

## Instantaneous Stimulus Paradigm: Cortical network and dynamics of figure-ground organization

**Lora T. Likova, Christopher W. Tyler**

The Smith-Kettlewell Eye Research Institute  
San Francisco, CA, USA

[lora@ski.org](mailto:lora@ski.org)

### ABSTRACT

To reveal the cortical network underlying figure/ground perception and to understand its neural dynamics, we developed a novel paradigm that creates distinct and prolonged percepts of spatial structures by instantaneous refreshes in random dot fields. Three different forms of spatial configuration were generated by: (i) updating the whole stimulus field, (ii) updating the ground region only (negative-figure), and (iii) updating the figure and ground regions in brief temporal asynchrony. fMRI responses were measured throughout the brain. As expected, activation by the homogenous whole-field update was focused onto the posterior part of the brain, but distinct networks extending beyond the occipital lobe into the parietal and frontal cortex were activated by the figure/ground and by the negative-figure configurations. The instantaneous stimulus paradigm generated a wide variety of BOLD waveforms and corresponding neural response estimates throughout the network. Such expressly different responses evoked by differential stimulation of the identical cortical regions assure that the differences could be securely attributed to the neural dynamics, not to spatial variations in the hemodynamic response function. The activation pattern for figure/ground implies a widely distributed neural architecture, distinct from the control conditions. Even where activations are partially overlapping, an integrated analysis of the BOLD response properties will enable the functional specificity of the cortical areas to be distinguished.

**Key words:** Cerebral cortex, Perceptual organization, Figure/ground, Asynchrony, Transients, Structure-from-transients, Neural response, BOLD Waveform.

### INTRODUCTION

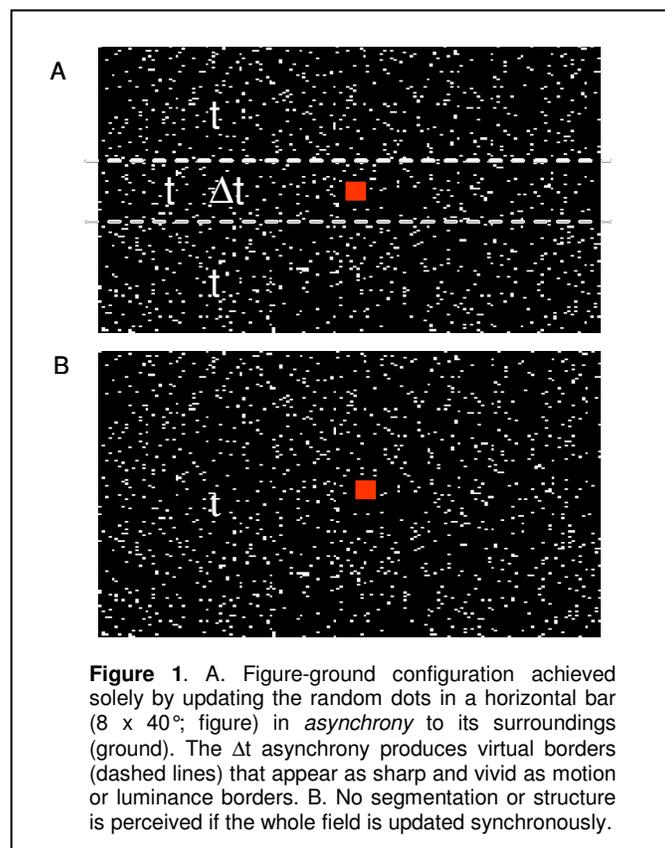
Segmentation and figure-ground organization are basic mechanisms involved in perception of visual scene. Utilizing functional magneto-resonance imaging (fMRI) we previously found, for the first time in the human brain, *suppressive top-down* modulation underlying the visual *figure-ground categorization*. The model accounting for the data throughout the occipital lobe identifies hMT+ as the source driving suppression in the V1/2 retinotopic representations of the *ground*-regions (Likova & Tyler, 2005). The figure/ground and the control structures were defined solely by temporal asynchrony between the noise transitions in corresponding regions of a field of visual noise. We term this phenomenon 'Structure-from-Asynchrony' (SfA). When a region meets the criteria for figure (e.g., smaller, surrounded) versus ground (larger, surrounding), the SfA is capable of supporting strong figure-ground percepts. Importantly, however, when these criteria are not met, the regional segregation mechanisms still operate but no categorization of the regions as figure versus ground is perceived.

