***Title page**

fMRI adaptation revisited

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Abstract

Adaptation has been widely used in functional magnetic imaging (fMRI) studies to infer neuronal response properties in human cortex. fMRI adaptation has been criticised because of the complex relationship between fMRI adaptation effects and the multiple neuronal effects that could underlie them. Many of the longstanding concerns about fMRI adaptation have received empirical support from neurophysiological studies over the last decade. We review these studies here, and also consider neuroimaging studies that have investigated how fMRI adaptation effects are influenced by high-level perceptual processes. The results of these studies further emphasize the need to interpret fMRI adaptation results with caution, but they also provide helpful guidance for more accurate interpretation and better experimental design. In addition, we argue that rather than being used as a proxy for measurements of neuronal stimulus selectivity, fMRI adaptation may be most useful for studying population-level adaptation effects across cortical processing hierarchies.

Key words: function imaging, adaptation, repetition suppression, surround suppression

Introduction

Adaptation has long been used in psychophysics and neuroscience to probe the nervous system. The usefulness of adaptation in understanding brain function is perhaps best illustrated by its revealing orientation-tuned mechanisms in the human brain (Blakemore & Campbell, 1969; Blakemore & Hague, 1972). In the early 2000s adaptation was embraced by the neuroimaging community with the use of "fMRI adaptation" to infer neuronal response properties in human brain areas in a wide variety of sensory stimuli and cognitive tasks (Grill-Spector & Malach, 2001). The basic logic of the approach is straightforward. Adaptation causes weakened responses to repeated or prolonged stimuli. If altering the properties of a stimulus causes fMRI responses to recover, this is evidence that a distinct population of neurons has been recruited by the stimulus manipulation. Equivalently, stimulus-specific adaptation effects on fMRI responses indicate the presence of neurons that are selective along the dimension of stimulus manipulation.

Despite its widespread use, fMRI adaptation has been criticized for the potentially complex relationship between neuronal and BOLD (blood oxygenation level dependent) adaptation effects, which can preclude accurate inferences about neuronal tuning. Perhaps partly as a result of this critique, fMRI adaptation has fallen out of favour and been largely superseded by multivariate pattern analysis (MVPA) as the method of choice for inferring neuronal response properties (Haxby et al., 2001; Kamitani & Tong, 2005). MVPA methods, however, have their own issues of interpretation (see Op De Beeck, 2010, for a review).

Here we revisit fMRI adaptation as an experimental approach, motivated by several new findings. First, there has been progress in understanding the neurophysiological effects of adaptation, with results that help clarify the interpretation of BOLD measurements. Second, whereas most of the original critique of fMRI adaptation focused on confounds arising from the underlying "low-level" neurophysiological mechanisms, recent work has shown that fMRI adaptation effects can also be influenced by high-level processes such as attention and expectation. We close by suggesting ways in which fMRI adaptation may still be useful for understanding perceptual and cognitive function.

What are the concerns with fMRI adaptation?

The pitfalls of using fMRI adaptation effects to infer neuronal response properties were reviewed by Krekelberg, Boynton, and van Wezel (2006); Bartels, Logothetis, and Moutoussis (2008); and Grill-Spector, Henson, and Martin (2006). Briefly, these perspectives identified three key issues. First, adaptation effects may involve a range of effects at the neuronal level, including fatigue, sharpened tuning, response facilitation, and altered response dynamics. Depending on the relative importance of these neuronal effects in a given experimental paradigm, one may see a range of behaviours in the BOLD response, making it difficult to infer accurately the underlying neuronal selectivity. Second, it is not clear when adaptation effects reflect changes in the imaged brain area, and when they reflect effects inherited from upstream areas. That is, adaptation can alter the signals sent from early sensory areas to subsequent processing stages, thereby altering the downstream responses. Interpreting adaptation effects as evidence of neuronal response selectivity in the imaged area may therefore be misleading. Third, adaptation effects in fMRI BOLD signal may reflect changes in neurovascular coupling rather than in neuronal responsivity. In the following, we focus on new experimental findings that allow insight into these issues.

