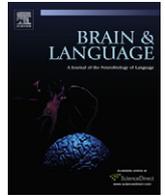


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fMR-Adaptation and the bilingual brain

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ABSTRACT

fMR-Adaptation, where a pair of identical stimuli elicits a smaller neural response than a pair of dissimilar stimuli has been extensively used to study object identification and classification as well as memory. Thus far this technique has found limited application in evaluating brain areas sensitive to meaning, language and control of language production. These studies are reviewed together with suggestions as to how varying inter-stimulus repetition lag, dimension of interest and evaluating inter-individual differences may shed new light on how different languages are acquired and represented in the brain.

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1. Introduction

An enduring set of questions in language research concerns how the brain is able to identify words, to differentiate similar looking or sounding words, and to assign meaning to different words. With two or more languages, how the brain controls the language in use is an additional area of interest. An important goal of functional brain imaging is the mapping of the different features of words—semantics, orthography and phonology to neural substrates. In addition to conventional task-related activation, fMR-Adaptation is a technique that could provide valuable insights into these questions

2. What is fMR-Adaptation?

Adaptation refers to the phenomenon where a pair of identical stimuli elicits a smaller neural response than a pair of dissimilar stimuli. This explains the technique's alternative name 'repetition suppression' (Grill-Spector, Henson, & Martin, 2006). Repetition suppression effects were first observed in the inferior temporal cortex of primates who were shown visual stimuli as electrophysiological recordings were made using intracranial electrodes (Li, Miller, & Desimone, 1993; Miller, Li, & Desimone, 1991). The reduced activation in ventral visual areas in response to repeated stimuli may reflect the reactivation of perceptual representations that have become sparse and selective as a result of prior experience (Wiggs & Martin, 1998). On the other hand, it is important to note that repetition enhancement can also occur under certain conditions (Henson, Shallice, & Dolan, 2000), and may reflect

spared access to existing representations by severely degraded input (Turk-Browne, Yi, Leber, & Chun, 2006b).

Based on similar underlying neurophysiological mechanisms, fMR-Adaptation (Grill-Spector & Malach, 2001; Henson, 2003) involves comparing the difference in BOLD signal elicited by pairs of visual stimuli that are identical and pairs that are dissimilar along some dimension(s) of interest. Adaptation can be used to show that clusters of neurons lying within the same brain region show differential sensitivity to a feature of interest—extending the modest spatial resolution of fMRI and better enabling us to characterize how information is coded in the brain.

3. fMR-Adaptation and repetition priming: a comparison

Repetition priming refers to the facilitated processing of a repeated stimulus. Behaviorally, priming is manifest as a reduction in response time. Neurophysiologically, it is associated with a reduction in the amplitude of evoked potentials and reduced fMRI signal in response to the repeated stimulus. Interestingly, the behavioral and physiological indicators of priming can sometimes be dissociated. This has been described for ERP (Thierry & Wu, 2007) as well as for functional imaging (Ganel et al., 2006; Maccotta & Buckner, 2004; Sayres & Grill-Spector, 2006), suggesting that physiological markers may index different facets of stimulus perception, classification, encoding or processing. As such, functional imaging may provide unique empirical information that simply cannot be inferred from behavior.

Whereas the classic fMR-Adaptation design involved paired or multiple repetitions of the original stimulus immediately following initial presentation, the term has recently been used by memory and attention researchers to refer to paradigms where the repeated stimulus only occurs after tens of seconds and after several

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intervening unrelated stimuli (Eger, Henson, Driver, & Dolan, 2004; Yi & Chun, 2005). This type of design is closer to that used in repetition priming experiments and as will be pointed out later, may index different processes from experiments using the classic design.

4. fMR-Adaptation as a tool to study bilingualism

Given the phonological differences between languages, semantics appeared to be the most suitable aspect to evaluate using adaptation (Chee, Soon, & Lee, 2003). An important attraction of the technique in this regard, is that it can be used to detect and differentiate groups of neurons sensitive to particular stimulus dimensions that are dispersed among neurons sensitive to other features. A distributed arrangement of word representations, ability to code for abstract rules (Wallis, Anderson, & Miller, 2001), as well as the capacity to reconfigure responses according to task demands (Freedman, Riesenhuber, Poggio, & Miller, 2001) constitute a neural architecture consistent with our apparently limitless capacity to categorize words along different dimensions. This architecture is consistent with the observation from numerous imaging studies that common brain regions are activated during semantic processing of different languages. This said, even cognates in different languages must be differentially represented at some level in the brain—a distinction that fMR-Adaptation allows us to make. To illustrate in depth how adaptation has been used to study the bilingual brain, three studies using this paradigm in different populations are reviewed.

