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Repetition priming and repetition suppression: Multiple mechanisms in need of testing

Stephen J. Gotts¹, Carson C. Chow², and Alex Martin¹

¹Section on Cognitive Neuropsychology, Laboratory of Brain and Cognition, National Institute of Mental Health (NIMH), National Institutes of Health, Bethesda, MD 20892, USA

²Laboratory of Biological Modeling, National Institute of Diabetes and Digestive and Kidney Diseases (NIDDK), National Institutes of Health, Bethesda, MD 20892, USA

Abstract

In our Discussion Paper, we reviewed four theoretical proposals that have the potential to link the neural and behavioral phenomena of Repetition Suppression and Repetition Priming. We argued that among these proposals, the Synchrony and Bayesian Explaining Away models appear to be the most promising in addressing existing data, and we articulated a series of predictions to distinguish between them. The commentaries have helped to clarify some of these predictions, have highlighted additional evidence supporting the Facilitation and Sharpening models, and have emphasized dissociations by repetition lag and brain location. Our reply addresses these issues in turn, and we argue that progress will require the testing of Repetition Suppression, changes in neural tuning, and changes in synchronization throughout the brain and over a variety of lags and task contexts.

Keywords

Repetition priming; Repetition suppression; Synchrony; Prediction; Bayesian

BAYESIAN EXPLAINING AWAY MODEL

Both Friston's and Henson's commentaries make the point that the Facilitation, Sharpening, Synchrony, and Bayesian Explaining Away models are not mutually exclusive. This is a point that we failed to clarify and that we fully endorse. The ideas are certainly mechanistically distinct, but they could all coexist with one another simultaneously, perhaps making separate contributions in explaining repetition priming. Efforts should be focused on assessing the contribution of any/all (none?) of these in a given experimental situation.

Friston's commentary clarifies his positions on the experimental predictions that we articulated. He re-emphasizes his commitment to anti-symmetrical bottom-up and top-down

Correspondence should be addressed to: Stephen J. Gotts, Section on Cognitive Neuropsychology, Laboratory of Brain and Cognition, National Institute of Mental Health (NIMH), National Institutes of Health, Bethesda, MD 20892, USA. gottss@mail.nih.gov.

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interactions, while he is less enthusiastic about the relative timing predictions. Between-region anti-symmetry is the central claim of this model. It predicts that top-down causal interactions should be more negative after stimulus repetition and that repetition suppression in lower-level areas should be due to feedback from higher-level areas. Friston also stresses the presence of repetition-dependent changes in the feed-forward direction with stimulus repetition, although with an inverse valence to the feedback effects (implementing a negative feedback loop). We view these clarifications as quite reasonable but differ with Friston on other aspects of his argument. Friston claims that near-optimal perceptual inference lends support to a Bayesian brain hypothesis in which top-down/bottom-up interactions are anti-symmetrical. We believe that it is difficult in principle and practice to distinguish between near-optimal and satisfactory inference given a set of stimuli to be identified and tasks to be performed. Many neural network models demonstrate good performance over a range of learning problems. For example, the Boltzmann machine (e.g., Ackley, Hinton, & Sejnowski, 1985) utilizes a “contrastive” Hebbian algorithm to modify synaptic strengths as the model is exposed to a set of patterns to be associated. The learning algorithm, often heralded for its “biologically plausibility” (e.g., O’Reilly, 1998), leads this model to improve gradually with experience, develop similarity-based internal representations, and perform “linearly inseparable” mappings such as the XOR problem (e.g., Minsky & Papert, 1969). It does all of this while developing *symmetrical* weights between units in higher- and lower-level pools of units. Influential models such as Adaptive Resonance Theory (e.g., Grossberg, 1976), the Interactive Activation Model (McClelland & Rumelhart, 1981), and the Biased Competition Model (Desimone & Duncan, 1995) all predict a symmetrical coding scheme. These models exploit the flexible advantages of top-down, selective excitation in domains ranging from perception to working memory, visual attention/search, and imagery. It will be interesting to see if the Bayesian brain hypothesis can be extended into these domains using a more anti-symmetrical scheme. We would also note that attempts to test the anti-symmetrical property of Mumford’s (1992) Bayesian theory in single-cell recordings with monkeys have found support for feedback excitation rather than feedback inhibition (e.g., Lee & Mumford, 2003). This is not necessarily problematic for Friston’s proposal, because the cells encoding the conditional expectation of perceptual causes are distinct from those encoding prediction error. Nevertheless, we do not believe that it is self-evident that the brain behaves in its details as a Bayesian neural network model, at least one that relies on anti-symmetrical coupling in the feed-forward versus feedback directions.