Tuning changes

Adaptation is usually thought to reduce neural activity, but there is clear evidence that it can also enhance responses. Numerous studies have shown that adaptation with a stimulus matched to the classical receptive field of a neuron causes a stimulus-specific loss of responsivity. As a result, neurons driven with their preferred stimulus become less responsive, and the tuning of neurons with slightly offset preferences is repelled away from the adapter (Muller, Metha, Krauskopf, & Lennie, 1999; Dragoi, Sharma, & Sur, 2000). By contrast, adaptation effects induced by stimuli larger than the receptive field can lead to a stimulus-specific reduction in surround suppression, and thus to disinhibition and response enhancement (Webb, Dhruv, Solomon, Tailby, & Lennie, 2005; Camp, Tailby, & Solomon, 2009; Wissig & Kohn, 2012). Because the adaptation-induced weakening of surround suppression is stimulus specific, it can also alter neuronal tuning—causing tuning to shift toward the adapter rather than be repelled from it (Kohn & Movshon, 2004; Patterson, Wissig, & Kohn, 2013). Thus, the distinct effects of adaptation on tuning considered by Grill-Spector, Henson, and Martin (2006) — suppression, sharpening and facilitation — can in fact be expressed in the same neurons, and which effects are observed will depend on the balance of excitatory and suppressive inputs that are recruited by the adapter and test stimuli (see Solomon & Kohn, 2014 for review).

fMRI adaptation relies on the logic that stronger adaptation effects—that is, a greater reduction in response to a stimulus matched to the adapter than to an altered test stimulus—indicate greater neuronal selectivity for the manipulated stimulus dimension. Often, fMRI adaptation studies have reported a gradual increase in adaptation magnitude in extrastriate visual areas compared to primary visual cortex (V1; e.g., Boynton & Finney, 2003; Fang, Murray, Kersten, & He, 2005; Larsson, Landy, & Heeger, 2006; Montaser-Kouhsari, Landy, Heeger, & Larsson, 2007; Larsson, Heeger, & Landy, 2010), suggesting greater selectivity in extrastriate cortex. However, these new neurophysiological findings offer an alternative explanation. Standard fMRI paradigms normally use relatively large stimuli, and neurons in higher-stages of cortical processing have larger spatial receptive fields. A large stimulus recruits progressively more excitation, and progressively less surround suppression, in higher stages of visual processing. Thus, one would expect a stronger loss of responsivity in higher cortex, where adaptation effects on surround suppression is reduced, even without a difference in underlying neuronal selectivity.

However, in many cases stronger adaptation effects in higher extrastriate areas have been shown to be consistent with known differences in response properties between areas. For example, stronger and more size-invariant adaptation to objects in ventral stream areas than in V1 corresponds to differences in neuronal stimulus selectivity measured by direct recording techniques (e.g. Sawamura, Orban, & Vogels, 2006; Kovács, Zimmer, Harza, & Vidnyánszky, 2007; Kovács, Cziraki, Vidnyánszky, Schweinberger, & Greenlee, 2008). Inter-areal differences in susceptibility to adaptation to motion-defined boundaries measured with fMRI match differences in neuronal selectivity for such boundaries between macaque visual areas (Larsson, Heeger, & Landy, 2010). Differences in susceptibility to adaptation across areas may therefore reflect a combination of differential disinhibition across areas, the inheritance in higher areas of effects induced in lower areas (discussed below), as well as genuine differences in neuronal stimulus selectivity. Disambiguating these different contributions is non-trivial.

A diagnostic way to control for the confounding influence of surround suppression on fMRI adaptation effects would be to measure how the magnitude of adaptation effects depends on stimulus size; larger stimuli would be predicted to induce stronger weakening of

suppressive surrounds, leading to a reduction in adaptation with increasing stimulus size. To our knowledge, no study has yet systematically addressed the effect of stimulus size on fMRI BOLD adaptation effects. Recent fMRI work does, however, provide evidence for both suppressive and facilitatory adaptation effects in the BOLD signal, consistent with neurophysiological data. Larsson and Harrison (2015) found that adaptation effects for small patches of gratings depend on the spatial relationship between the adapter and subsequent test stimuli. When the adapter was in the same location as the test, BOLD responses in V1 decreased following adaptation (response suppression). When the adapter was displaced relative to the test, responses in V1 instead increased (facilitation), consistent with adaptation of suppressive surrounds in human visual cortex.