4.1. Chee et al. (2003)

The first study investigating the bilingual brain using fMR-Adaptation involved the analysis of responses to passively viewed Chinese characters and English words (Chee et al., 2003). The goal of the investigation was to determine if a word and its translational equivalent share a common neural substrate and whether or not words with the same meaning elicit repetition effects in areas known to be involved in semantic processing. Four different types of stimulus pairs were presented: repeated English concrete nouns, different English concrete nouns, Chinese concrete nouns and their English equivalents, and Chinese concrete nouns and non-equivalent English nouns. Words (or characters) were visually presented for 300 ms and separated by an interval of 400 ms. Volunteers were simply asked to consider the meaning of each word as it was presented.

Meaning-sensitive effects were found in the left prefrontal (inferior as well as dorsal), left mid temporal and left parietal regions for both languages. Language sensitive regions were found in the dorsolateral prefrontal and lateral temporal areas macroscopically overlapping with those sensitive to word meaning. Higher activation in the mixed-language condition could mean that switching costs were incurred, engaging the frontal executive in the process. However, the alternative explanation is that different neuronal arrays were involved in the processing of L2 and L1. Taken together, the findings concerning sensitivity to word meaning as well as language were interpreted as supporting a model of brain organization in which neuronal networks with differential sensitivity to semantics and language co-exist in the same broad location, but are differentiable at a finer level for language (see Fig. 1).

4.2. Klein et al. (2006)

Klein and her colleagues (Klein et al., 2006) had their French-English bilingual volunteers passively listen to auditory words

without any specific task instructions. There were eight types of stimuli which took into account language, meaning and translational equivalence (i.e. a $2 \times 2 \times 2$ (just to be consistent) design). This design served to evaluate differences in within-language and between-language repetition effects. Meaning-sensitive effects were observed in the left superior temporal gyrus and inferior frontal region. While many brain regions were common to L1 and L2, the authors also observed differences in adaptation in the mixed-language conditions for forward translation from L1 to L2. The results were interpreted as supporting the idea that at the lexical level, the neural substrates for L1 and L2 are shared but some neurons within these shared regions showed language specific responses. Thus, this study showed broadly concordant findings to Chee et al.; 2003, extending the original findings to the auditory word domain.

4.3. Crinion et al. (2006)

This study used fMR-Adaptation to evaluate how the brain distinguishes and controls the language in use (Crinion et al., 2006). Three groups of bilingual subjects made a semantic decision on the second word of visually presented, prime-target pairs, for example: locust-SALMON. The semantic decision involved evaluating one of three pre-designated types of perceptual features (relating to leg length, coloration and handle-type). The primes and targets were manipulated in a $2 \times 2 \times 2$ design so as to be similar or different with respect to the language used e.g. lachs-TROUT (semantically related but not identical referents in different languages); trout-SALMON (semantically related in the same language), item relatedness e.g. bathtub-SPOON (semantically unrelated in the same language); and the language of the target word.

The investigators ensured that their experiment focused on evaluating differences in word meaning and language by controlling for the effects of order of language of presentation (which might engender translation direction effects), item specific effects, orthographic and phonologic similarity, as well as response priming.

The most interesting feature of the work was the finding that language-dependent semantic priming selectively involved the left caudate. The authors cited clinical neuropsychological and electrical stimulation studies to support the notion that the caudate may have language production-control functions. This result was corroborated in a later study that found language control processes to be engaged in contexts requiring both languages to remain active (Abutalebi et al., 2007).

Extending prior work that has shown the temporal lobe to be part of a network of brain regions involved in semantic processing (Martin & Chao, 2001; Mummery, Patterson, Hodges, & Price, 1998), the left anterior temporal region was found to be sensitive to word meaning without being sensitive to the language used. Semantic priming occurred regardless of whether the prime and target were in the subjects' first language. Compared to the two prior bilingual studies using the adaptation paradigm (Chee et al., 2003; Klein et al., 2006), the brain region showing sensitivity to meaning was far more restricted. This might have arisen from the different inter-stimulus intervals used (250 vs. 400 ms) as well as the requirement to make very specific feature judgments in this study, a point we next turn to.