Figure-ground is a basic mechanism of perceptual organization with critical importance for theories of shape, object recognition, and attention. The region categorized by the brain as a 'figure' appears closer to the observer, the contour 'belongs to it' and thus a shape is encoded for the figural region only, while the ground is 'shapeless' and perceived as extended behind the figure and the contour (Rubin, 1921). Recent neurophysiological and fMRI studies (Kourtzi & Kanwisher, 2000; Baylis & Driver, 2001) support its determinative role in shape perception. However, conceptualizing figure-ground as an active *categorization* process instead of simply the figure-ground assignment both gives it the status of a more general paradigm for studying object recognition and perceptual categorization, and implies a mechanism that itself incorporates top-down feedback from yet higher cortical areas like the inferotemporal and dorsolateral prefrontal cortices (which are known to be active in object recognition tasks (Hayes et al., 2004; Pihlajamaki et al., 2005; Hautzel et al., 2002; Mottaghy et al., 2002; Pollmann & von Cramon, 2000)). In spite of the long-standing interest in figure/ground organization, its underlying mechanism is still not known. What neural architecture allows local and global information to be combined in a rapid way, as necessary for figure-ground? Our previous study revealed that even at the level of the occipital cortex there is a network with an interesting architecture, incorporating a suppressive feedback. Is this the whole story? Do the perceptual organization mechanisms, and in particular, the figure/ground mechanism, extend beyond the occipital lobe?

The present study has a three-fold purpose: (i) To establish the whole brain network for figure/ground categorization, (ii) to dissect the processing stream to understand its dynamics, and (iii) to probe if variations in BOLD waveforms can

be a basis for “reading” the underlying *neuronal* activity. For these purposes we developed and employed a novel paradigm that creates distinct and prolonged percept of spatial structures by *instantaneous* refreshes in random dot fields. To our knowledge this is the first fMRI study to employ an instantaneous paradigm. Our paradigm assures strong measurable and differentiating BOLD signals for a stimulus input effectively equivalent to an instantaneous (Dirac) impulse, with effectively zero duration. This methodological innovation has important theoretical advantages and consequences for the future analysis of temporal dynamics and time-resolved fMRI explorations because measured response can be treated as an impulse response kernel for linear analyses of the responses to all other stimulus waveforms.

Three different classes of spatial configurations were developed. (i) A non-structured change was generated by refreshing the random dots synchronously in the *whole* stimulus field, (ii) a figure-ground configuration was generated by brief temporal asynchrony (SfA) and (iii) and negative figure (‘hole’) was generated by refreshing the ground region only. The SfA paradigm employs perceived borders defined solely by transient asynchrony between refreshed regions of random-dot fields. Kandil & Fahle (2001, 2003; see Blake & Lee, 2005, for a review) have shown that accurate shape processing is possible with such transient asynchrony borders. Regions of the field that undergo synchronous noise replacement are perceptually integrated into unified zones (despite the fact that the noise is spatially uncorrelated from frame to frame), while the boundaries defined by asynchrony are seen as sharp segmentations between the regions.



To estimate the dynamics of the neural activation to these stimulus types, we compared the BOLD signal waveforms for each stimulus type throughout the cerebral cortex. In many studies, cortical activation is determined by convolution of the measured BOLD signal with a standard response kernel of the blood-specific hemodynamic response function (HRF). This approach generates the cortical activation pattern under the assumption that the HRF has a *uniform* waveform in all parts of the cortex (although it may differ from subject to subject, and the exact waveform for a given subject is often empirically determined; Friston, 2005; Handwerker et al., 2004).