Ewbank and Henson appear to take issue with our use of the label “Explaining Away” when referring to Friston’s Bayesian model, preferring instead “Predictive Coding”. Our rationale was simply to use a label that better distinguished the anti-symmetrical property in this model from the variety of models that utilize “prediction” in very different ways (e.g., Elman nets, Temporal Difference learning, forward models, etc.). Ewbank and Henson emphasize the difficulty in testing subtle predictions about brain connectivity using fMRI methods when the separate contributions of different cell types to the BOLD signal are unknown. We certainly agree that local estimates of the BOLD response in a given voxel will reflect an unknown mixture of various influences (a small fraction of which are neural). However, given the importance of the anti-symmetrical property to the Bayesian model articulated above, we think that it would be unwise to dispatch with this prediction

prematurely. Causal modeling approaches that are capable of assessing directional influences between anatomically connected cortical regions (e.g., DCM, Grainger, etc.) should detect net inhibitory coupling in the feedback direction—even when local activity represents an average over different cell types that are present in unknown proportions. If the feedback is net excitatory, what would serve as the basis of repetition suppression? If the problem is the ability of causal modeling approaches to infer directional influences appropriately among interrelated variables, then this problem will apply in a similar manner to the analyses of experiments using alternative methods such as EEG/MEG (e.g., Kiebel, Garrido, Moran, & Friston, 2008). However, we agree that EEG/MEG studies of inter-areal interactions constitute a promising direction for future research.

FACILITATION AND SHARPENING MODELS: THE SHORT AND LONG OF IT

In his separate commentary, Henson makes the case that it is too soon to dismiss the Facilitation model. While he admits that supporting evidence from single-cell recordings has been lacking, he raises the possibility that accelerated neural responses may be commonplace in EEG/MEG. We concur with him about the basic puzzle: How is it that electrical/magnetic field data can become decoupled from spike data? This decoupling extends even to the basic latency of stimulus-evoked responses in microelectrode recordings from occipital areas in animals (firing-rate latencies ranging from 30–50ms, whereas field measurements often show onsets closer to 70–100ms). Our best guess for a resolution is that it involves some form of field cancellation of the earliest responses. In any case, accelerated responses at the single-cell level should be obtainable if the Facilitation model is to hold. Having said that, a very recent study (since the submission of our paper) has provided some more direct support for the Facilitation model, as well as the Sharpening model, in recordings from monkey inferior temporal cortex (Woloszyn & Sheinberg, 2012). This study involved an extensive training period of several months (like other studies providing support for Sharpening), but it still suggests that Facilitation may apply in some cases. We are therefore happy to concede the point to Henson that it is too early to dismiss the Facilitation model.

The Riesenhuber, Weiner and Grill-Spector, and McMahon commentaries all mention the issue of how repetition lag (short versus long) relates to the observation of proportional scaling versus Sharpening. Riesenhuber makes the case that evidence on long-lag repetitions and Sharpening is not mixed but paints a consistent picture, with proportional scaling effects limited to lags typically involved in fMRI rapid adaptation paradigms (repetitions separated by a few seconds). We agree that results from experiments employing very long lags (and/or practice durations) versus very short lags have been reliably associated with Sharpening and scaling, respectively (see also McMahon's commentary). However, results for lags of an intermediate range (minutes or longer within a single testing session) do not fit cleanly into this picture. For example, Li et al. (1993) showed independent effects of short- and long-lag repetitions on single-cell firing rates in monkey inferior temporal cortex, with proportional scaling observed for long-lag repetitions (~ tens of minutes). As noted by Weiner and Grill-Spector, Weiner et al. (2010) found results in human fMRI for long lags that were consistent with proportional scaling in all but one of the regions that they examined (medial ventral temporal cortex). Given that these more intermediate lags are the ones involved in most

