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## Interactions between sensory and motor components of adaptation predicted by a Bayesian model

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Adaptation of reaching movements under shifted visual feedback consists of (at least) three distinct components - visual, proprioceptive and motor [2]. The sensory (visual and proprioceptive) components correspond to shifts in spatial perception, as measured through alignment tests in which the unseen left hand is aligned with the perceived location of either a visual target or the right hand [3]. In addition to sensory adaptation, there is a motor component of adaptation which is specific to the reaching task performed during exposure and does not transfer to subsequent tracking or alignment tasks [2].

Traditionally, sensory adaptation has been considered to be purely driven by the discrepancy introduced between the visual and proprioceptive estimates of hand location, and independent of any motor component of adaptation [1, 3]. Here, we argue for an alternative, unified view in which sensory and motor adaptation are jointly driven by optimal Bayesian inference of the true cause of an observed performance error.

We consider a generative model of a reaching movement from the subject's perspective (Figure 1). On trial  $t$ , the subject selects a (known) motor command  $u_t$ . This results in a final hand position  $y_t$ , which also depends on some (unknown) motor disturbance  $r_t^y$  and motor noise  $\epsilon_t^y$ . We assume that the final hand position is given by

$$y_t = u_t + r_t^y + \epsilon_t^y, \quad (1)$$

where  $\epsilon_t^y \sim N(0, \sigma_u^2)$ . The experimenter measures performance according to the hand position  $y_t$ , however this is not directly observed by the subject. Instead, noisy and potentially shifted observations are available through vision and proprioception,

$$v_t = y_t + r_t^v + \epsilon_t^v, \quad (2)$$

$$p_t = y_t + r_t^p + \epsilon_t^p, \quad (3)$$

where the observation noises  $\epsilon_t^v$  and  $\epsilon_t^p$  are zero-mean and Gaussian with variances  $\sigma_v^2$  and  $\sigma_p^2$ , respectively. The shifts  $r_t^v$  and  $r_t^p$  correspond exactly to the errors in the visual and proprioceptive alignment tests.

In addition to this model of a single reach trial, we assume the subject has some beliefs, based on prior experience, about how the total disturbance  $\mathbf{r} = (r^v, r^p, r^y)^T$  is liable to vary over time:

$$\mathbf{r}_{t+1} = A\mathbf{r}_t + \boldsymbol{\eta}_t, \quad (4)$$

where  $A$  is a diagonal matrix and  $\boldsymbol{\eta}_t$  is Gaussian noise with diagonal covariance matrix (diagonal since each disturbance evolves independently). We propose that subjects adapt by optimally inferring the disturbance  $\mathbf{r}_t$  given the observations. Under our assumptions of linearity and Gaussian noise, this inference is straightforward and equivalent to a Kalman filter.

Our model is able to account for the distributed nature of visuomotor adaptation across sensory and motor components. More importantly, our model makes the surprising prediction that force field adaptation will also result in sensory as well as motor adaptation, even though there is never any discrepancy between senses. We tested this prediction experimentally: 11 subjects made reaching movements in a velocity-dependent lateral force field ( $F_x \propto \dot{y}$ ), the strength of which was slowly increased over the course of 50 trials. These reach trials were interleaved with visual and proprioceptive alignment tests. We found that subjects did indeed exhibit sensory adaptation in addition to motor adaptation (Figure 2). Fits of our model to data (Figure 3) demonstrate a close agreement with the trial-to-trial adaptation in the reach and alignment test performance.

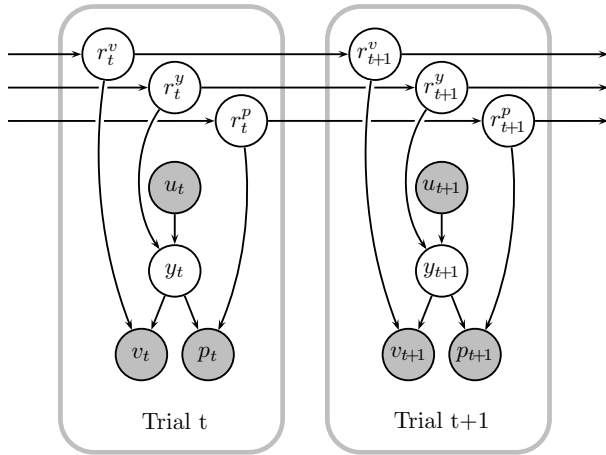


Figure 1. A generative model of reaching from the subject's perspective.  $r_t^v$ ,  $r_t^p$ ,  $r_t^y$  = disturbances,  $u_t$  = motor command,  $y_t$  = hand position,  $v_t$  = visual observation,  $p_t$  = proprioceptive observation. Shading indicates observed variables.

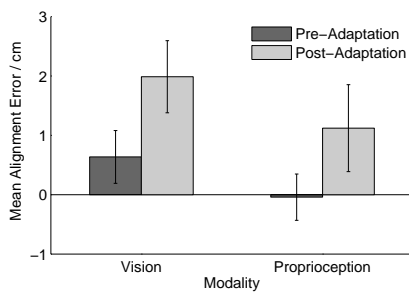


Figure 2. Comparison of visual and proprioceptive alignment test performance before vs after force field adaptation. Bars represent average alignment error (i.e. in the direction of the force field) across 11 subjects. Error bars indicate SEM. One-tailed paired t-tests confirmed significance of the shifts in both modalities ( $p < 0.05$  in both cases). There was no significant shift in the perpendicular direction, where there was no force (data not shown).

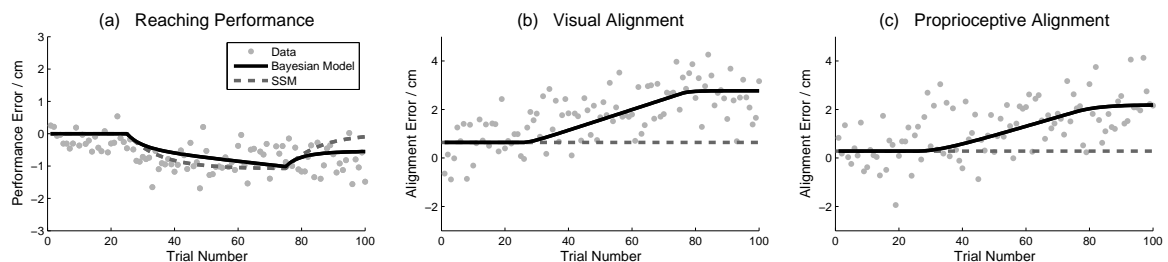


Figure 3. Trial-by-trial data, averaged over subjects, and model fits. State space model fits are included for comparison. Force field strength was increased linearly from zero at trial 25 to maximum at trial 75. (a) Reaching performance error, (b) Visual alignment test error, (c) Proprioceptive alignment test error.

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