The uniform HRF approach (see Figure 6A, as well) is also based on the implicit assumption that the neural response to a given stimulus has a stereotypic waveform throughout the cortex, or at least that it is not sufficiently different to significantly impact the shape of the HRF. This assumption was evaluated by Handwerker et al. (2004) for alternating checkerboard stimuli with a 2 sec period. For most subjects, there were only minor differences across the cortex that

could be attributed to difference in the vascular structure in different brain regions (DeZwart et al., 2005), although such effects would be expected to be small if the BOLD response analysis was restricted to voxels lying within the cortex itself. However, in some cases there were large differences in the BOLD waveform, particularly in the degree of inhibitory rebound, among cortical regions. It seems likely that these differences reflected differences in the neural responses driving the BOLD signal. Substantial BOLD differences with tasks involving different behavioral delays have been reported by Bandettini & Cox (2000), Miezin et al. (2000), Richter et al. (2000), and d'Avossa et al. (2003).

What had never been studied is the differential neural involvement response waveforms to *ultra-brief* stimuli of various types *within the same* cortical regions. It is generally assumed that, despite their perceptual differences, such stimuli would all generate the same BOLD waveform for all stimulus types. Thus, revealing any significant deviation from that prediction in the BOLD waveform elicited in *one and the same* cortical area can contribute to revealing the specifics of the underlying neural processing and enhance the understanding of the recurrent network of extended perceptual responses to complex stimulus configurations.

## METHODS

### Stimuli

Based on our ultra-brief paradigm of sparsely distributed over time instantaneous updates that differ only in their location throughout the random dot field, three stimulus types were generated: (i) *Uniform Field* - by updating the random dots in the whole stimulus field, (ii) *Negative Figure (or 'hole')* - by updating the background only, and (iii) the *Figure-Ground* configuration was defined by brief temporal asynchrony between updates in the figure and the background region. The delay between the two regional updates was 60 msec, but the updates were instantaneous in each region. The SfA paradigm, applied in the figure/ground stimulation, differs from the standard approaches by introducing asynchrony in the noise updates in specified zones of a large field of random noise dots to achieve spatiotemporal segmentation. The noise elements were 'featureless' pixel-size dots with uncorrelated positions from frame to frame.

Stimuli for the sparse event-related fMRI design consisted of presenting in a random order each of the three types of instantaneous stimulus transition to a new stationary dot field. The time between the instantaneous events was 18 sec on average. All stimuli were random dot fields of 24 x 20°. The experiment was repeated 10 times in different random orders in the same session.

### Scanning procedure

The fMRI responses were collected with an 8-channel head coil in a GE Signa 3T scanner at the University of California, San Francisco. There were 40 axial slices at 1.5 s TR, with TE of 30 ms and flip angle 70°, providing 3 x 3 x 3 mm voxels throughout the whole brain. The stimuli were presented in an Avotec system at 1024 x 768 pixel resolution. Observers were required to maintain fixation on a red 4 x 4 pixel fixation point at the center of the stimulus. To equate attention between the test and the null stimuli a global dimming task was incorporated: the observers were asked to detect the instantaneous changes in the luminance of the stimulus at an average rate of 1 per 20 frames.

