WHAT HAS VISION SCIENCE TAUGHT US ABOUT FMRI?

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The field of vision science, like other domains of cognitive neuroscience, has widely adopted functional MRI as one of its core tools. This has led some researchers to ask how much, if anything, have we learnt about the human visual system from fMRI. A recent symposium at the annual meeting of the Vision Sciences Society was dedicated to this question (Puce et al., 2021). Here, we draw attention to the fact that many vision scientists have used fMRI to answer the opposite question:

What has our existing knowledge of the visual system taught us about functional MRI?

fMRI's potential as a tool for advancing our understanding of brain function depends, in part, on the properties of the tool and the signal it measures. We observe that vision science has been especially fruitful in characterising the fMRI measurement, helping to address many basic questions, such as:

1. What biophysical properties are measured by fMRI?
2. What types of neural signals are measured by fMRI?
3. Does the fMRI signal obey temporal linearity?
4. Does a negative response in blood-oxygen-level-dependent (BOLD) signal arise from a reduction in neural activity?
5. Does the fMRI signal reflect the activity of large veins or small veins, and can these be distinguished?
6. What is the smallest spatial scale of neural activity that can be resolved by fMRI?
7. What are appropriate large-scale parcellations of cortex, as measured by fMRI?
8. Can we link fMRI measures to neural tuning properties? Or is it too coarse-scale a measure?
9. Can we link fMRI to the information content represented in brain areas?
10. Are computational fMRI methods reproducible?

In the long run, scientists and clinicians are more interested in understanding brain function than the tools used to measure it. But the former depends on the latter. Here, we focus on how the systematic nature of vision science has been used to address the questions above.

WHAT BIOPHYSICAL PROPERTIES ARE MEASURED BY FMRI?

Early fMRI studies deduced that neural activity was linked to oxygen consumption (Belliveau et al., 1991; Ogawa, Lee, Kay, et al., 1990; Ogawa, Lee, Nayak, et al., 1990). However, it was unknown whether neural activity causes the BOLD signal to increase (due to increased supply of oxygenated blood) or decrease (due to increased consumption of oxygen). Ogawa and colleagues (1992) found that visual stimulation increased the water proton signal (which is influenced by the nearby substrate) in primary visual cortex (V1), and this change could be followed in time. Shortening the TE reduced the fMRI signal, indicating that signal changes are caused by a change in T_2* relaxation. This was the first human study to show that a stimulus drives an intrinsic contrast agent (changes in the concentration of deoxyhemoglobin in cerebral blood) and that this is what fMRI measures. This study used visual stimulation because the researchers knew where in the cortex to look for responses and because they knew what stimulus to use to produce strong neural activity that could be easily controlled. It would have made little sense to attempt to make discoveries about the neural basis of perception while simultaneously trying to learn how fMRI works.

WHAT TYPES OF NEURAL SIGNALS ARE MEASURED BY FMRI?

A major question in the history of fMRI is: what aspects of neural activity give rise to the BOLD signal? It is likely that many facets of neural activity influence the BOLD signal and there is not a single, simple answer to this question (and we do not attempt to answer this question here). However, vision science found a useful way to reframe and address this question, by using known properties of the visual system in specific brain areas and well-oiled stimulus regimes.

For example, Rees and colleagues (2000) used visual map hMT+ to explore the neural basis of the fMRI signal. The signal in hMT+ increased linearly with stimulus motion coherence, as did prior measurements of average single neuron firing rates in monkey MT, linking these two signals together. This found support in a follow-up from Heeger and colleagues (2000) who compared the fMRI signal in human V1 with electrophysiological recordings of neural firing from monkey V1. Both measurements were driven by stimuli that systematically varied in contrast. Moreover, there was a proportional relationship between fMRI signal and the firing rate of V1 neurons. Similarly, Gardner and colleagues (2005) established a quantitative link between the fMRI and the electrophysiological contrast response. Using an adaptation experiment, they were able to match the horizontal shift of the adapted fMRI contrast response function with the shift found in previous animal studies (Ohzawa et al., 1982; Sclar et al., 1990), thereby validating that the fMRI contrast response function behaves similarly to that from electrophysiology.