Recent neurophysiological studies thus highlight the interplay of excitation and suppression in shaping the effects of adaptation on visual neurons. Adaptation effects in fMRI BOLD measurements are likely to reflect changes in the sensitivity of classical receptive field, suppressive mechanisms, or both, depending on the configuration of the adapting and test stimuli. This interplay is likely to be a significant source of variance in previous fMRI adaptation measurements. These observations also help provide guidance for interpretation of fMRI adaptation effects, particularly if the experimental design includes parametric variations of stimulus size. Finally, the neurophysiological work provides testable predictions about population adaptation effects measured by fMRI (see Box).

Inherited adaptation

Recordings from neurons in the visual pathway indicate that adaptation effects that emerge at early stages of visual processing propagate to downstream areas. For example, spatial adaptation in V1 may reflect convergence of adaptation effects at the level of LGN (Dhruv & Carandini, 2014). Similarly, adaptation effects in extrastriate area MT seem to be inherited from early visual cortex, at least when the stimuli are composed of oriented contours (Kohn & Movshon, 2003, Patterson, Duijnhouwer, Wissig, Krekelberg, & Kohn, 2014*).* Under other stimulus conditions, however, adaptation effects may arise in area MT itself *(*Priebe, Churchland, & Lisberger, 2002*)*. Thus, neural recordings have shown that adaptation effects can propagate through inter-areal circuits, causing robust effects in downstream areas.

Converging evidence also suggests that inherited adaptation effects can influence downstream processing in unexpected ways. In behavioural studies, adaptation to low-level cues (e.g. orientation) can distort high-level face and shape perception (Xu, Dayan, Lipkin, & Qian, 2008; Xu, Liu, Dayan, & Qian, 2012; Dickinson & Badcock, 2012; Dickinson, Mighall, Almeida, Bell, & Badcock, 2013*).* In single neurons, adaptation can alter selectivity for stimulus features other than those present in the adapter, for the simple reason that complex selectivity is built from the representation of simpler properties (Patterson, Wissig, & Kohn, 2014). Adaptation effects in low-level representations can thus derail downstream selectivity for distinct features. Consistent with this, adaptation effects may even induce response selectivity where there was none previously: for example, direction-selective responses in V4 may emerge following motion adaptation (Tolias, Keliris, Smirkanis, & Logothetis, 2005; but see also Ferrera & Maunsell, 2005). Moreover, the effects of adaptation to low-level stimulus features (e.g., local contrast boundaries) in early visual areas may propagate to high-level areas, resulting in a much higher degree of stimulus specificity than expected from the unadapted tuning in these areas (Sawamura, Orban, & Vogels, 2006).

Many fMRI studies have also found evidence of widespread adaptation to low-level

features across extrastriate cortical areas, consistent with inheritance of adaptation effects from V1 (e.g. Murray, Olman, Kersten, 2006; Larsson, Landy, & Heeger, 2006). Three lines of evidence suggest that the bulk of extrastriate adaptation to such simple features originates in V1: first, the tuning of motion adaptation in area MT is very similar to that in V1 (Lee & Lee, 2012), and contrast adaptation in V2 and V3 (but not V4) is nearly identical to that in V1 (Gardner et al., 2005); second, the spatial specificity (i.e. tuning) of direction-selective and orientation-selective adaptation in extrastriate areas is identical to that in V1 (Larsson & Harrison 2015); third, adaptation to motion induces strong motion-selective responses in areas that normally lack such selectivity, including area V4 (Larsson & Harrison 2015).

This evidence for propagation of adaptation effects from lower (upstream) to higher (downstream) areas implies that unless the relative contributions of inherited and intrinsic adaptation can be dissociated, fMRI adaptation effects cannot be interpreted as evidence of neuronal tuning in the imaged areas. Fortunately, single-unit (Priebe, Churchland, & Lisberger, 2002, Kohn & Movshon, 2003) and fMRI studies (Larsson & Harrison 2015) offer a way to dissect the influence of inherited and intrinsic components: by measuring the spatial specificity of adaptation effects and comparing these to the receptive field sizes of the imaged areas. If displacing the test stimulus from the adapter results in a recovery of the fMRI response, then it suggests that the adaptation effect was induced in an area where the receptive field size is smaller than the distance of the displacement. Using new tools to estimate population receptive field sizes from fMRI measurements (Larsson, Landy, & Heeger, 2006; Dumoulin & Wandell 2008) and an understanding that shifting the location of a test stimulus may enhance responses (Larsson & Harrison, 2015), one can compare the spatial extent of adaptation effects to estimates of receptive field size in multiple visual areas, potentially allowing localization of fMRI adaptation effects to specific areas.