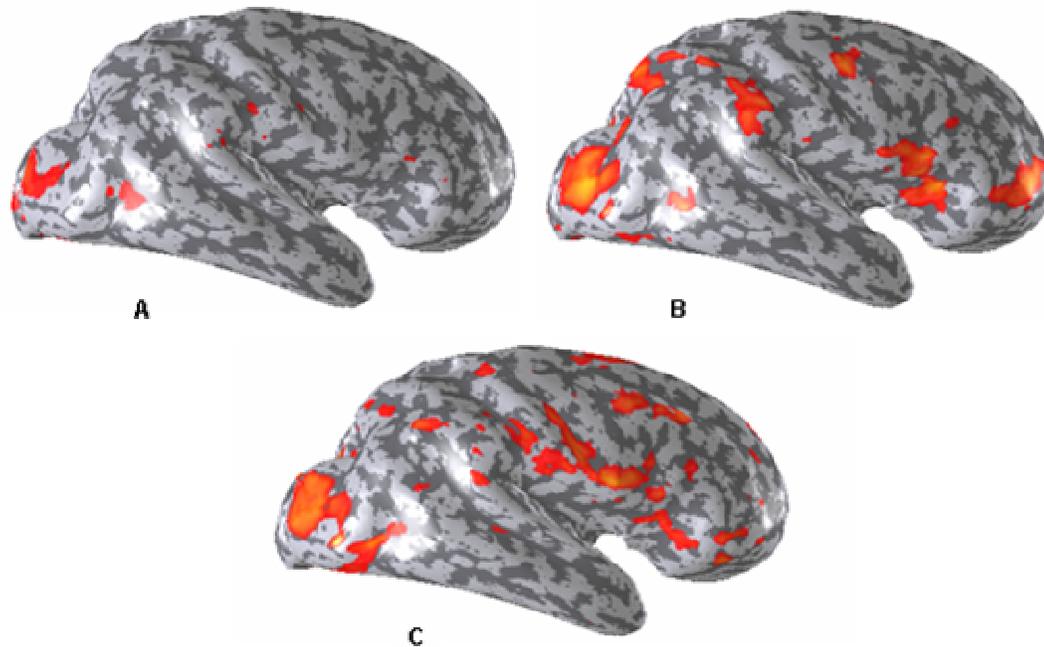
### Data analysis and visualization

The blood-oxygenation-level-dependent (BOLD) fMRI response to the differential stimulation for each condition was extracted in accordance with a general linear model of the event-related sequence, with the BOLD waveforms for each event type as free parameters. The initial response transient to stimulus onset was excluded by beginning visual stimulation 9 s before the analysis was initiated. A high-resolution anatomical (T1-weighted) volume scan of the entire brain was also obtained for each observer (voxel size = 0.94 x 0.94 x 1.2 mm). Gray (cortex) and white (nerve fiber) matter were segmented for each observer using the Vistasoft software. The cortex was specified as a manifold extending 3 mm above the segmented gray/white matter boundary, which was used to reconstruct 3D views of the whole cerebral cortex. The differential fMRI activity profile within the cortical voxels was then mapped directly onto the 3D cortical map, to allow visualization of the response properties over complete cortical areas. (Gyri are coded in lighter gray than the sulci).

## RESULTS

### The activation networks

The network for activation by pure temporal transients defining no coherent spatial structure (*uniform field*) is shown in Fig. 2A. Significant activation is restricted to the occipital pole and a lateral region coincident with the human motion complex (hMT+), which is expected to be responsive to dynamic field of transients. For the case of the *negative-figure* (Fig. 2B) a more extensive occipito-parietal network is activated, together with some frontal and prefrontal sites. The *figure/ground* stimulus, exhibits a similar pattern of activation in the dorsolateral occipital cortex, but increased occipito-temporal activation, strongly reduced parietal, and a lot of widely distributed frontal and prefrontal activation, including the central sulcus, the supplementary and the frontal eye fields and the ventrolateral prefrontal cortex. Thus, the three different instantaneous stimuli engaged three distinct cortical networks.



**Figure 2.** The activation (yellowish-orange color) patterns for the three stimulus types:  
 (A) *Uniform Field* - synchronously updated random-dot field  
 (B) *Negative Figure* - only the random dots in the ground region were refreshed  
 (C) *Figure/Ground* - generated by asynchronous figure/ground structure

