

The Identification of a rapidly-decaying, high-precision proprioceptive sensory memory & its effects on motor adaptation

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Although working memory is generally recognized as the short term store that dominates the cognitive processing of information, an even more transient form of memory has been identified in both the visual and auditory systems. These vivid “sensory memories” are modality specific and can have a resolution that far exceeds that of working memory. In visual sensory memory, also known as iconic memory, capacity increases of several-fold compared with working memory have been repeatedly demonstrated (Sperling 1960). Visual sensory memory has a duration of only a few hundred milliseconds, whereas auditory sensory memory, also known as echoic memory, has generally been reported to last several seconds (Cowan 1998). Interestingly, sensory memory has not been reported for proprioception. Here, we demonstrate the existence of a high-precision, rapidly decaying proprioceptive sensory memory that can double the endpoint precision when reaching to a remembered location. We find that this memory decays with a time constant of just 1-2 seconds and its presence is associated with altered visuomotor adaptation.

We began by examining the extent to which visuomotor rotation learning depends on movement-vector-based versus goal-location-based representations of movement (Figure 2A-B). In two experiments, we trained a 30° rotation to one target while giving veridical feedback at two other targets. The training resulted in near-complete learning of the imposed rotation, which could in principle be achieved by any combination of goal location and movement vector remapping. We dissociated these possibilities by examining how the learning generalized to one test movement that matched the trained movement in terms of movement vector but not goal location, and another test movement that matched goal location but not movement vector. As shown in the middle panel of Figure 2, the test movements in both cases were clearly affected by the adaptation, indicating that both movement vectors and goal locations adapt. However, we find that the adaptation coefficient associated with movement-vector-based adaptation is 4-fold stronger than for goal-location-based adaptation ($K_{MV} = 0.69 \pm 0.03$ vs $K_{GL} = 0.17 \pm 0.01$, measured as a portion of the training period adaptation, $p < 10^{-6}$ in both cases). We hypothesized that this disparity arises because the fidelity of sensory information about movement direction is substantially better than for hand position. This hypothesis stems from a Bayesian view of motor adaptation whereby the reliability of sensory information about a perturbation would determine the extent to which it is weighed during adaptation.

Interestingly, an analysis of how the adaptation coefficients evolved in time, revealed that K_{GL} increased dramatically when the time since the goal location was last visited was small (Figure 3). Remarkably, this increase was most pronounced at latencies of just 2-4 seconds, suggesting that the reliability of sensory information about the goal location improved dramatically at these very short latencies. This finding suggests the existence of a rapidly-decaying high-resolution proprioceptive memory analogous to the visual and auditory sensory memories that have previously been reported.

To investigate this possibility, we designed a task to measure the reliability of proprioceptive information as a function of the duration of proprioceptive memory. As diagrammed in Figure 4A, subjects began in the center with visual feedback to establish a proprioceptive calibration. They then move away (movement 1) and wait for a variable time between 0 and 25 seconds before returning to the center without visual feedback (movement 2). After the return movement, subjects adjust their position and press a key to indicate alignment with the center target. We find that the variability of these keypress locations is dramatically reduced at small time delays with a 46% reduction in variance at a delay of 2s in contrast to a reduction of only 3% at 6s, as illustrated in Figure 4B-C. This striking increase in the precision of the proprioceptive sense with low time delays is very similar to short term performance increases observed in vision and audition (Sperling 1960; Cowan 1998). This finding points to short-duration proprioceptive sensory memory that can be used to improve the reliability of movements to recently visited locations by nearly a factor of two.

Upon consideration, the parallel increase in the goal location adaptation coefficient (K_{GL}) that spurred our search for this proprioceptive sensory memory may give new insight into the mechanism for Bayesian integration in the motor system. Although a host of recent studies have demonstrated Bayesian-like integration in motor control whereby decreases in reliability of the prior or increases in the reliability of the sensory likelihood lead to greater sensory weighting, these studies have generally relied on designs in which participants have ample opportunity to observe the relevant changes in reliability. In contrast, the changes in reliability that we demonstrate in the last experiment could not be readily observed in the K_{GL} measurement experiment because the observations associated with a particular movement would have to include trials at a number of different latencies. The fact that the K_{GL} adaptation coefficient increases dramatically at low latencies therefore suggests that the motor system has direct access to both the content and reliability of each proprioceptive memory. This could only be the case if the reliability of the proprioceptive memory were intrinsically encoded alongside its content as suggested in several intriguing theoretical models of neural encoding (Ma et al. 2006) for which direct experimental evidence is scant.



Figure 1: Experiment setup.

