Cerebellum-based implicit learning contributes to savings

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Savings, manifested as faster relearning than initial learning, is the hallmark of long-term retention of motor adaptation. However, what cognitive and neural mechanisms underlie savings is still under debate. The error memory account asserts that enhanced sensitivity to errors during initial learning causes savings (e.g., Herzfeld et al., 2014). On the other hand, the explicit strategy account asserts that cognitive strategy formed during initial learning is quickly recalled during relearning and principally contributes to saving effect (e.g., Morehead, et al., 2015). Both accounts receive empirical supports but the debate is not resolved since error exposure and strategy formation co-occur in typical research paradigms. Here we use novel behavioral paradigms to prevent strategy formation in visuomotor rotation adaptation and confirm that error exposure itself can lead to savings. Furthermore, we successfully improved the "pure" implicit learning by applying anodal transcranial direct-current stimulation (tDCS) on the cerebellum, the locus of sensory prediction error-based learning. More importantly, using the same tDCS to directly upregulate error sensitivity, we also induce otherwise-absent savings following the learning of a gradually-induced perturbation.

In Exp1 we used error-clamp paradigm which reliably induces implicit learning without explicit learning (Morehead et al., 2017). Participants reached a target with their unseen hand while a cursor moved synchronously with the hand but spatially locked at 30° counter-clockwise (CCW) to the target direction. Instructed to ignore the cursor, participants would unknowingly deviate their hand to "counter" the clamped cursor, indicating a prediction error-based, implicit learning. Critically, significant savings was observed when they later adapted to an abrupt 30° CCW, as compared to a control group who learned and relearned the same abrupt perturbation (Fig 1). The reports of the aiming direction indicated that the savings consisted of faster implicit learning and a marginally-significant faster explicit learning.

In Exp2 we used gradual learning paradigm where adaptation to a gradually-induced 30° perturbation could not lead to savings in a subsequent adaptation of an abrupt perturbation (Herzfeld et al. 2014; our replicating exp). However, if participants were required to report their aiming directions, we observed robust savings. In fact, 12 of 28 participants never developed an explicit strategy during initial learning and their savings largely consisted of an enhanced implicit learning, accompanied by a *decrease* in explicit learning (Fig 2). The rest 16 participants developed strategies (though with small angles) and their savings was still caused by enhanced implicit learning; their use of strategy was initially large but quickly diminished (Fig 3). Thus, simply asking people to report aiming directions can cause other-wise absent savings, possibly due to enhanced error saliency by explicit reports. Furthermore, people showed idiosyncratic but persistent learning patterns in terms of distinct reliance on implicit/explicit learning.

The above behavioral findings were corroborated by Exp3, which used cerebellar anodal tDCS to selectively enhance implicit learning. Two new groups of participants performed the error-clamp task and demonstrated the prediction error-based, implicit learning (Fig 4A). Critically, we found that the group with anodal tDCS during clamp learning showed larger though not faster implicit learning than the sham group. Next, we recruited new groups of participants to test whether this enhanced implicit learning by anodal tDCS could render savings which is otherwise impossible after gradual perturbation without aiming report. Indeed, cerebellar tDCS applied during gradual learning led to faster learning of subsequent 30° perturbation than sham stimulation (Fig 4B). In fact, stimulated participants' learning rate was as fast as the relearning rate of the control group; the sham group's learning rate was as slow as the initial learning rate of the control group. These results thus suggest that enhancing implicit learning by anodal cerebellar tDCS can facilitate the savings.

Consistent with the error memory account, our findings demonstrated that in certain conditions people can implicitly learn visuomotor adaptation and show savings without the aid of explicit strategy. Previous studies found that anodal cerebellar tDCS benefits initial learning but not retention overnight (Galea et al., 2011) but this effect is not robust (Jalali et al., 2017). Our data highlight that cerebellar tDCS selectively improves implicit learning and facilitates savings, possibly by enhancing the error saliency during initial learning (Jiang et al., 2018).