5. The role of attention in fMR-Adaptation effects

Early studies used passive viewing of stimuli whereas more contemporary work has examined repetition effects related to a specific task that engages attention in a more consistent manner.

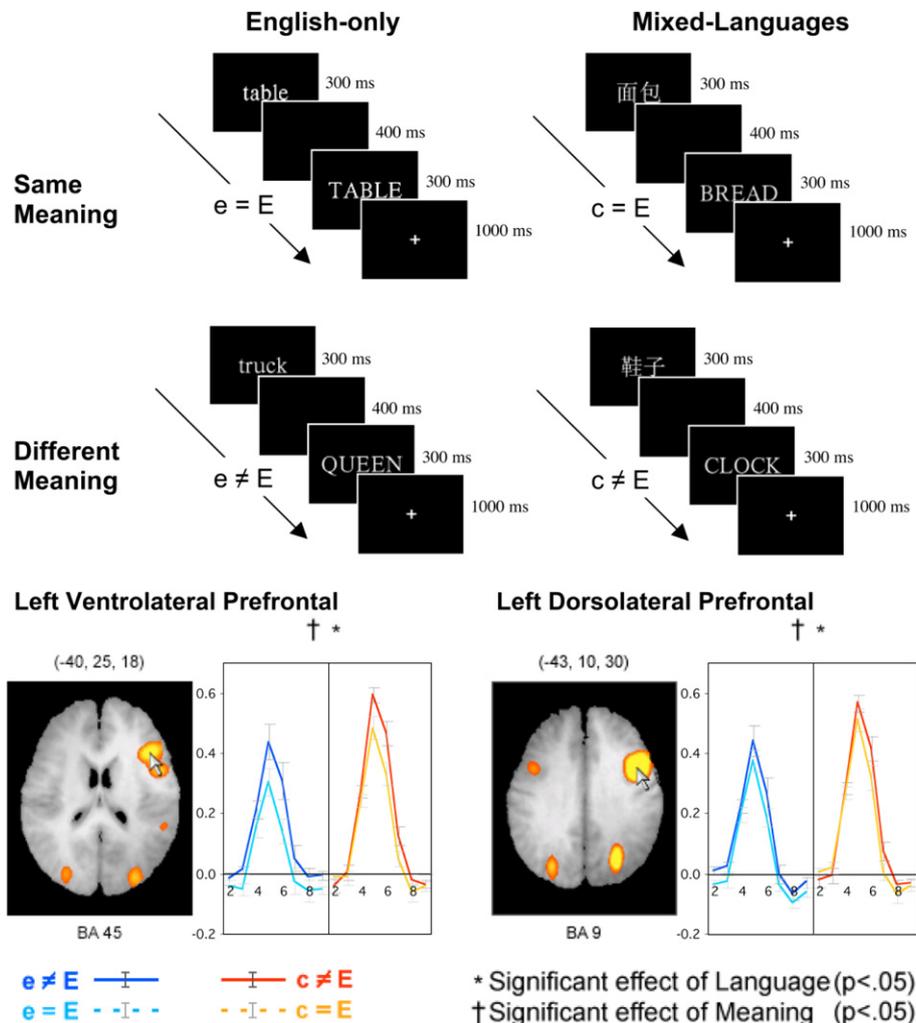


Fig. 1. Upper panel: schematic showing four conditions employed as well as the stimulus timing used in a fMR-Adaptation experiment evaluating the reduction in activation elicited by repeated words in the same language and across languages. Lower panel: group level activation maps relating to the event-related experiment showing particular regions of interest (ROI) and their corresponding average responses to individual conditions. The Talairach coordinates for the activation peak in the ROI are shown above each axial section. The error bars represent ± 1 SE. The horizontal axis shows image number and the vertical axis is percent change in BOLD signal. ROI showing significant effect(s) in the repeated measures ANOVA are marked (Adapted from: Chee et al. (2003)).

Attention has been shown to be critical for adaptation (Eger et al., 2004; Murray & Wojciulik, 2004; Vuilleumier, Schwartz, Duhoux, Dolan, & Driver, 2005; Yi & Chun, 2005). Focusing attention to specific features in the presented stimuli may serve to restrict further processing such that repetition effects become more selective, possibly leading to a smaller locus of adaptation effect, which might explain the findings of the Crinion study.

