Repetition Suppression during Movement Execution Reflects Different Mechanisms in the Striatum than in the Neocortex

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Abstract:

Repetition suppression (RS) provides an important tool to investigate brain representations. Repetition of the same stimulus evokes a reduction in elicited brain activity. While the reduction in activity is consistently observed across modalities and species, it is unclear what mechanisms drive this effect. Several models of RS have been proposed, which vary in their prediction of stimulus 'tuning' in the second repetition. Here we examined RS mechanisms in two motor cortical areas and the striatum while participants executed motoric finger sequences, twice in a row. We distinguished the RS models by investigating the changes in the sequence-dependent fMRI activity patterns in concert with the changes in overall activity. In the striatum, we observed that the tuning for individual sequences is 'sharpened' on the second execution, whereas in the cortex we found a 'fatigued' representation. This dissociation might indicate different computational roles along the cortico-striatal circuitry, with the striatum solving the selection problem, and signaling its novelty to the cortex.

Keywords: repetition suppression; fMRI; striatum; movement;

Mechanisms of repetition suppression

When the same stimulus is presented twice, its repetition leads to a reduction of neural activity (Gross, Schiller, Wells, & Gerstein, 1967). This observation is commonly referred to as adaptation, or repetition suppressions (RS). Multiple potential mechanisms for RS have been proposed, amongst which are the *'fatigue model'*, the *'sharpening model'*, and the *'scaling model'* (sketched in Fig. 1; Grill-Spector, Henson, & Martin, 2006). The fatigue model proposes that firing of neurons reduces especially for those neurons that were highly active during the initial response. For instance, neurons with the highest firing rate on the first execution of a finger tapping sequence A would reduce their firing the most upon second execution. This would lead to a less distinguishable activity pattern for different sequences on second execution, i.e. to reduced 'tuning' (Fig. 1A - reduced angle for between population responses for sequence A and B; $\alpha > \beta$). In contrast, the sharpening model suggests that only the neurons most tuned for sequence A will respond on the second execution, leading to an enhanced tuning (Fig. 1B: $\alpha < \beta$). Alternatively, all neurons could reduce their firing rate

by the proportion, resulting in no net change in the shape of the tuning function (Fig. 1C: $\alpha = \beta$). Therefore, examining both elicited activation and stimulus tuning allows us obtain new insights into the underlying mechanisms of RS. Here, we addressed the question of how movement repetition affects the fine-grained fMRI activity patterns in the primary motor cortex (M1), the dorsal premotor cortex (PMd), and the dorsal striatum (putamen).
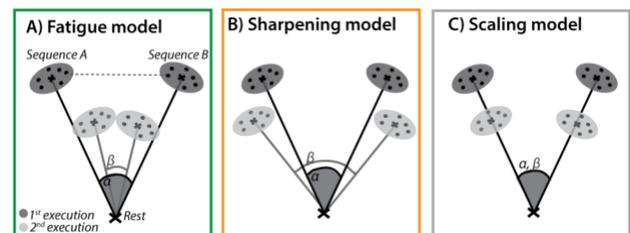

Figure 1: Models of repetition suppression shown in a space of activity patterns. Individual dots refer to the activity pattern measured during a single run, and the crosses the average activity pattern. The length of the vector relative to the rest activity pattern corresponds to the strength of the activation. The example dashed line is the distance between two sequence patterns. The models differ in whether they predict that the average angle between patterns increases or decreases.

Cortex displays repetition fatigue, striatum sharpening

Eighteen participants performed twelve 9-digit finger-tapping sequences on a piano-like device, while we recorded their brain activity with a 7T MRI (voxel size: 2 mm isotropic). We examined the elicited activation above resting baseline for first and second execution of each finger sequence, as well as the distance between activation patterns for all possible pairs of sequences.

Our results show reduction in elicited activation from first to second execution across both cortical areas, as well as in the putamen (Fig. 2A). Next, we examined the crossnobis distance (Walther et al., 2016) between activation patterns for different sequences, separately for the first and second