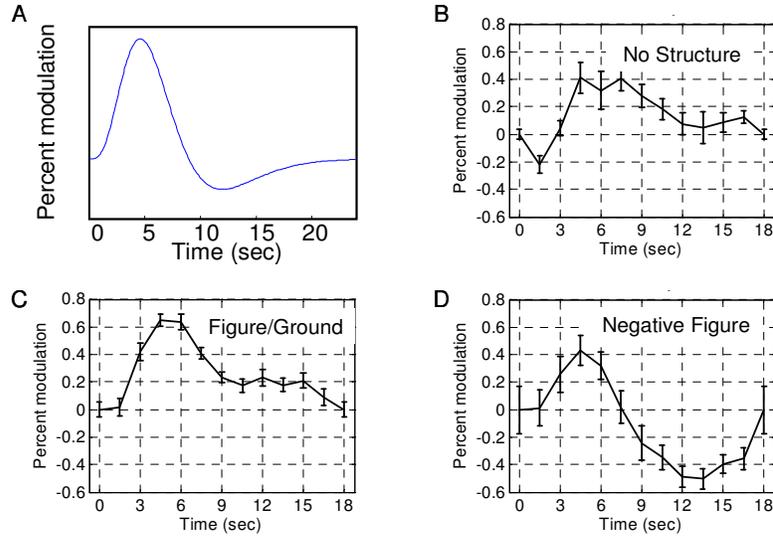
### DYNAMICS OF THE NETWORK

To study the network dynamics, we took advantage of the instantaneous paradigm that provides maximum resolution of the response dynamics because the stimulating event is simply an instantaneous transition between two stationary states. As a result, the expected BOLD waveform is equivalent to the HRF, whose canonical form provided in the SPM5 analysis software is depicted as Fig. 3A. Thus, a waveform very close to this should be expected in every cortical area showing significant response under our paradigm.

#### Area V3A

One of the most posterior areas responding to our set of stimuli is area V3A. The typical pattern of activation for the three stimulus types are shown in Fig. 3B-D. Note, that none of these response waveforms follow the canonical HRF prediction. The response to the *uniform-field* update rises to the expected peak, but instead of falling back through zero within about 8 s, it stay positive for about 16 s. Thus, paradoxically, the response to a purely transient event is predominantly sustained. We attribute this sustained response to the texture processing as the neurons in the V3A region digest the structure of the random pattern. Note that the response also exhibits an early negative dip, which has been attributed to the metabolic demand of the neural response per se rather than the adaptive vascular response to this demand. This is a feature that has been reported for high-field strength fMRI but has been difficult to replicate at 3T. None of the studies looking for it have used an instantaneous paradigm, however. It may be that this paradigm is particularly effective in revealing this early negativity.

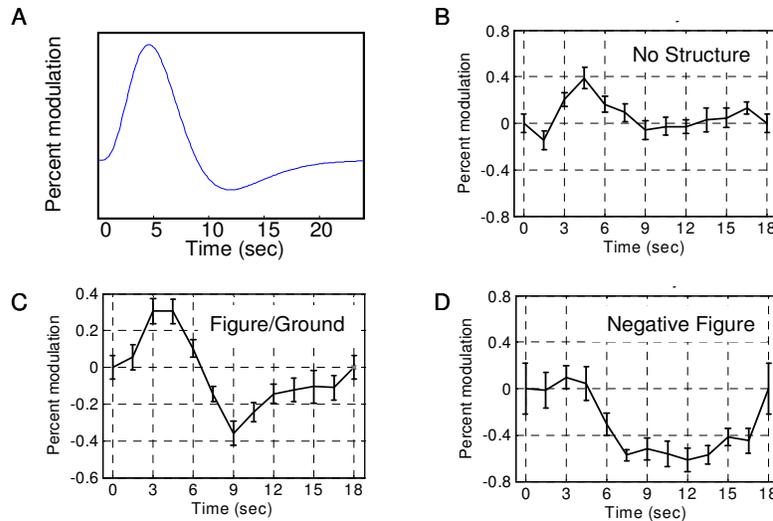
The *figure/ground* stimulus type also produced a predominantly sustained response in V3A (Fig. 3C), the waveform is largely similar to that for the uniform noise update, but without the initial negative dip. We have proposed elsewhere (Likova & Tyler, 2005) that V3A processes contour structure and segmentation, but not figure/ground per se. The similarity of the responses in these two conditions is consistent with this interpretation. Finally, the response of this cortical area to the *negative figure* condition shows a markedly different response after the early peak. Rather than staying positive, the signal swings strongly negative in the second half of the epoch. This may relate to a suppressive signal from another cortical area discussed next.