5.1. New developments in the use of fMR-Adaptation to study cognition

Until recently, adaptation has most commonly been used to study classification or representational properties of visually presented stimuli (Grill-Spector, 2004; Grill-Spector & Malach, 2001). Apart from the studies on language cited, adaptation has attracted interest as a tool to study memory (Epstein, Higgins, & Thompson-Schill, 2005; Turk-Browne, Yi, & Chun, 2006a) and the effects of attention on visual processing (Chee & Tan, 2007; Eger et al., 2004; Murray & Wojciulik, 2004; Vuilleumier et al., 2005; Yi & Chun, 2005).

Adaptation studies, originally involving immediate repetition of test items, have been expanded to include paradigms in which the

repeated stimulus only occurs after a delay and several other unrelated stimuli (Eger et al., 2004; Yi & Chun, 2005). Whether short-lag repetition effects evaluate the same neural processes as repetition over a longer lag is the subject of active investigation (Bentin & Moscovitch, 1988; Henson, Rylands, Ross, Vuilleumier, & Rugg, 2004; Nagy & Rugg, 1989). Although there appear to be no major qualitative differences in adaptation as a function of repetition lag in human fMRI data (Henson et al., 2004), primate electrophysiology data suggest otherwise (Baylis & Rolls, 1987; McMahon & Olson, 2007). Repetition effects involving short-lags and no intervening stimuli result in larger signal differences between novel and repeated items.

Recently, a short repetition lag (<1 s) paired-picture presentation experiment found both larger responses to novel stimuli and greater adaptation to repeated stimuli in individuals with better recognition memory (Chee & Tan, 2007). Short-lags between repeated and novel stimuli generate significantly larger effects than longer lags (Baylis & Rolls, 1987; McMahon & Olson, 2007), and may be better suited to evaluating differences in perceptual processing or word classification.

To illustrate, in a within-language study, one can evaluate how homophones engage different parts of the language network to

varying extents for example, determining if naming “carat” followed by “carrot” will elicit adaptation. For readers in whom phonological processing has priority, adaptation would be expected, whereas for those in whom orthographic or semantic processing has priority, adaptation would be expected to be weak. Across languages, and in the context of learning, this method can be applied to examine how a particular individual attends to semantics, orthography or phonology at various stages of novel word learning. Short-lag repetition designs also serve to eliminate interference effects from intervening stimuli arising from semantic similarity (Klaver et al., 2007).

In contrast, long-lag experiments may be useful in evaluating the durability of memory for novel words or novel word sounds (i.e. words in a foreign language) and in explaining the basis for inter-individual differences in the mastery of new languages. A greater degree of adaptation for repeated, newly learned words would be expected to correspond to a greater degree of learning. This has been shown for spatial navigation skills (Epstein et al., 2005), but it would be of interest to determine if this observation generalizes to language learning.

5.2. Potential application of fMR-Adaptation in studying implicit translation

Cross-language priming is an area that may benefit from the amalgamation of clever experimental design and new methods. Until recently, it was unclear if a fluent bilingual performs internal translation of L2 to L1 automatically (Kroll & deGroot, 1997). A problem with existing designs is that the use of mixed languages during testing encourages automatic translation. A recent ERP study suggests that unconscious translation of L2 to L1 does occur during reading, at least in moderately fluent bilinguals (Thierry & Wu, 2007). This clever experiment involved presenting monolingual English speakers, English–Chinese bilinguals and Chinese monolingual speakers with English prime–target pairs that in some instances had a Chinese translation that shared one (of two) characters. In this way, the effect of hidden repetition priming of Chinese characters could be uncovered. Interestingly, whereas there was no evidence of behavioral priming for the Chinese equivalents of covertly translated words, this was evident in the N400 ERP recording. It would be fascinating to evaluate the neuronal networks involved in unconscious translation process using brain imaging methods.

To investigate how the direction of translation or order of language switching affects brain activation, an event-related fMRI design alternating between initially presenting L1 and initially presenting L2 might be useful. For example, it has been shown that switches from L1 to L2 incurring higher switch costs manifest as higher caudate and anterior cingulate activation (Abutalebi et al., 2008).