execution. The scaling model predicts that the distance between two sequence patterns reduces at the same rate as the length of the overall activity vector. We calculated this expectation from the observed distance on the first execution (dashed line in Fig. 2B). Our observed distance on second execution was significantly lower than expected under scaling in cortical regions M1 and PMd. In contrast, the observed second distance in the putamen was significantly higher than expected from scaling in both regions. This suggests that while the RS mechanism in the cortex reflects the *'fatigue'* model, the observations in the putamen follow the *'sharpening'* model.
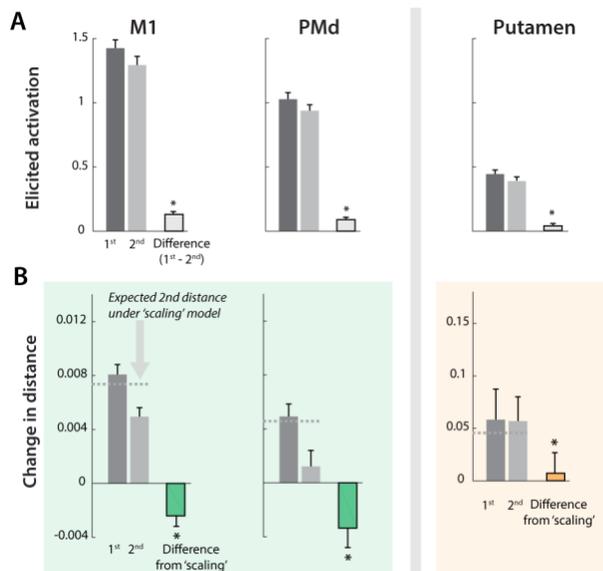

Figure 2: A) Repetition suppression in activation. B) Repetition mechanism: "fatigue" in the cortex, "sharpening" in the striatum.

Learning accentuates the repetition effects

After the scanning session, we trained participants on half of the performed sequences over a period of five weeks, and re-tested them in the scanner on performance of all twelve sequences. We observed that the RS of the overall activation was increased as compared to the baseline session, and more so for the trained than control sequences (Fig. 3A – greater red bar for difference in elicited activation on $1^{st} - 2^{nd}$ execution). We also examined how distance between activation patterns on second execution changed compared to what would be expected under the 'scaling' mechanism. We again observed that compared to scaling prediction, distances were smaller in cortex and larger in striatum (Fig. 3B). Additionally, this effect was increased for the trained sequences in PMd and putamen. This suggests that learning accentuates the underlying neuronal dynamics for the repetition – leading to a stronger 'fatigue' effect in the cortex, and more 'sharpening' in the striatum.
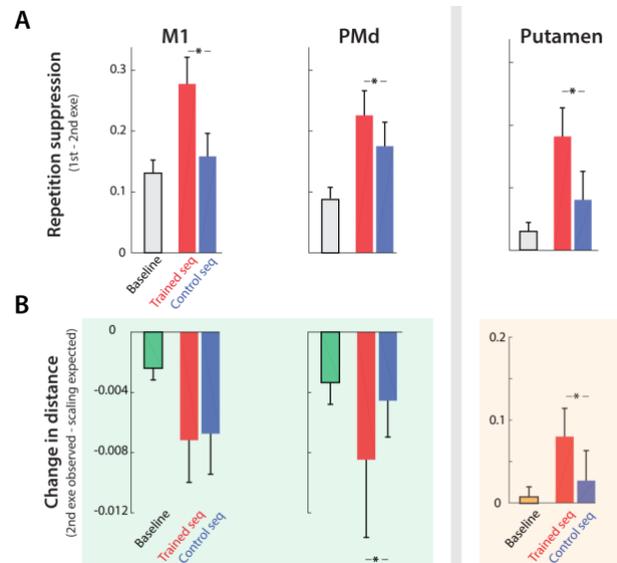

Figure 3: Repetition effects after 5 weeks of training on half of the sequences from baseline scan. Fatigue and sharpening mechanisms become facilitated with learning.

Novelty signal driving dissociating RS effects across cortex and striatum?

We observed a qualitatively different mechanism of repetition suppression across different brain structures, with striatum displaying a 'sharpening' effect, and cortex 'fatigue' for the second movement repetition. The striatal circuit has been proposed to be specialized device for action selection (Gurney, Prescott, & Redgrave, 2001). Receiving contextual inputs, it uses reciprocal inhibitory connections to select a 'winner' option (e.g. which finger sequence to execute), sending a 'go' signal for the choice back to the cortex. With repetition, the lingering inhibition of non-chosen options could maintain, or enhance the support for the winner, leading to the observed sharpening.

References

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, *10*(1), 14–23. http://doi.org/10.1016/j.tics.2005.11.006

Gross, C.G., Schiller, P.H., Wells, C., Gerstein, G. L. (1967). Single-unit activity in temporal association cortex of the monkey. *Journal of Neurophysiology*, *30*(4), 833–843.

Gurney, K., Prescott, T. J., & Redgrave, P. (2001). A computational model of action selection in the basal

ganglia. I. A new functional anatomy. *Biol Cybern*, *84*(6), 401–410. http://doi.org/10.1007/PL00007984

Walther, A., Nili, H., Ejaz, N., Alink, A., Kriegeskorte, N., & Diedrichsen, J. (2016). Reliability of dissimilarity measures for multi-voxel pattern analysis. *NeuroImage*, *137*, 188–200. http://doi.org/10.1016/j.neuroimage.2015.12.012