Similarly, Winawer and colleagues (2013) measured the spatial summation of visual stimuli to investigate the relation between the fMRI BOLD signal and electrocorticographic (ECoG) responses in visual cortex. BOLD and broadband ECoG responses had the same sub-additive spatial summation, whereas stimulus locked ECoG responses did not. They concluded that asynchronous broadband signals (closely correlated with spiking) are an important contributing factor to the BOLD signal. Other studies have used carefully controlled stimuli and a neural model to confirm that the broadband response in ECoG is well matched to the BOLD signal, but that some additional variance in the BOLD signal is related to the power of low frequency oscillations in ECoG (Hermes et al., 2019). This finding supports the claim that the BOLD signal is influenced by neural signals other than spiking (Logothetis & Wandell, 2004).

It was not necessary to complete simultaneous measurements in these studies because a quantitative link was enabled by matching stimulus parameters and recording locations. These studies shed light on the neural basis of the fMRI signal not by directly comparing the fMRI response to neural activity (which have different units) but by comparing them with reference to parametric variations in the visual stimulus. Recently, these 'stimulus-referred' approaches have been expanded to 'image computable' approaches (Kay et al., 2008), which can provide deeper understanding of how responses at the neural level translate to population responses measured by fMRI (Gardner & Merriam, 2021; Roth et al., 2018).

DOES THE FMRI SIGNAL OBEY TEMPORAL LINEARITY?

Many fMRI analyses and experimental designs (especially fast, event-related designs) rely on the assumptions that the fMRI signal sums approximately linearly in time and can be averaged across trials. Boynton and colleagues (1996) hypothesised and tested a *'linear transform model'* of the fMRI signal, in which V1 neural activity is a nonlinear function of stimulus contrast and the corresponding fMRI signal is a linear transform of this neural activity. Stimulus contrast and duration influenced the fMRI signal; increasing stimulus contrast monotonically scaled the magnitude of the fMRI signal and shortening the stimulus duration decreased the fMRI signal. The linear transform model was consistent with their data; the stimulus-

evoked fMRI responses could be predicted by convolving the predicted neural time-course with a *shift-invariant linear temporal filter* (Boynton et al., 2012). Thus, the hemodynamic response function (HRF) is approximately linear in time. One caveat is that the brief stimuli gave a larger than expected response predicted by this linearity, perhaps due to neural adaptation or transient effects. Further, Dale & Buckner (1997) investigated whether selective averaging techniques could be applied to visually evoked fMRI responses. They found that the fMRI signal can be linearly summed across both short and intermixed trials. These two studies, using simple contrast patterns of variable duration, laid the basis for thousands of subsequent event-related fMRI studies; however, the nature of the fMRI signal itself had to be first established.

DOES A NEGATIVE BOLD RESPONSE ARISE FROM A REDUCTION IN NEURAL ACTIVITY?

Shmuel and colleagues (2002) addressed a fundamental question in neuroimaging: does a negative BOLD response imply a reduction in neural activity or is it a purely vascular phenomenon (Wade, 2002)? They answered this by characterising negative BOLD in human V1-V3. Stimulus-contrast and stimulus-duration dependent changes in positive BOLD were mirrored in negative BOLD. To establish that the BOLD signal was negative, they defined a meaningful baseline as the response to a uniform field (mean luminance). They justified this choice based on classic vision science findings from Hubel & Wiesel (1962) that demonstrated that the responses of neurons in early visual cortex are largely insensitive to mean luminance, driven instead by contrast. To probe the coupling between positive and negative BOLD, Schumel and colleagues (2002) interleaved fMRI BOLD scans and scans that measured cerebral blood flow. Clusters of negative BOLD were spatially correlated with reductions in cerebral blood flow, indicating that negative BOLD is due to a decrease in the rate of oxygen consumption, reflecting a decrease in neural activity in response to neural suppression. The locations of positive and negative BOLD on the cortical surface, combined with stimulus selection, enabled the researchers to interpret the results in terms of neural receptive fields (surround suppression). This finding was supported in a follow-up study, where Shmuel and colleagues (2006) showed that negative BOLD is associated with local decreases in neural activity measured from electrophysiology. Again, the value in these studies was a new characterisation of one part of the fMRI signal, rather than a discovery of how visual circuits work.