repetition priming studies, the evidence supporting the involvement of Sharpening in repetition priming does indeed appear to be mixed. Even if we were to grant a larger role to Sharpening at these lags, additional assumptions would still be required to explain Repetition Priming. We concur with McMahon that the Synchrony model is well situated to explain priming at the shorter lags that tend to produce scaling, and it may participate at longer lags (and/or practice durations) as well.

DIFFERENT LOCATIONS DO NOT NECESSARILY IMPLY DIFFERENT MECHANISMS

The Weiner and Grill-Spector, Horner, and Wig commentaries all highlight the fact that studies of Repetition Suppression often report findings that vary by brain location. Weiner and Grill-Spector note the challenges facing the Synchrony model in explaining the region- and lag-dependent nature of Repetition Suppression in occipital and temporal brain regions. While no model can currently explain this range of data, we agree that this should be the goal. We would note that while synchrony is a mechanism at one level of description, it is also an emergent phenomenon with multiple possible underlying mechanisms that can apply differentially at different lags and potentially in different brain regions (e.g., spike-frequency adaptation and synaptic depression, electrical synapses between interneurons, spike-timing-dependent plasticity, etc.). Our current experimental focus is simply to detect whether synchronization is occurring in the appropriate experimental contexts and whether it is quantitatively related to the magnitude of repetition priming. In his commentary, Horner rightly makes the point that Repetition Suppression is most strongly related to priming in the prefrontal cortex and that this central issue should not be lost in the discussion. Wig counters, appropriately in our view, that just because occipital Repetition Suppression is more weakly related to repetition priming in certain tasks does not imply that it is irrelevant to priming magnitudes in all tasks. Would a task that emphasizes information represented in occipital areas (e.g., fine shape discriminations) yield a stronger association between occipital Repetition Suppression and priming (see also Martin & Gotts, 2005)? More generally, we would argue that Repetition Suppression effects that are dissociable by brain region or task do not necessarily imply qualitatively distinct lower-level mechanisms. Future experiments will need to clarify the region- and lag-dependence of Repetition Suppression, changes in neural tuning properties, as well as changes in Synchrony. One issue raised by Weiner and Grill-Spector that we would dispute is the exclusive role of high versus low frequency oscillations in local versus long-distance cortical interactions, respectively. Modulations of local synchrony can be in lower frequencies (theta, alpha, beta: E.g., Anderson et al., 2008; Gilbert et al., 2010; Gregoriou, Gotts, & Desimone, 2012) and modulations of long-distance synchrony can be in higher frequencies (gamma: E.g., Buschman & Miller, 2007; Gregoriou et al., 2009a).

NEGATIVE PRIMING AND OTHER PARADIGMS

In the final commentary, Dyson and Alain argue that our proposal has failed to consider the influences of task, time, and context on repetition priming. They cite evidence from EEG/ERP studies in the auditory modality, noting conflicting evidence from negative

priming, perceptual learning of speech tokens, and sensory gating. Some of the differences with our literature review may involve genuine differences between visual and auditory modalities. However, we would reiterate the difficulty of using scalp EEG/ERP measurements to rule out a proposal cast at the level of underlying neural sources. Too many ambiguities are present. Results from paradigms such as negative priming that involve multiple simultaneous stimuli and additional processes (selective attention) may also not be directly comparable to simple identification paradigms with sequentially presented single stimuli.

The Commentaries offered in response to our Discussion Paper highlight the importance and interest in uncovering the mechanism(s) linking Repetition Suppression to one of nature's most powerful learning phenomena, Priming. We again thank our colleagues for their thoughtful and thought-provoking comments on our proposal.

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