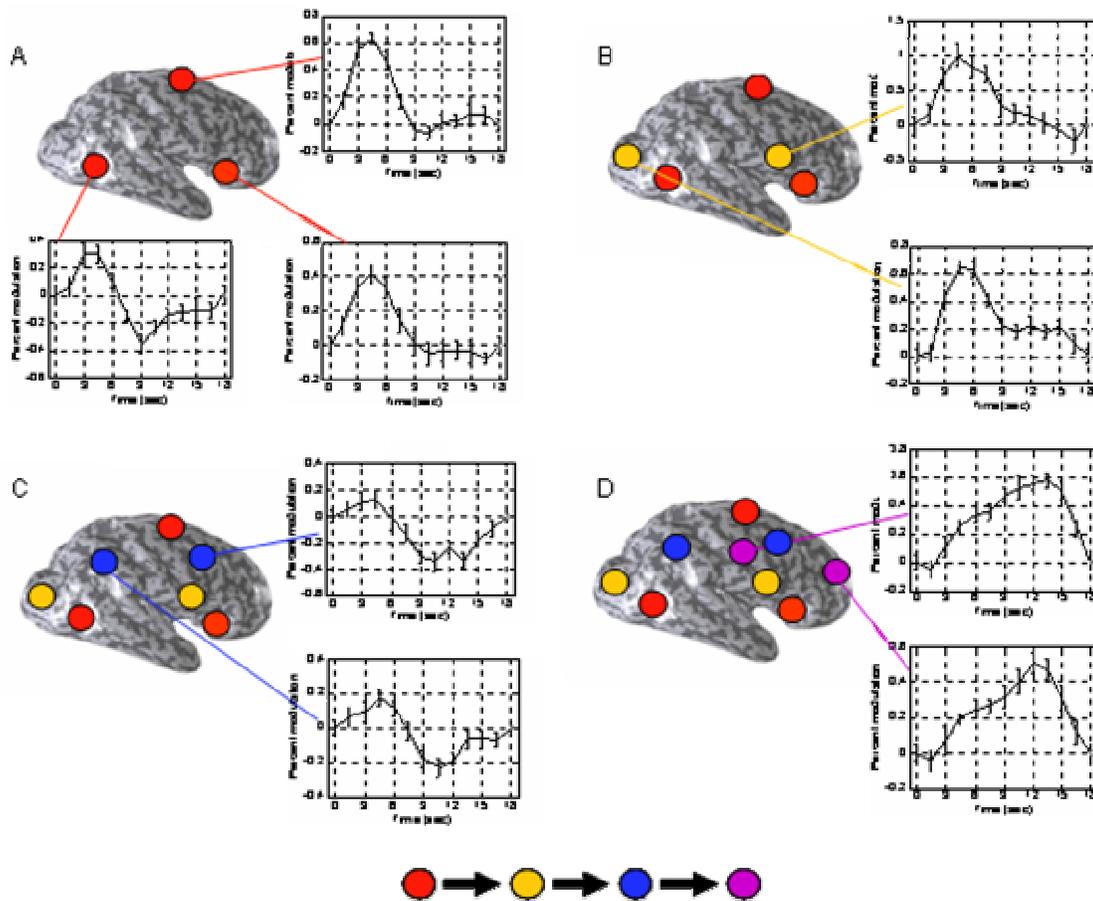
**Figure 3.** A. Canonical BOLD HRF (from SPM-5). B-D. Percent BOLD responses to each of the three stimulus types in the posterior ROI corresponding to retinotopic area V3A. Error bars are 1 standard error of the means. Note dramatic differences in response waveform *within the same* cortical area, implying that these differences are due to different underlying *neural* responses.