DOES THE FMRI SIGNAL REFLECT THE ACTIVITY OF LARGE VEINS OR SMALL VEINS, AND CAN THESE BE DISTINGUISHED?

Artefacts in the fMRI signal can have vascular origins. Vascular draining can contaminate fMRI signal from any region of the cortex in which large veins exist, posing a potentially fundamental problem of interpretation of the fMRI signal: *"The realization in 1993 of the large vein contribution was highly disturbing to us. Large veins drain blood from large patches of cortex and their distribution is spatially sparse. Therefore, they cannot provide high spatial fidelity to neuronal activity in functional imaging."* (Menon et al., 1993; Uğurbil, 2018). Understanding this complication for the entire field of fMRI was best addressed by harnessing known properties of neural circuits. Vision science enables specific predictions about expected fMRI responses, including their location, strength, and the timing of their activation. Thus, visual stimulation is well-suited to detect anomalous responses and then link these responses to vascular artefacts (e.g. Lee et al., 1995; Winawer et al., 2010). Recent studies have used visual experiments and computational modelling to clarify the ability (and limit) of fMRI to distinguish neural effects from vascular confounds at high spatial resolution (Kay et al., 2019, 2020). The general findings are that while vessel-related limits are certainly real, fMRI can nonetheless be used to reliably probe neural function at the millimetre scale.

WHAT IS THE SMALLEST SPATIAL SCALE OF NEURAL ACTIVITY THAT CAN BE RESOLVED BY FMRI?

The organisation of visual areas into spatial maps enables estimation of the point-spread or line-spread function--the spatial extent of activation on cortex from a small stimulus. In V1, the line spread function (full width at half max) was estimated to be about 3.5 mm (Engel et al., 1997). To determine whether neural activity can be resolved by fMRI at an even finer scale than the line function, the spatial pattern of neural activity must be precisely tailored. Vision science provided the theory on how to do this. The organisation of ocular dominance columns in V1 was established in animal models many years before their initial measurement using fMRI (Horton & Hocking, 1996; Hubel & Wiesel, 1963; Wiesel & Hubel, 1963). It was already known that ocular dominance columns are ~1 mm wide and each column's ocular selectivity varies at a fine scale. Thus, ocular dominance columns were an ideal model for investigating the spatial resolvability of the fMRI signal, which may be limited by vascular blurring. Indeed, fMRI signals driven by visual input to the left or right eye can be reliably resolved by some fMRI sequences (Cheng et al., 2001; Yacoub et al., 2007), confirming the submillimeter resolvability of the fMRI signal. These findings provided guidance to other researchers seeking to find new structures in the human brain at a fine spatial scale.

WHAT ARE APPROPRIATE LARGE-SCALE PARCELLATIONS OF CORTEX, AS MEASURED BY FMRI?

One benefit of fMRI over other methods of probing brain function is its large field of view: one can sample the BOLD signal across the whole brain every second or so. This gives rise to the possibility of using fMRI to understand how (and whether) the brain is organised into discrete areas. One proposal for delineating cerebral cortex into discrete areas is by function, cytoarchitecture, connectivity, and topography (Van Essen & Maunsell, 1983). These criteria have been used to understand the parcellation of visual cortex and validate fMRI-based parcellation methods across the cerebral cortex. For example, Laumann and colleagues (2015) used resting state functional connectivity to parcellate a highly-scanned individual's cortex, whereas Glasser and colleagues (2016) used a semi-automated neuroanatomical approach to parcellate group-level multimodal data from the Human Connectome Project (HCP). However, these criteria for parcellation do not necessarily lead to unique solutions. The computed parcellations were validated via their correspondence with retinotopic maps, especially V1-V3, as their borders are well-defined. Where parcellation schemes differed from known retinotopic maps, the authors could identify limitations in the method and possible artefacts in the fMRI signal.

CAN WE LINK FMRI RESPONSES TO NEURAL TUNING PROPERTIES? OR IS IT TOO COARSE-SCALE A MEASURE?