Missing links between the BOLD signal and single-neuron adaptation effects

Interpreting adaptation effects in fMRI BOLD response requires understanding if adaptation changes the relationship between neural and vascular activity (neurovascular coupling). There is a lack of direct evidence for adaptation-induced changes in neurovascular coupling, but a recent study by Moradi and Buxton (2013) reported that adaptation changes the coupling between local oxygen metabolism ($CMRO_2$, a measure of energy consumption thought to closely parallel local neural activity) and blood flow, such that BOLD measurements underestimate the magnitude of adaptation effects. Specifically, $CMRO_2$ showed sub-linear summation when doubling the duration of a stimulus block (consistent with adaptation), whereas BOLD responses increased linearly with stimulus duration (consistent with no adaptation). Little is known about the effects of adaptation on neurovascular coupling at finer spatial or temporal scales and no study to date has directly compared neural activity and blood flow during adaptation. More research is needed, both to understand the mechanisms linking neural activity, metabolic demand, and BOLD signals, and in particular how these mechanisms are affected by adaptation.

A closely related issue is that fMRI measurements are inherently population-based, whereas most neurophysiological work has concentrated on individual neurons. As a result, we have a limited understanding of how adaptation affects population neural responses. Several recent studies have compared adaptation effects in single units and local field potentials (LFP), an indirect measure of neuronal population activity. Some of these studies have found population-level effects consistent with those observed in single neurons (De Baene & Vogels 2010; Kaliukhovich & Vogels 2012; von der Behrens,

Bäuerle, Kössl, & Gaese, 2009), but others report conditions where this is not the case (Jia, Smith, & Kohn, 2011). Notably, for long interstimulus-intervals (ISIs) adaptation appears to reduce both the temporal coordination and amplitude of neural population responses (Kaliukhovich & Vogels 2012), whereas for short ISIs coordination can increase even though spiking activity decreases following adaptation (Hansen & Dragoi 2011; see Gotts, Chow, & Martin, 2012 for review). Since hemodynamic responses appear to be related to the coordination of neuronal activity as well as its amplitude (Niessing et al., 2005), adaptation-induced changes in BOLD may reflect changes in either network coordination or firing rates, or both.

In summary, it is clear that linking BOLD measurements to neuronal spiking activity is not trivial. This is not specific to fMRI adaptation, and reflects the greater issues of inferring single-unit properties from population measurements and of understanding to what extent BOLD signals are driven primarily by synaptic activity (see Logothetis & Wandell, 2004 for a review) or spiking output (Lima, Cardoso, Sirotin, & Das, 2014). This difficulty need not preclude the use of fMRI to measure adaptation effects, but does point to a need for better understanding of the relationship between neuronal adaptation effects and adaptation effects as measured by BOLD, ideally by simultaneous measurements of neuronal and hemodynamic responses.

Low-level vs high-level effects of adaptation: attention and expectation

The neurophysiological evidence reviewed above suggests that fMRI adaptation effects will be influenced by multiple low-level ("bottom-up") processing mechanisms. Recent neuroimaging work suggests that additional, high-level ("top-down") effects, can also modulate fMRI adaptation effects. For instance, it is well established that the deployment of attention can confound the interpretation of fMRI adaptation effects, as highlighted in the controversy over one of the first applications of adaptation to fMRI: the demonstration of motion aftereffects (MAE) in human MT+ complex by Tootell et al (1998). The adaptation-induced change in BOLD, interpreted by Tootell et al. as a neural correlate of the MAE, was subsequently shown to depend on attention, in that the effect disappeared when attention was diverted from the adapting and test stimuli (Huk, Ress, & Heeger, 2001). To minimize such attentional confounds, most subsequent fMRI adaptation studies have used attention-demanding tasks to maintain a constant level of attention across conditions.

The use of an attention-demanding task can be problematic, however, if the task involves attending to the adapter or test stimuli. Recent studies suggest that under such circumstances, novelty or "expectation" effects can significantly influence fMRI BOLD adaptation effects. For example, in work aimed at understanding the source of "repetition suppression" (a reduction in responses to repeated presentations of stimuli), Summerfield, Trittschuh, Monti, Mesulam, and Egner (2008) studied the effects of repetitive presentation of face stimuli on BOLD signals in the fusiform face area (FFA). BOLD signals were larger when the stimulus was less frequent (i.e. unexpected), than when they were more frequent. Summerfield et al. concluded that repetition effects were more likely to reflect stimulus expectation, rather than adaptation. Crucially, however, the study required subjects to attend to the adapting stimuli. Larsson and Smith (2012) replicated the results of Summerfield et al., but showed that the effect of expectation disappeared when subjects performed a demanding task at fixation, diverting attention from the adapting stimuli. Nonetheless, repetition suppression was still observed when attention was diverted, consistent with neuronal adaptation effects.