#### Area hMT+

The motion area, hMT+, shows further important differences. The response to the *uniform-field* update is purely transient, as might be expected for a predominantly motion-responsive region. Note that it replicates the early dip, although in reduced extent relative to V3A. The response to the *figure/ground* stimulus is strong, but again more transient than in V3A. The response to the *negative figure* condition is purely negative, and strikingly different in waveform from the canonical HRF. It is not simply an inverted version of the HRF, with a negative peak at 5 s, but a negativity that does not leave its baseline until 5 s and then reaches maximum at about 8 s, remaining negative for the remainder of the epoch. This behavior seems diagnostic of a late inhibitory response whose role is to suppress the figural interpretation and turn the figure region into a ‘hole’ (or ‘ditch’, for the elongated configuration of the present study). Based on the results of Likova & Tyler (2005) our interpretation is that this inhibition then invades V3A to generate its late inhibitory response. It presumably also returns recursively to V1 and V2 to provide retinotopic inhibition in the figure region, but that is not analyzed in the present work.



**Figure 4.** A. Canonical BOLD HRF (from SPM-5). B-D. Percent BOLD responses to each of the three stimulus types in the posterior ROI corresponding to retinotopic area hMT+. Error bars are 1 standard error of the means. Note dramatic differences in response waveform from the same cortical area, implying different underlying *neural* responses.



**Figure 5.** The waveforms of the signals in the main cortical areas activated during the figure/ground stimulation are presented. Based on their characteristics the responses are grouped in four categories. The order of plots A-D and red-to-purple color coding (see icon) roughly reflect the latency of the peak.

To give an insight into the rich temporal dynamics of the *figure/ground* network, the waveforms in the activated areas throughout the lateral surface of the brain are shown in Fig. 5. The activation peaks earliest in hMT+, in the supplementary eye fields, and in an anterior region in a ventrolateral prefrontal cortex. This activation is closely followed by activation in posterior occipital regions, and in the ventrolateral precentral sulcus. Two widely separated areas – a parietal region and the frontal eye fields – have predominantly negative biphasic responses, well synchronized between the two areas in spite of their large spatial separation. The slowest responses are found in a more dorsal region in the precentral sulcus and a prefrontal area. This pair of areas, again synchronized across a long distance, exhibits a cumulative response with peaks at 12 and 13 sec respectively, but with rapid offsets. The full interpretation of these results is beyond the scope of this paper, but they clearly demonstrate how much more information may be extracted from fMRI with a paradigm that allows a full temporo-spatial analysis.

## DISCUSSION

The three classes of stimulus structure activated three distinct cortical networks. The stimuli that elicited global perceptual organization (i.e., the *figure/ground* and the *negative-figure* stimuli) activated distributed networks extending far beyond the occipital lobe into the parietal and frontal cortex. Conversely, the non-structured *uniform-field* stimulus of noise transition engaged structures mainly restricted to the occipital lobe.

The instantaneous stimulus paradigm generated a wide variety of BOLD waveforms, demonstrating that the main assumptions of the standard GLM approach are seriously violated. Moreover, the data show dramatic differences in the BOLD waveforms properties (e.g., latency, sign, amplitude and width) even *within* the *same* brain areas as a function of the stimulus type. As there can be no vascular heterogeneity within the same area, these dramatic waveform

variations must be attributed to differences in the underlying *neural dynamics*, not to spatial variations in the HRF. Such results imply that the BOLD fMRI has the potential to capture them through an appropriate approach.

The implications for the form of the neural activation are captured in the extended model of the BOLD activation schematically presented in Fig. 6. In the standard approach, the stimulus is convolved with what is known as a hemodynamic response function (the “HRF”), on the assumption that the neural activation follows the stimulus waveform and that the main function coupling the neural response to the paramagnetic BOLD response is the hemodynamics (Fig. 6A). The present data show that this assumption is violated even in individual cortical regions, since the drastic waveform variations can only be attributable to differences in the neural responses (rather than hemodynamics or glial metabolic factors that should remain constant for a given cortical region). We therefore propose the more accurate view that the *neural response* is obtained by convolution of the stimulus with a *neural response kernel*,  $n(t)$  (although there may also be nonlinearities in the resulting neural response), and that the neural response is coupled to the paramagnetic signal by a compound *metabolic response kernel*,  $m(t)$ , which includes the chain of neural *metabolic demand*, the *glial response function* to the metabolic demand and the *hemodynamics* of the vascular response to the glial metabolic demand. The net metabolic kernel  $m(t)$  is presumed to be invariant for a given cortical region (and, indeed, is unlikely to vary greatly across cortical regions, as long as the BOLD signal is restricted to voxels within the cortex). Thus, the main variation among the signals on Fig. 3 and 4 is attributable to large changes in the neural responses within and between cortical regions.

