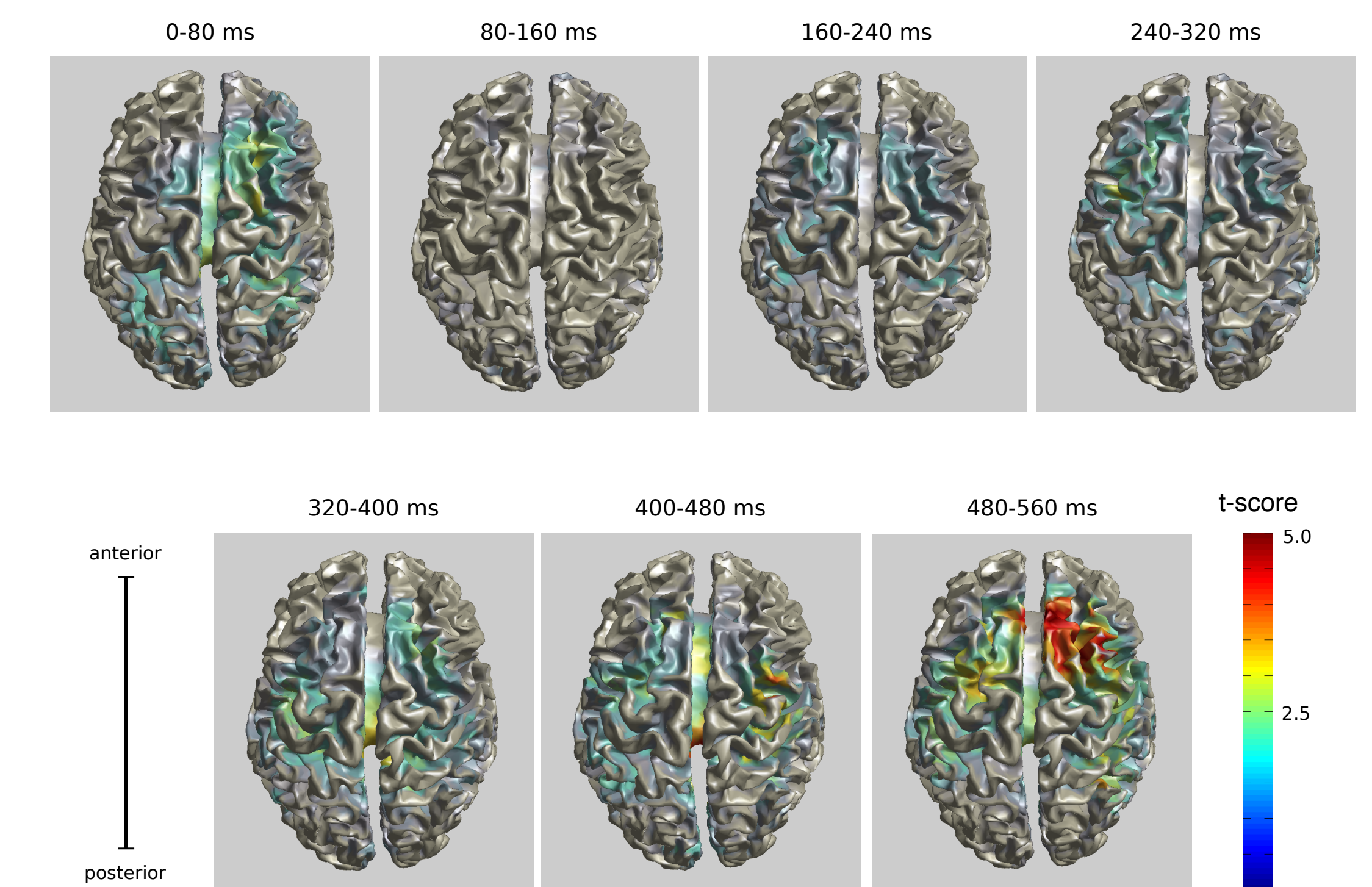
Unexpected events are associated with a late, positive-going ERP at midline electrodes (VExPR). There is no evidence of an earlier component that would parallel the error response negativity (ERN).

The VExPR is similar in timing and topography to the error positivity (Pe), which has been associated with error awareness.

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Source-localizing the VExPR

Using BESA's implementation of the sLORETA algorithm, we calculated the neural sources of ERPs to expected and unexpected path segments.



Above, the unexpected-expected comparison shows that the greatest difference is in posterior medial frontal areas, which are also involved in other error-monitoring and response-conflict paradigms.

Sequence expectations build quickly.

The one-shot learning that we see in performance, in eye movements, and in ERPs reflects the use of familiarity-based prediction to better-encode the sequence on subsequent presentations.

Errors in expectation cause different neural activity than errors in responding.

Although both expectation errors and response errors cause a mismatch between prediction and outcome, there is no ERN-like neural response within the first 100 ms of an unexpected segment. The early mechanisms of these two forms of monitoring are different.

Posterior medial frontal cortex comprises a prediction- and error-monitoring system.

These regions are active in the error positivity, in the VExPR, and in paradigms where responses are in conflict. Late (300 ms) activity in all of these contexts reflects a need for some response to an unanticipated event, such as a change in behavior or a more-thorough encoding of new information.