6. Future directions

The adaptation paradigm is ripe for use by researchers interested in studying the bilingual brain. By observing individual differences in responses to selectively repeated items, one may evaluate between-subject variation in how associations are formed between words in L1 and L2 and even between words in the same language. This might also prove useful as a tool to study inter-individual differences in the development of semantic or phonological associations required for naming and understanding novel words.

To illustrate, it was recently advanced that the left anterior hippocampal formation and caudate are involved in the buildup of orthographic representations. Words in German, words in a dialect, and pseudowords organized in miniblocks were repeatedly

named; and inference regarding learning was made by observing regional attenuation of fMRI signal with the repeated naming of dialect words (Abutalebi et al., 2007). Using an adaptation design that allows analyses to be confined to successfully learned words instead of a block design that included unlearned words might render such a conclusion more specific to learning.

Thus far, experiments have primarily been focused on visual words and on semantics. There is certainly room to explore how auditory words are processed, evaluating possible strategic differences that prior language experience imposes on phonological processing of novel and familiar word sounds. Finally, as more laboratories become appropriately equipped, there are tremendous opportunities to gain fresh insights from the combination of fMRI and simultaneous event-related studies of word processing using this paradigm.

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References

- Abutalebi, J., Annoni, J. M., Zimine, I., Pegna, A. J., Seghier, M. L., Lee-Jahnke, H., et al. (2008). Language Control and Lexical Competition in Bilinguals. *An Event-Related fMRI Study Cereb Cortex*, 18, 1496–1505.
- Abutalebi, J., Brambati, S. M., Annoni, J. M., Moro, A., Cappa, S. F., & Perani, D. (2007). The neural cost of the auditory perception of language switches: An event-related functional magnetic resonance imaging study in bilinguals. *Journal of Neuroscience*, 27, 13762–13769.
- Abutalebi, J., Keim, R., Brambati, S. M., Tettamanti, M., Cappa, S. F., De Bleser, R., et al. (2007). Late acquisition of literacy in a native language. *Hum Brain Mapp*, 28, 19–33.
- Baylis, G. C., & Rolls, E. T. (1987). Responses of neurons in the inferior temporal cortex in short term and serial recognition memory tasks. *Experimental Brain Research*, 65, 614–622.
- Bentin, S., & Moscovitch, M. (1988). The time course of repetition effects for words and unfamiliar faces. *Journal of Experimental Psychology. General*, 117, 148–160.
- Chee, M. W., Soon, C. S., & Lee, H. L. (2003). Common and segregated neuronal networks for different languages revealed using functional magnetic resonance adaptation. *Journal of Cognitive Neuroscience*, 15, 85–97.
- Chee, M. W., & Tan, J. C. (2007). Inter-relationships between attention, activation, fMR adaptation and long-term memory. *NeuroImage*, 37, 1487–1495.
- Crinion, J., Turner, R., Grogan, A., Hanakawa, T., Noppeney, U., Devlin, J. T., et al. (2006). Language control in the bilingual brain. *Science*, 312, 1537–1540.
- Eger, E., Henson, R. N., Driver, J., & Dolan, R. J. (2004). BOLD repetition decreases in object-responsive ventral visual areas depend on spatial attention. *Journal of Neurophysiology*, 92, 1241–1247.
- Epstein, R. A., Higgins, J. S., & Thompson-Schill, S. L. (2005). Learning places from views: Variation in scene processing as a function of experience and navigational ability. *Journal of Cognitive Neuroscience*, 17, 73–83.
- Freedman, D. J., Riesenhuber, M., Poggio, T., & Miller, E. K. (2001). Categorical representation of visual stimuli in the primate prefrontal cortex. *Science*, 291, 312–316.
- Ganel, T., Gonzalez, C. L., Valyear, K. F., Culham, J. C., Goodale, M. A., & Kohler, S. (2006). The relationship between fMRI adaptation and repetition priming. *NeuroImage*, 32, 1432–1440.
- Grill-Spector, K. (2004). The functional organization of the ventral visual pathway and its relationship to object recognition. In N. Kanwisher & J. Duncan (Eds.), *Functional neuroimaging of visual cognition A* (pp. 171–193). Oxford: Oxford University Press.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Science*, 10, 14–23.
- Grill-Spector, K., & Malach, R. (2001). fMR-Adaptation: A tool for studying the functional properties of human cortical neurons. *Acta Psychologica*, 107, 293–321.
- Henson, R. N. (2003). Neuroimaging studies of priming. *Progress in Neurobiology*, 70, 53–81.
- Henson, R. N., Rylands, A., Ross, E., Vuilleumier, P., & Rugg, M. D. (2004). The effect of repetition lag on electrophysiological and haemodynamic correlates of visual object priming. *NeuroImage*, 21, 1674–1689.
- Henson, R., Shallice, T., & Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. *Science*, 287, 1269–1272.
- Klaver, P., Schnaidt, M., Fell, J., Ruhlmann, J., Elger, C. E., & Fernandez, G. (2007). Functional dissociations in top-down control dependent neural repetition priming. *NeuroImage*, 34, 1733–1743.