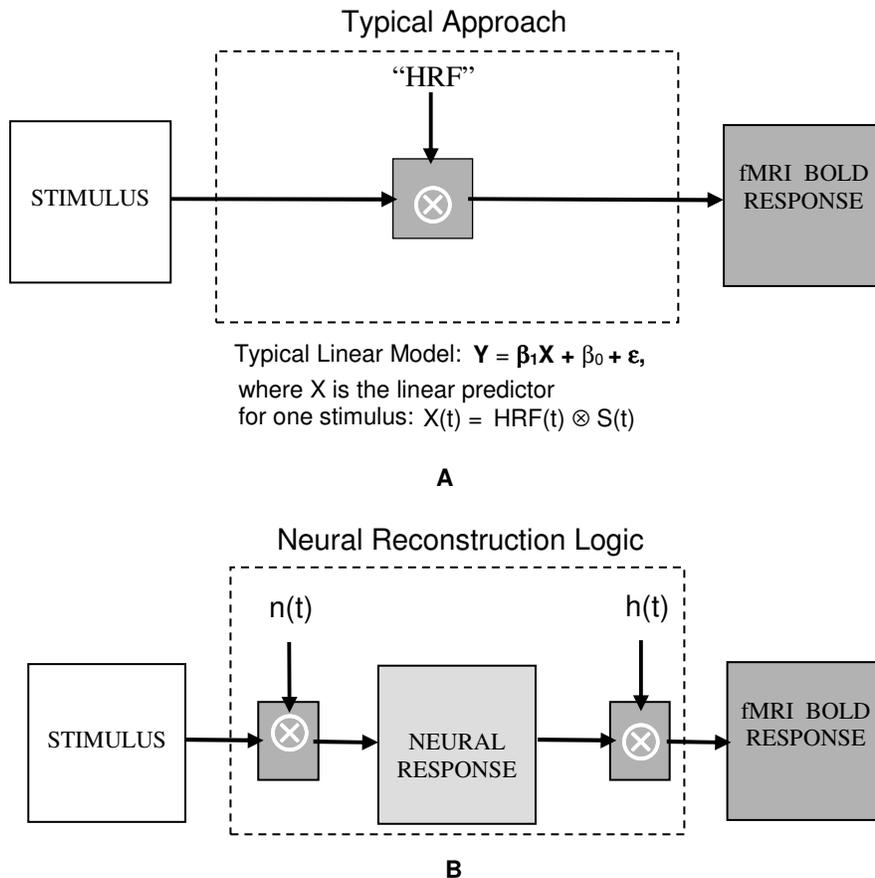


Figure 6. Schematic comparison of the typical approach and an approach based on a neural reconstruction logic allowing to extract the characteristics of the neural processing.

**Conclusion:** The unique paradigm of instantaneous and simple visual stimuli was able to create a variety of prolonged global percepts. Moreover, strong BOLD signals were obtained for each of the stimulus types in spite that they were constituted by a single brief transition from one to another field of visual noise. The data also reveal three distinct cortical networks underlying the three classes of perceptual organization: the figure/ground, the negative figure (hole),

and the transient uniform field. Expressly different responses evoked by brief, but differential stimulation of identical cortical regions, assure that the differences could be securely attributed to the neural dynamics, not to spatial variations in the HRF. Where networks partially overlap the temporal analysis of the BOLD can help to resolve whether the co-located regions perform the same or different functions under different stimulus conditions. The variety of response types from our instantaneous paradigm have important consequences both for the design and analysis of event-related experiments and for the development of methods to estimate the underlying neural responses from the BOLD signals.

### Acknowledgements

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