The population receptive field (pRF) model (Dumoulin & Wandell, 2008) provides a quantitative framework to link the fMRI signal with neural response properties. This framework is the genesis of many computational approaches to fMRI. The pRF model is defined in terms of input parameters that are informed by theory of visual receptive fields. Since its inception and initial application, the pRF model has been used to understand topographic organisation in regards to other stimulus types and cortical regions: somatosensory cortex (Puckett et al., 2020; Schellekens et al., 2021; Wang et al., 2021), auditory cortex (Thomas et al., 2015), numerosity maps in parietal cortex (Harvey et al., 2013; Harvey & Dumoulin, 2017; van Dijk et al., 2021), sensory substitution (Hofstetter et al., 2021), and semantic space (Huth et al., 2012). Having a domain like vision science, in which some of the results are expected from prior knowledge, has provided a solid foundation for the extension of this approach to other domains; for example, the pRF model has

been expanded to assess canonical computation of normalisation that is thought to occur throughout the brain (Aqil et al., 2021). This forward modelling approach provides an alternative to the subtraction approach (measuring contrast maps between stimuli, task, or groups) (Van Orden & Paap, 1997), affording greater generalisation and explanatory depth.

CAN WE LINK FMRI TO THE INFORMATION CONTENT REPRESENTED IN BRAIN AREAS?

Popular classification and pattern-analysis fMRI analyses were first developed using vision experiments. Multivariate pattern analysis was developed using fMRI responses to faces, objects, and grating orientation in visual cortex (Haxby et al., 2001; Kamitani & Tong, 2005), and representational similarity analysis was developed using fMRI responses to categorical visual object representations in ventral temporal cortex (Kriegeskorte et al., 2008). Similarly, the fMRI-adaptation studies were first developed by assessing fMRI responses to changes in the properties of object stimuli in lateral occipital complex (LOC), and is now used to study the functional properties of cortical neurons across different neural systems (Grill-Spector & Malach, 2001).

ARE COMPUTATIONAL FMRI METHODS REPRODUCABLE?

Attention has been placed on the reproducibility of psychology (Open Science Collaboration, 2015) and neuroimaging studies (Botvinik-Nezer et al., 2020; Poldrack et al., 2017). Human retinotopic maps are highly reproducible (Benson et al., 2018; Himmelberg et al., 2021; Lage-Castellanos et al., 2020; Lerma-Usabiaga et al., 2020; van Dijk et al., 2016) and large, publicly available datasets of fMRI responses in visual cortex, such as the HCP Retinotopy (Benson et al., 2018) and NSD datasets (Allen et al., 2022), are at the forefront of understanding brain function. This high level of reproducibility is due to the implementation of an explicit computational approach in characterising the fMRI signal.

WHY HAS VISION SCIENCE BEEN SO USEFUL FOR FMRI?

The methods underlying vision science guide us on how to drive the system with large signals that are spatially and temporally precise. For example, established knowledge of visual processing tells us that spatial and temporal contrast are more important stimulus parameters than luminance, and these parameters will drive the largest fMRI signal. One probably would not want to use, for example, emotion, as a tool to test the temporal linearity of the BOLD response, as experimenters cannot precisely control its onset, offset, and intensity (however, one might apply the linearity findings from visual neuroimaging to help model the responses in a study of emotion). Likewise, the organisation of the visual system is well-documented, allowing for highly accurate localisation. Finally, vision science equips us with tools to parametrically manipulate the strength of the neural signal. We know that contrast is the currency of the visual system, and we understand how varying the contrast of a stimulus will drive both fMRI and neural signals. This allows researchers to define the fMRI response in units of visual stimulus and compare the fMRI response with measurements from other instruments.

The systematic (albeit tedious) nature of vision science has paid off; it has advanced our understanding of fMRI, starting with the BOLD signal and more recently with the development of computational models to characterise the fMRI response. Although we have focused on fMRI, a similar approach can be used to better understand other forms of brain measurement technology, such as functional ultrasound (Macé et al., 2011) or portable modular quantum magnetometer systems (Tierney et al., 2019). Overall, the advancement in our understanding of fMRI afforded through vision science has benefited psychology, by

allowing psychologists to non-invasively measure the neural basis of a whole array of human behaviours, thereby shaping the way we think about human psychology, and medicine, by allowing medical researchers to detect changes in cortical neural circuit functioning in response to disease or therapy.

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