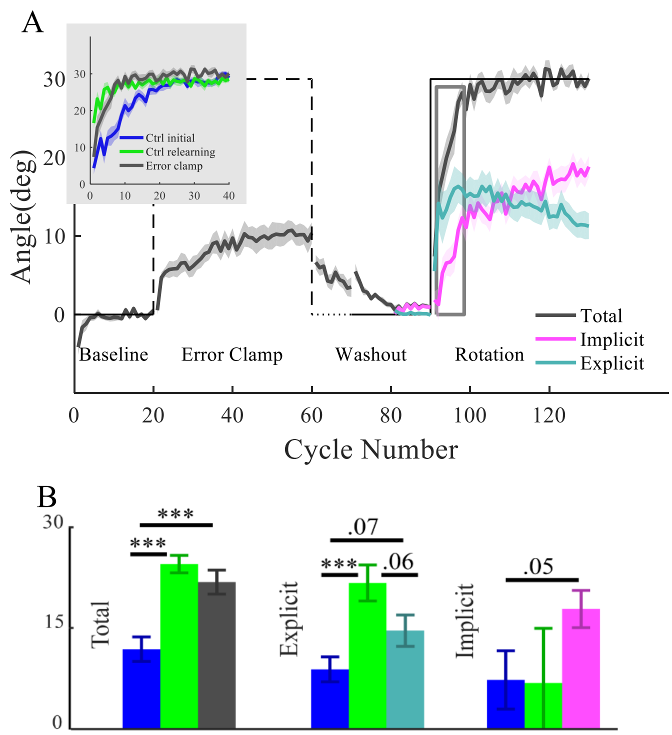


Fig1: Learning performance of the error-clamp group. (A) Participants learned implicitly during error clamp. After washout, they showed faster learning than the control group (blue and green) when both groups adapted to the same 30° abrupt perturbation for the first time (inset). Savings is computed over cycle 2-8, highlighted by a box. (B) The total, implicit and explicit learning during cycle 2-8 are compared between groups. *** p<.001

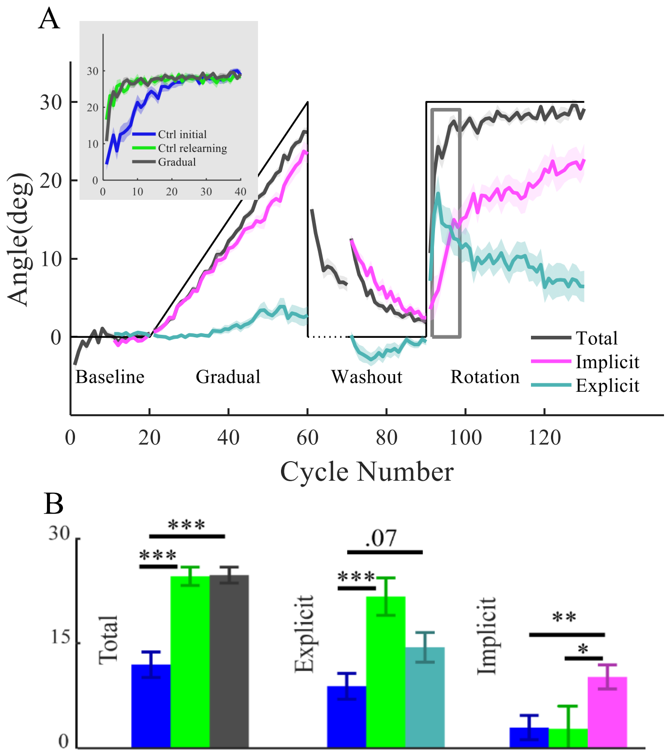
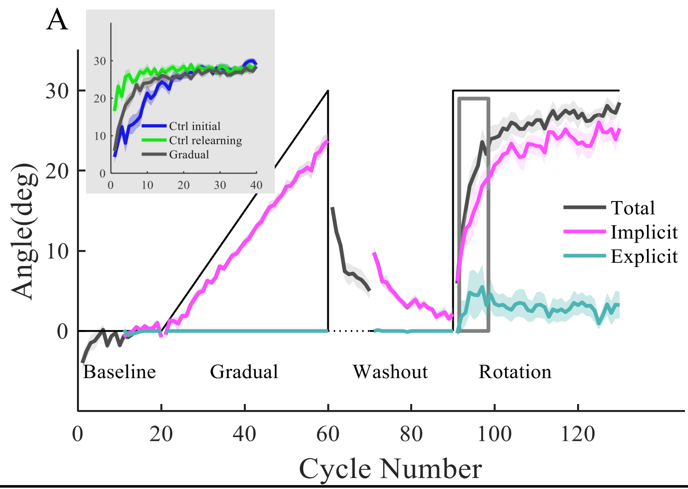


