Fast-adapting Bayesian prior for visual motion speed in the smooth pursuit eye movement system

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Actions are guided by a complex interaction between past experience and current sensory information. When sensory information is weak, behaviors tend to be guided by experience whereas strong sensory information defeats prejudices instilled by experience. The Bayesian framework formalizes the interaction between past experience and sensory information, where past experience is the "prior", current sensory information is the "likelihood", and behavior is the "posterior". Importantly, the Bayesian framework seems to be a fundamental feature of human and animal behavior. It can explain complex phenomena including eye movements, arm movements, visual perception, and multisensory perception. The Bayesian framework has received much attention in behavioral and theoretical studies. Here, we take the next step of asking how Bayesian-like behavior arises from the operation of a neural circuit. We examine how a Bayesian prior for speed is represented in the neural circuitry of the smooth pursuit eye movement system.

Previous work from our lab showed that the Bayesian framework describes pursuit behavior. Eye speed during the initiation of pursuit was lower in response to the weak visual motion of a low-contrast sine wave grating versus the strong visual motion high-contrast patch of dots. A Bayesian model accounts for the effect of contrast on pursuit eye speed if it includes the "zero-speed" prior previously used to describe the effect of contrast on speed perception. Here we show that this speed prior is adaptable according to the recent history of visual motion speed, and that the behavioral adaptation has interesting neural correlates in the pursuit circuit.

<u>Methods</u>: We trained two Rhesus macaques to fixate and smoothly track moving visual targets. We carefully contrived a behavioral paradigm that allowed for control over the statistics of visual motion speed and the strength of visual motion signals. To control the statistics of visual motion speed, we utilized an alternating 50-trial block design. In a "fast-context" block, 80% of the trials moved at 20 deg/s and 20% of the trials moved at 10 deg/s. In a "slow-context" block, 80% of the trials moved at 2 deg/s and 20% of the trials moved at 10 deg/s. A "control" block consisted of 20 trials, all at 10 deg/s. A 100% contrast patch of dots was used for strong visual motion and a 6% contrast sine-wave grating was used for weak visual motion. These different targets were interleaved randomly through-out all of the blocks. Importantly, we obtained similar results using targets that were matched in form and differed only in contrast. Acute single-unit extracellular recordings were made in the smooth eye movement region of the frontal eye fields (FEFsem) while the monkeys performed the behavioral task.

<u>Results</u>: The fast- and slow-context have consistent effects on both pursuit behavior and the responses of neurons in the FEFsem. Eye speed during the fast-context block is faster than eye speed during the slow-context block in response to 10 deg/s visual motion (**Figure 1A and B**). Furthermore, modulation of eye speed by context was larger for the low-contrast stimulus compared to the high-contrast stimulus (**Figure 1C and D**), consistent with the Bayesian framework. Our electrophysiological recordings in FEFsem revealed that the recent history of target speeds was encoded by preparatory ramps of activity occurring prior to visual motion onset. The example cell had a stronger ramp in activity during the fast context compared to the slow context (**Figure 2A**). The scatter plot shows greater modulation of preparatory activity during the fast context compared to the slow context across our population of cells (**Figure 2B**). We also examined the effect of speed context on the pursuit-related responses of these cells and how any effect depended on the strength of visual motion. Our example cell has a stronger pursuit response to the 10 deg/s visual motion during the fast context compared to the slow context. This modulation is greater when weak visual motion was presented (**Figure 3A-C**). This finding was consistent across our population of cells (**Figure 3D and E**). We conclude that preparatory activity in FEFsem encodes the expectation of upcoming target speed according to the recent history of visual motion speeds encountered. The effect of this expectation on pursuit-related FEFsem responses and ultimately behavior depends on the strength of visual motion provided.