- Klein, D., Zatorre, R. J., Chen, J. K., Milner, B., Crane, J., Belin, P., et al. (2006). Bilingual brain organization: A functional magnetic resonance adaptation study. *NeuroImage*, *31*, 366–375.
- Kroll, J. F., & deGroot, A. M. B. (1997). Lexical and conceptual memory in the bilingual mapping from to meaning in two languages. In J. F. Kroll & A. M. B. deGroot (Eds.), *Tutorials in bilingualism: Psycholinguistic perspectives* (pp. 169–199). Mahwah: Lawrence Erlbaum Association.
- Li, L., Miller, E. K., & Desimone, R. (1993). The representation of stimulus familiarity in anterior inferior temporal cortex. *Journal of Neurophysiology*, *69*, 1918–1929.
- Maccotta, L., & Buckner, R. L. (2004). Evidence for neural effects of repetition that directly correlate with behavioral priming. *Journal of Cognitive Neuroscience*, *16*, 1625–1632.
- Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: Structure and processes. *Current Opinion in Neurobiology*, *11*, 194–201.
- McMahon, D. B., & Olson, C. R. (2007). Repetition suppression in monkey infratemporal cortex: Relation to behavioral priming. *Journal of Neurophysiology*, *97*, 3532–3543.
- Miller, E. K., Li, L., & Desimone, R. (1991). A neural mechanism for working and recognition memory in inferior temporal cortex. *Science*, *254*, 1377–1379.
- Mummary, C. J., Patterson, K., Hodges, J. R., & Price, C. J. (1998). Functional neuroanatomy of the semantic system: Divisible by what? *Journal of Cognitive Neuroscience*, *10*, 766–777.
- Murray, S. O., & Wojciulik, E. (2004). Attention increases neural selectivity in the human lateral occipital complex. *Nature Neuroscience*, *7*, 70–74.
- Nagy, M. E., & Rugg, M. D. (1989). Modulation of event-related potentials by word repetition: The effects of inter-item lag. *Psychophysiology*, *26*, 431–436.
- Sayres, R., & Grill-Spector, K. (2006). Object-selective cortex exhibits performance-independent repetition suppression. *Journal of Neurophysiology*, *95*, 995–1007.
- Thierry, G., & Wu, Y. J. (2007). Brain potentials reveal unconscious translation during foreign-language comprehension. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 12530–12535.
- Turk-Browne, N. B., Yi, D. J., & Chun, M. M. (2006a). Linking implicit and explicit memory: Common encoding factors and shared representations. *Neuron*, *49*, 917–927.
- Turk-Browne, N. B., Yi, D. J., Leber, A. B., & Chun, M. M. (2006b). Visual quality determines the direction of neural repetition effects. *Cerebral Cortex*.
- Vuilleumier, P., Schwartz, S., Duhoux, S., Dolan, R. J., & Driver, J. (2005). Selective attention modulates neural substrates of repetition priming and “implicit” visual memory: Suppressions and enhancements revealed by fMRI. *Journal of Cognitive Neuroscience*, *17*, 1245–1260.
- Wallis, J. D., Anderson, K. C., & Miller, E. K. (2001). Single neurons in prefrontal cortex encode abstract rules. *Nature*, *411*, 953–956.
- Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current Opinion in Neurobiology*, *8*, 227–233.
- Yi, D. J., & Chun, M. M. (2005). Attentional modulation of learning-related repetition attenuation effects in human parahippocampal cortex. *Journal of Neuroscience*, *25*, 3593–3600.