Fig2: Learning performance of a subgroup of participants (n=16) from the gradual learning exp, plotted similarly as Fig1. (A) They developed their strategy (small reported angles) during gradual learning and exhibited savings. Note large explicit learning was evidenced during initial exposure to 30° abrupt perturbation but the savings was mainly caused by implicit learning. (B) The total, implicit and explicit learning are compared between groups.



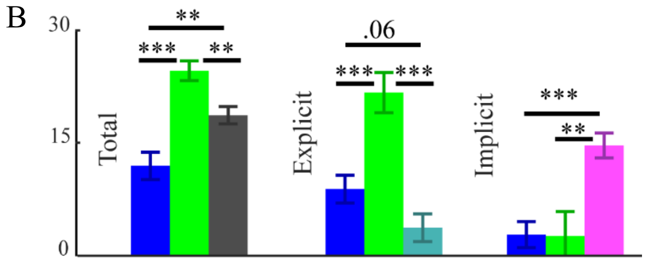


Fig3: Learning performance of the rest of participants (n=12) from the gradual learning exp. (A) They did not develop an explicit strategy during gradual learning but still exhibited savings. Explicit learning was small and implicit learning dominates. (B) The total, implicit and explicit learning are compared between groups. *** p<.001, ** p<.01.

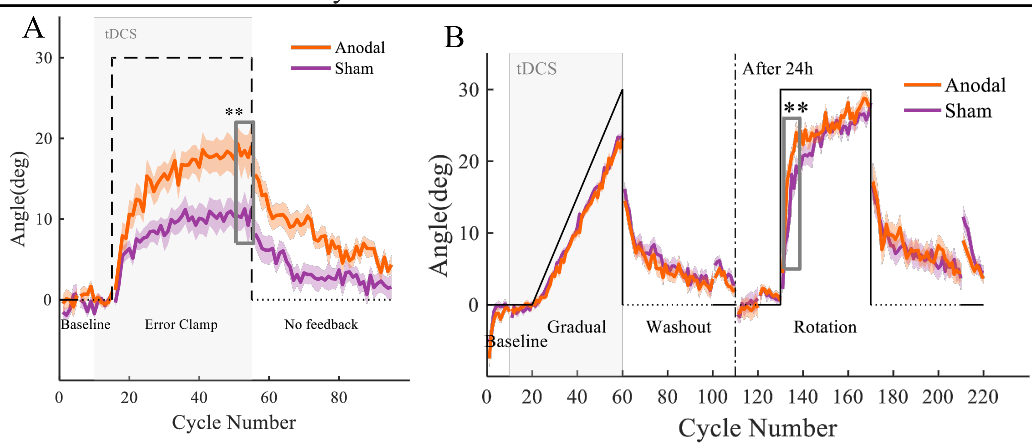


Fig4: Learning performance of the tDCS groups. (A) The anodal tDCS group showed significantly more implicit learning than the sham group. (B) A second anodal tDCS group showed significantly faster learning than the sham group when adapting to 30° abrupt perturbation on day2. Overnight control group is not shown here.

Reference: Herzfeld, D.J., et al., *Science*, 2014. 345(6202): p. 1349-1353. Morehead, J.R., et al. *Journal of Neuroscience*, 2015. 35(42): p. 14386-96. Morehead, J.R., et al., *Journal of cognitive neuroscience*, 2017. 29(6): p. 1061-1074. Galea, J.M., et al., *Cerebral Cortex*, 2011. 21(8): p. 1761. Jalali, R., R.C. Miall, and J.M. Galea, *Journal of neurophysiology*, 2017. 118(2): p. 655-665. Jiang, W., et al., *Journal of neurophysiology*, 2018.