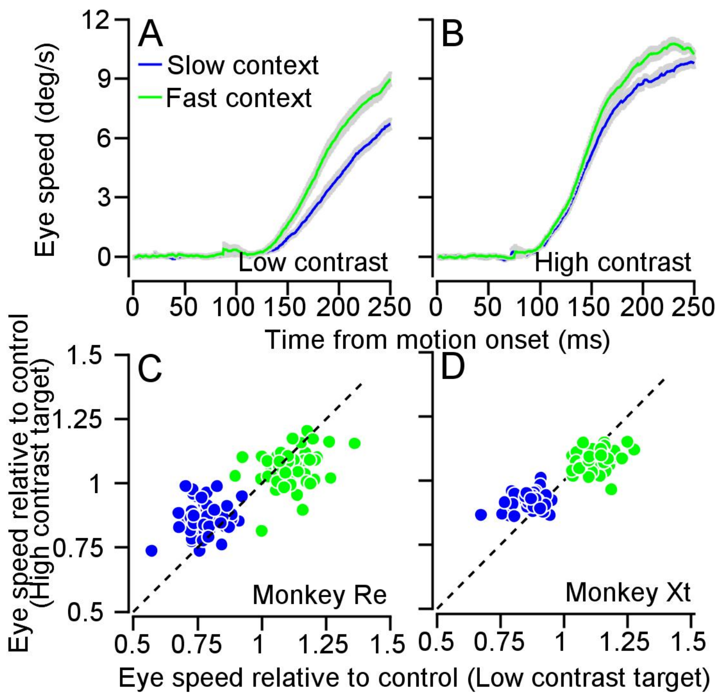

Figure 1. Influence of speed context on eye speed. A, B: Each graph contains trial-averaged eye speed in response to target motion at 10 deg/s with a low (**A**) or high (**B**) contrast target for one experiment. Green and blue traces represent eye speed during the fast and slow context. Error bars represent the SEM. **C, D:** Summarizes data across many experiments in two different monkeys. Green and blue symbols represent eye speed in response to 10 deg/s target motion during the fast and slow context normalized to eye speed during the control blocks for the high versus the low contrast target.

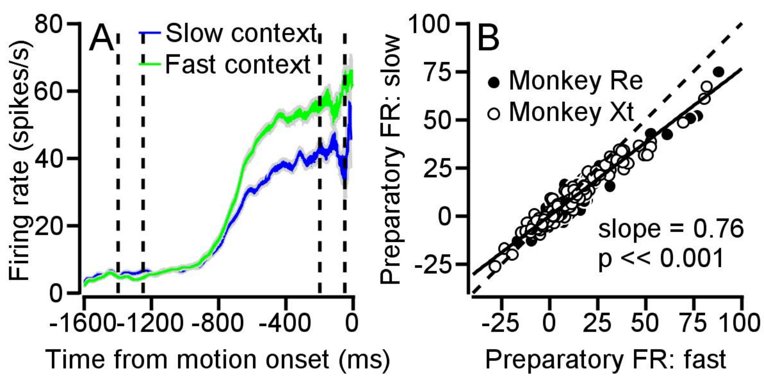

Figure 2. Influence of speed context on preparatory ramps of activity in FEFsem. A: The green and blue traces plot trial-averaged firing rate for one example cell during the fixation period in the fast and slow context. Error bars represent SEM. **B:** Summarizes data across our population of cells collected in two monkeys. Each symbol represents the average preparatory modulation of firing rate during the slow versus fast context. Modulation was estimated by subtracting the FR at the beginning of fixation from the FR at the end of fixation (dashed lines in **A**). The dashed line represents unity and the solid line represents the linear regression curve fit to the data.

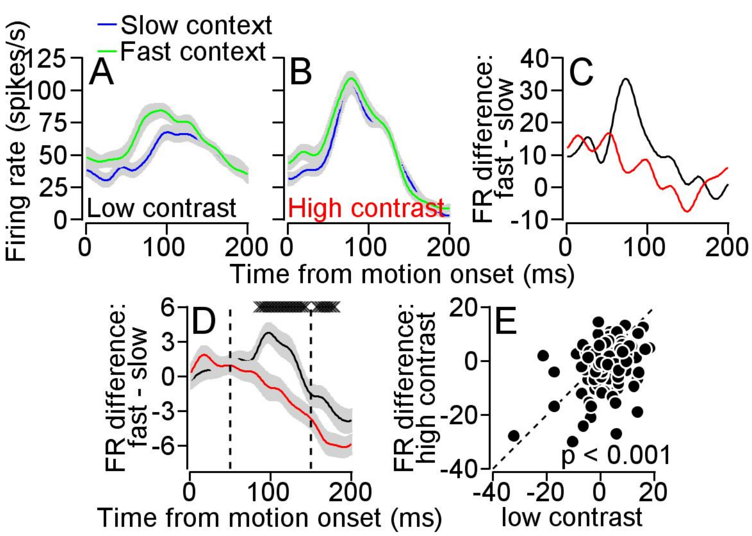

Figure 3. Influence of speed context on pursuit-related activity in FEFsem. A, B: The green and blue traces represent trial-averaged firing rate in the fast and slow context for one example cell during the period following visual motion onset of the low or high contrast target at 10 deg/s. Error bars represent SEM. **C:** The black and red traces represent the average difference in firing rate found by subtracting the green traces from the blue traces in **A** and **B** for the low and high contrast targets. **D:** The black and red traces represent the difference in firing rate between the fast and slow context for low and high contrast targets, averaged across our population of cells collected from both monkeys. Black cross-hairs represent points where the two traces significantly differ ($p < 0.05$, 2-sample t-test). **E:** Symbols summarize the difference in firing rate between the fast and slow context found by averaging in the period marked by dashed-lines in **D** for the low versus high contrast targets. The dashed line indicates unity and the FR difference statistically differed for high versus low contrast targets ($p < 0.001$, paired t-test).