

match (or interfere with) the resonance frequency of the oscillation in the spiking responses.

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## Focusing on the frontal cortex

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**Abstract:** Gotts et al. provide a timely review of the major neural models of repetition suppression (RS) and priming. They justifiably call on researchers to focus their attention on the extent to which these phenomena can be explained by changes in synchrony between cortical regions. They are relatively agnostic as to which regions may be critical to RS and priming. Here I argue we should devote more attention to the role of frontal regions, and suggest that there is a need to engage with more cognitive accounts of priming in order to develop a comprehensive neurocognitive account of priming and RS.

Gotts et al. present four neural models designed to capture the complex relationship between repetition suppression (RS) and behavioral priming (henceforth referred to as priming). They support the idea that synchrony, temporally correlated neural firing that allows for increased efficiency of communication between spatially distinct cortical regions, underlies this relationship. I strongly support Gotts et al.'s call for more research focusing on the interaction between cortical regions following stimulus repetition. Their discussion, however, was relatively agnostic concerning the cortical regions we should focus on in order to understand such interactions. I would argue that the prefrontal cortex, more specifically the inferior frontal gyrus (IFG), and its interactions with more posterior perceptual regions, should be the focus of our attention.

Firstly, the IFG has been perhaps the only region that has consistently demonstrated RS across multiple stimulus types including visual objects (e.g., Koutstaal et al., 2001), faces (e.g., Henson et al., 2003), and written (e.g., Barton, Fox, Sekunova, & Iaria, 2010)

and spoken (e.g., Gagnepain et al., 2008) words. Secondly, the IFG has consistently been shown to correlate with priming (e.g., Dobbins, Schnyer, Verfaellie, & Schacter, 2004). Thirdly, transcranial magnetic stimulation to the IFG has been shown to disrupt priming and RS (Wig, Grafton, Demos, & Kelley, 2005). Finally, using magnetoencephalography, visual object repetition has been shown to increase synchrony between frontal and occipitotemporal regions (Ghuman, Bar, Dobbins, & Schnyer, 2008).

It seems the IFG plays a critical and causal role in the production of priming and is therefore a key region on which to focus our attention. Two questions emerge from this discussion: (1) Why has the IFG been relatively overlooked despite this evidence and (2) What role does the IFG play in priming and RS? With regard to the former question, the first possible reason is due to the legacy of particular cognitive accounts of priming, which were largely adopted by the neuroimaging community, that suggest priming relates to the modification of perceptual (and conceptual) representations (Henson, 2003). The second reason is that RS, as measured by fMRI, is often maximal in occipitotemporal perceptual regions. Thus, regions known to be involved in perceptual processing, such as lateral occipital and fusiform regions in the case of object recognition, were (and still are) the pre-dominant cortical regions of focus.

What role does the IFG play in priming and RS? In recent years, there has been a resurgence of interest in the idea that bindings between a stimulus (e.g., a visual object) and a response (e.g., a "yes" decision) can facilitate response selection processes (Logan, 1990). Such stimulus-response (S-R) contributions have now been shown to drive RS in frontal regions (Horner & Henson, 2012). Furthermore, S-R learning has been shown to explain a large proportion of priming variance during long-lag visual classification studies (Horner & Henson, 2009). As such, it seems the IFG may play an important role in the selection of task-appropriate responses, possibly integrating information from multiple cortical sources including, though not limited to, posterior perceptual regions. Importantly, given the localization of S-R contributions to frontal regions and the dominant role it plays in priming, it would seem appropriate to focus our efforts on understanding RS in frontal regions, and how this region communicates with more posterior perceptual regions.

Finally, the above discussion serves to highlight the need to embed cognitive theories of priming and RS (e.g., episodic vs. abstractionist accounts) within

models of the neural mechanisms that underlie such effects (e.g., sharpening vs. synchrony). For example, not only do we need to state how RS results in priming but also what information is being learned (i.e., what representations are being encoded/modified) in order for such phenomena to manifest. Each level of account should serve to shape and constrain the other, allowing for a fuller understanding of the neurocognitive mechanisms that give rise to RS and priming.

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## Repetition suppression and repetition priming are processing outcomes

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**Abstract:** There is considerable evidence that repetition suppression (RS) is a cortical signature of previous exposure to the environment. In many instances RS in specific brain regions is accompanied by improvements in specific behavioral measures; both observations are outcomes of repeated processing. In understanding the mechanism by which brain changes give rise to behavioral changes, it is important to consider what aspect of the environment a given brain area or set of areas processes, and how this might be expressed behaviorally.

Different structures of the brain engage in different forms of information processing. One way of defining the function of a specific brain structure is to examine its methods of computation in service of learning (e.g., Doya, 1999). There is considerable anatomical, neurophysiological, and theoretical evidence to suggest that the cerebral cortex engages in unsupervised learning to reflect the statistics of the environment by forming efficient cortical representations of the organism's experiences. Moreover, different areas of the cerebral cortex learn the statistics of distinct features of the environment, and RS may be a neural signature of this statistical learning. Identifying a mechanism by

which RS produces the behavioral changes that typically accompany repeated processing (i.e., repetition priming) necessitates careful consideration of how RS reflects the processing outcomes of a specific area or set of areas, and what the appropriate behavioral metric for this processing outcome may be.

Drawing from empirical and theoretical sources, Gotts and colleagues describe four potential mechanisms for how RS may result in repetition priming. The authors provide clear and testable predictions for evaluating how these mechanisms may link RS to behavioral facilitation. Their article will be a key source of reference in moving forward with this important endeavor.

In studying the mechanism by which RS may result in repetition priming, it is imperative to remember that both RS and repetition priming are independent measurements of the processing outcomes of repeated experience. It is not necessary that observations of RS in a collection of areas be clearly linked to changes in the observed behavior, or any clear or measurable behavioral measures for that matter. If RS is a neural signature of cortical learning, it is likely that RS observed in different areas is a consequence of different processing outcomes. As such, different areas may reveal that they've learned the statistics of the environment via distinct behavioral measures.

As an example, speeded response times following repeated semantic classification of visually responsive objects is typically accompanied by RS within numerous brain areas including regions of the inferior frontal gyrus, inferior temporal lobes, and occipital cortex. While the behavioral improvements may be a product of increased synchrony between a subset of regions that are involved in decision processes (e.g., between areas within the frontal and temporal cortex; see Ghuman, Bar, Dobbins, & Schnyer, 2008), other regions exhibiting RS need not be directly linked to the measured classification-time improvements.

RS can be eliminated or diminished in certain regions using transient disruption (i.e., TMS; Wig, Grafton, Demos, & Kelley, 2005) or changes in stimulus-to-decision mapping (e.g., Dobbins, Schnyer, Verfaellie, & Schacter, 2004; Horner & Henson, 2008; Wig, Buckner, & Schacter, 2009). The disruption of RS is also accompanied by reductions in the observed behavioral improvements (e.g., response time during semantic classification). However, despite these region-specific reductions in RS, RS is still prominent in other regions that are likely involved in task performance (e.g., regions of the visual cortex—see Figure 4 of Wig