Predictability engenders more efficient neural responses

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The neural response to a stimulus diminishes with repeated presentations, a phenomenon known as repetition suppression. We here use neuroimaging to demonstrate that repetition suppression appears to be a special case of "prediction suppression"—that is, the brain shows diminishing activity when subsequent stimuli in a train are predictable. This demonstration supports the hypothesis that the brain dynamically leverages prediction to minimize energy consumption.

Repetition suppression can be measured in neural firing rates using single cell electrophysiology[1,2], in event related potentials using electroencephalography [3], in the BOLD response using functional magnetic resonance imaging [4] and using PET[5] and MEG [6]. Explanations for such stimulus-specific adaptation include neural fatigue and sharpening of neural network representations[7].

Not only the neural response, but the perceived duration of a stimulus as well is found to contract with repetition[8-11]. We have previously hypothesized that this correlation is not accidental, but that subjective duration is a direct reflection of the amplitude of neural responses[8,9]. Interestingly, duration contractions can be demonstrated using non-repeating stimuli that are nonetheless predictable[8], which suggested the possibility that repetition suppression is a special case of what we term "prediction suppression." To test this hypothesis, we performed a neuroimaging experiment using presentations of predictable and unpredictable stimuli. Participants viewed series of 5 words that belonged to a sequential category (e.g. months of the year, days of the week), presented either in their natural order (Ordered condition, e.g. *March, April, May, June, July*) or in a scrambled order (Scrambled condition, e.g. *May, February, October, March, January*). In control trials, participants were presented with words that belonged to a non-sequential category (Non-sequential condition, e.g. *Peach, Plum, Apple, Pear, Banana*). Stimuli in the first 2 conditions were letters, numbers, days of the week or months of the year. Stimuli for the non-sequential condition were names of fruits, makes of car, types of furniture, or animals (**Table 1** and **Supplementary Methods**).

We localized cortical regions that were selectively involved in processing sequential stimuli (random-effects contrasts between the Non-sequential trials and either the Ordered or Scrambled sequences; see **Supplementary Methods** for details). The regions comprised a cluster in the right temporoparietal junction (TPJ) and a cluster in the right middle temporal gyrus (MTG). Within these right hemisphere regions we find that the neural response to predictable stimuli ("Ordered sequence") spans a smaller volume than the response to unpredictable stimuli ("Scrambled sequence"; **Fig. 1**). Importantly, the peak coordinates remain the same while only the size of the activated voxel cluster changes. This difference in cluster sizes is not an artifact of the chosen statistical threshold, as the effect is clear across a range of threshold choices (**Supplementary Fig. 1**). Two other clusters appear in the Scrambled condition (left temporoparietal junction, peak activation -60, -24, 16 and left inferior frontal gyrus, peak activation, -52, 8, 16), but not in the Ordered condition, suggesting that they too drop out of the active cortical network with increasing predictability.

This finding that scrambled sequences result in a greater volume of neural activation than unscrambled sequences supports the idea that predictable stimuli, like repeated stimuli, induce more efficient coding[7], perhaps via sharper tuning of neural populations[12] and/or dynamic tuning of synaptic strengths[13]. Our results are in agreement with other studies indicating that repetition suppression is a manifestation of satisfied perceptual predictions[14]. While it has recently been shown that suppression can be modulated by predictions based on immediate context[14], we present here evidence that such predictions can also be founded from past experience.

Table 1 | Example stimuli from the three categories (Ordered sequence, Scrambled sequence and Non-sequence) presented during the experiment.

	Ordered sequence	***Scrambled sequence***
Months	February March April May June	February April January October July
Days	Wednesday Thursday Friday Saturday Sunday	Tuesday Thursday Sunday Monday Wednesday
Letters	G H I J K	C J A V L
Numbers	1 2 3 4 5	4 7 9 1 6

	Non-sequence
Fruit	Pear Peach Banana Apple Grape
Animals	Dog Cat Bear Monkey Rat
Cars	Mercedes Honda Toyota Lexus Ford
Furniture	Chair Table Desk Bed Sofa

Further, note that the TPJ shows increased activation in response to viewing a movie in reverse, a condition in which predictability is degraded[15].

Traditional repetition suppression experiments involve the repetition of a single stimulus, and are thus unable to rule out low level properties of the stimulus (such as details of the visual form). By using stimuli that change each time, either predictably or unpredictably, we are led to suggest that the diminishing neural response seen with stimulus repetition may be a special case of a more general phenomenon of prediction suppression.

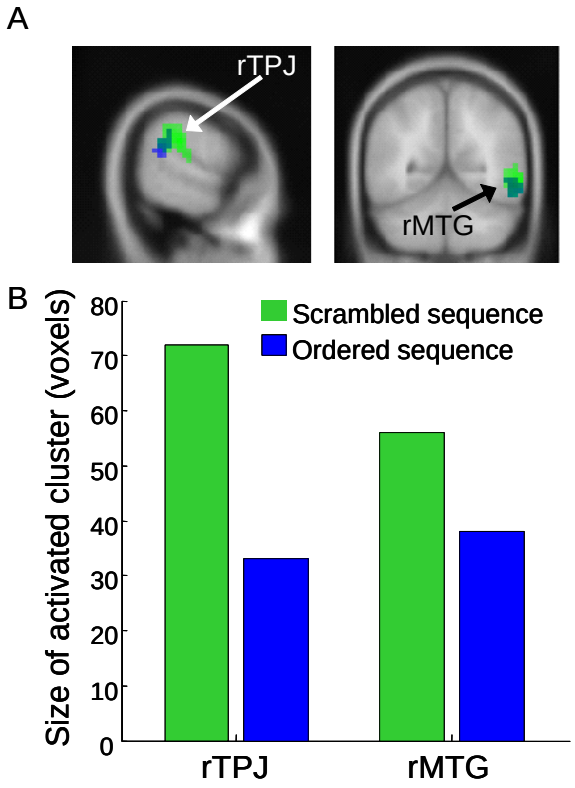

Figure 1 | Processing of predictable stimuli recruits smaller cortical networks. Participants viewed 5 words that were presented serially while in an fMRI scanner. The words belonged to a sequential category in their natural order ("Ordered sequence") or in a scrambled order ("Scrambled sequence"), or to a non-sequential category ("Non-sequential"). (**A**) Sagittal (x=64) and coronal (y=-56) sections showing increased activation in the right temporoparietal junction (TPJ, peak activation 64,-44,20) and right middle temporal gyrus (MTG, peak activation 56,-64,0) in response to sequential stimuli (whether ordered or scrambled). The figure overlays two contrasts: Ordered sequence greater than non-sequence (blue), and Scrambled sequence greater than non-sequence (green). (**B**) Although the peak cluster activation remained the same, a greater volume of voxels was activated in response to the Scrambled sequence (unpredictable) condition than the Ordered sequence (predictable) condition. Clusters $p<0.005$ with at least 20 continuous voxels; **Supplementary Fig. 1** demonstrates the same effect over a variety of parameter settings.

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