Nevertheless, it remains possible that expectation influences fMRI adaptation effects even

without a confounding influence of attention. For example, Gardner et al. (2005) found that the effects of contrast adaptation on BOLD responses in V4 more closely reflected stimulus novelty (or expectation) rather than contrast changes, even though a demanding task at fixation was used to divert attention from the adapting stimuli (notably, in V1-V3 there was no effect of novelty). Moreover, expectation effects in EEG measurements (known as mismatch negativity) have been found even when attention is diverted or subjects unconscious (see Stefanics, Kremlacek, & Czigler, 2014 for a review).

Further studies will be necessary to determine how task manipulations (e.g. varying the relative probability of stimulus repetitions vs. non-repetitions) can influence and control for top-down effects, and how to dissociate between bottom-up and top-down contributions to fMRI adaptation effects. It is also not clear to what extent top-down effects due to attention and/or expectation might directly interact with adaptation, for example by sharpening the tuning of neuronal responses (Kok, Jehee, & de Lange, 2012). Further complicating matters is the fact that single-unit recordings from non-human primates have found no evidence for expectation effects in neuronal spiking responses (Kaliukhovich & Vogels 2011; Fishman & Steinschneider, 2012; Kaliukhovich & Vogels, 2014), raising the question of whether fMRI is particularly susceptible to such effects or, alternatively, whether expectation effects are unique to the human cortex. fMRI studies in non-human primates and other model species may provide a way to resolve this issue.

What can be done?

The original critiques fMRI adaptation focused on the difficulty of reliably relating BOLD effects to underlying neuronal response properties. Work over the last decade has reinforced these concerns. Many of the initial confounds have been confirmed by experimental studies, and new observations further complicate interpretation of fMRI adaptation effects.

Nevertheless, we believe it is a mistake to conclude that measuring adaptation effects with fMRI has no purpose. fMRI adaptation as a measure of neuronal selectivity suffers from the limitations outlined above, but (at least compared to MVPA techniques) the approach does have the virtue of directly tapping into comparatively well defined underlying neurophysiological mechanisms, allowing testable assumptions to be made about mechanistic links between neurophysiology and BOLD measurements. Provided the results are interpreted with caution, and the experiments are carefully designed to minimize the confounds reviewed above, fMRI adaptation studies can help guide and provide impetus for more direct measurements. The use of parametric experimental designs is critical, since these allow the various low-level and high-level influences on adaptation effects to be systematically disentangled. Used in this manner, fMRI adaptation can be a useful complement to other measurements, even though it may not always provide conclusive evidence on its own.

In addition, we believe that fMRI adaptation has particular promise and merit in light of its capacity to study population-level consequences of adaptation in its own right. Specifically, the ability of fMRI to simultaneously measure correlates of neural activity across multiple brain regions means that fMRI adaptation is particularly suitable to addressing questions about how adaptation cascades across sensory hierarchies, particularly in brain areas that are not easily accessible with direct neuronal recordings or invasive neuronal population measurements, such as LFP or optical imaging. In this context, methods to trace the inheritance of adaptation effects using spatially selective adaptation (Larsson & Harrison, 2015) hold promise, as well as techniques that measure the tuning of adaptation across

cortical areas (Lee & Lee, 2012). A full understanding of the relationship between single-neuron and population measurements of adaptation effects will also require concerted effort to conduct parallel and directly comparable experiments with fMRI and direct neuronal recordings. Key to progress in this area is a better understanding of the mechanisms of neurovascular coupling and how these may be affected by adaptation.

BOX: Open questions

Does adaptation to specific stimulus features occur at multiple stages in the visual hierarchy, or are effects induced at a particular stage?

Do mechanisms and properties of adaptation differ between early and high levels of visual processing?

How does adaptation affect neurovascular coupling at different spatial scales?

How do high-level adaptation effects affect responses at earlier levels?

What is the relationship between adaptation of single neurons and populations?

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