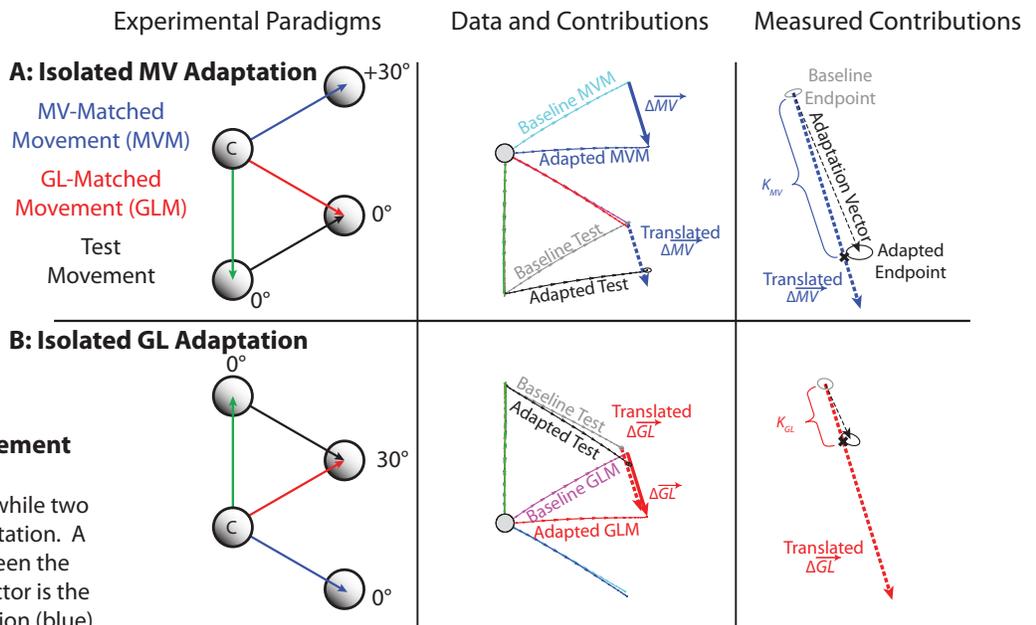


Figure 2: Experimental dissociation of movement and goal location based adaptation.

Experiment A. A 30° rotation is learned at one target while two other targets, spaced 60° apart, are trained with 0° rotation. A test movement is then made without feedback between the unrotated targets, where the required movement vector is the same as the vector that had been trained with a rotation (blue). The second panel shows that the test movement after training is rotated from the test movement before training, but not by the full 30°. The right panel shows the difference between adapted and baseline test movements and a vector representing the full motor adaptation that was learned during training. The projection of the test movement onto the full training-period adaptation, denoted K_{MV} , indicates the extent of movement vector adaptation; this value is 0.69 ± 0.03 .

Experiment B. A 30° rotation is learned at one target while a 0° rotation is learned at targets spaced 60° away on either side. A test movement from a non-rotated target to the rotated target requires a non-rotated movement vector. The middle panel shows that subjects bias their movements toward a remapped goal location. The right panel shows the difference between adapted and baseline test movements alongside the full adaptation vector from training. The projection of the test movement endpoint onto the full training-period adaptation, denoted K_{GL} , indicates the extent of goal location adaptation; this value is 0.17 ± 0.01 .

Figure 3: Time-dependence of movement vector and goal location adaptation.

The amount of goal location adaptation, K_{GL} , increases by over 300% when returning to a recently-visited target. An exponential fit has time constant of 3.4s, indicating a fast decay. In contrast, the amount of movement vector adaptation, K_{MV} , shows very weak dependence on the time since the same movement vector was performed. Since K_{MV} is much greater than K_{GL} , it contributes to a greater portion of adaptation. This difference is reduced when returning to recently-visited targets.

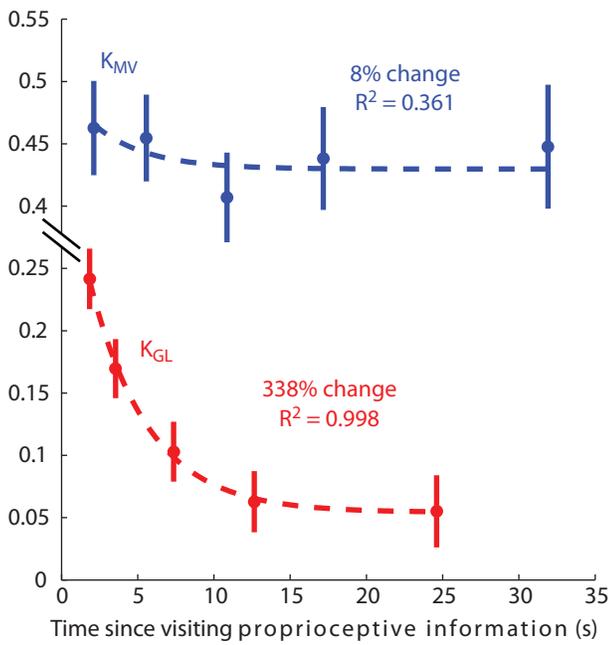


Figure 4: Time-dependence of sensory precision

(A) Beginning in the center, subject reached to the top (movement 1), then waited for a randomly chosen time between 0 and 25 seconds. Their return to the center (movement 2, red) was analyzed for variability as a function of time since leaving the center. (B) The endpoints were binned into eight bins for each subject, according to the time since leaving the center. Three bins are shown for a subject corresponding to a short (blue), medium (red), and long (green) delay. (C) A nearly 2-fold increase in precision is obtained for the endpoints of short delay return movements. The time constant for an exponential fit is 1.4s.

