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What causes non-monotonic tuning of fMRI response to noisy images?

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Although images are defined both by the *amplitude* and *phase* of their Fourier components, it is phase structure that is the major determinant of their appearance [1–3]. Rainer *et al.* [4] recently examined how phase structure impacts on cortical activity by measuring the BOLD fMRI signal in anaesthetized monkeys that were shown stimuli containing a blend of phases from images and noise. They showed that cells in V1 respond most strongly to natural images, most weakly to 50:50 image–noise blends, and then recovered for pure noise images. Given the strict monotonic dependence of psychophysical detectability on signal-to-noise ratio, this non-monotonicity was surprising and generated some excitement [5]. The authors’ interpretation centres around the notion that *sparseness* is a desirable property of a cortical visual code [6–8]. They reasoned that the non-monotonicity is a trade-off between a few V1 cells responding vigorously to natural images versus many V1 cells responding weakly to noise images. Here, we offer another explanation: Rainer *et al.*’s phase blending fails to consider the directional nature of phase which leads to an over-representation of near-0° phase-components in their stimuli. This has the side-effect of altering the second-order (contrast) and fourth-order (kurtosis/sparseness) statistics of stimuli in a manner broadly consistent with observed changes in the BOLD signal. These changes do not inevitably arise from phase blending: using the weighted mean phase (WMP) produces monotonic changes in all of these statistics.

We conclude that one cannot rule out an explanation of BOLD non-monotonicity based on simple image statistics rather than a cortical trade-off.

We used a subset of eight of the images used in the original study; all had identical amplitude spectra, and were zero-mean in the range (-127,127). We estimated image phase (ϕ_{image}) and the phase of uniform random noise images (ϕ_{noise}) using the Fast Fourier transform. Two ways of combining (ϕ_{image}) and (ϕ_{noise}) were compared (see text box below). For both techniques $w = 1$ indicates full signal and $w = 0$ indicates full noise. The difference between the techniques lies in what phase distributions result at intermediate values of w . Equation (1) fails to take into account the directional nature of phase, and using it to combine large numbers of phases will systematically over-represent angles close to 0° simply because there are many more ways for two arithmetically weighted directions to sum to 0° than to any other direction.

Figure 1B shows that the over-representation of 0° phase introduces bright blobs at the corners of the images blended with the Rainer *et al.* technique. Although these were not visible in their study [4], as images were spatially vignettted prior to presentation, they substantially reduce the contrast of the central portion of the image compared to the equivalent WMP blended stimulus (Figure 1C). We wondered if such blending might alter not only second-order

statistics, such as contrast, but fourth-order statistics such as *kurtosis* — important for the representation of phase structure [9]. To look at changes in such statistical properties we generated 100 sequences from each of the eight images, with each sequence progressing from 0–100% phase coherence in 12.5% phase coherence increments, using Rainer and WMP blending techniques (14400 images in total). Images were spatially vignettted, but, as in the original paper not re-normalised, and we computed:

1. The grey-level standard deviation or RMS contrast;
2. The sample-corrected phase-only kurtosis (Δk) [9];
3. The average magnitude of response of a Gabor model [4] where a random selection of 500 patches were drawn from each image and multiplied by a Gabor filter (s.d. = 13 pixels, horizontal or vertically oriented, random selection).

Figure 1F shows the RMS contrast and Gabor model response to blended stimuli. We replicate the non-monotonic behaviour of the Gabor model, but note that this is only the case for images generated with Rainer *et al.*’s blending technique. Furthermore, Rainer *et al.* [4] posit that this pattern of results reflects a dense-low, sparse-high trade-off. However it simply reflects the amount of contrast energy present which in turn fluctuates due to an over-representation of 0° phase combined with spatial windowing (Figure 1F). Could this explain the fMRI results? Figure 1E shows

Ranier *et al.* blend [4]

$$\phi_{\text{final}} = w\phi_{\text{image}} + (1 - w)\phi_{\text{noise}} \quad (1)$$

Weighted mean phase (WMP)

$$\phi_{\text{final}} = \bar{\phi} = \begin{cases} \tan^{-1}(C_{\phi}/S_{\phi}) & S_{\phi} > 0, C_{\phi} > 0 \\ \tan^{-1}(C_{\phi}/S_{\phi}) + \pi & C_{\phi} < 0 \\ \tan^{-1}(C_{\phi}/S_{\phi}) + 2\pi & S_{\phi} < 0, C_{\phi} > 0 \end{cases} \quad (2)$$

where:

$$S_{\phi} = w \sin(\phi_{\text{image}}) + (1 - w)\sin(\phi_{\text{noise}}) \quad (3)$$

$$C_{\phi} = w \cos(\phi_{\text{image}}) + (1 - w)\cos(\phi_{\text{noise}}) \quad (4)$$

For both techniques, w is in the range [0,1].

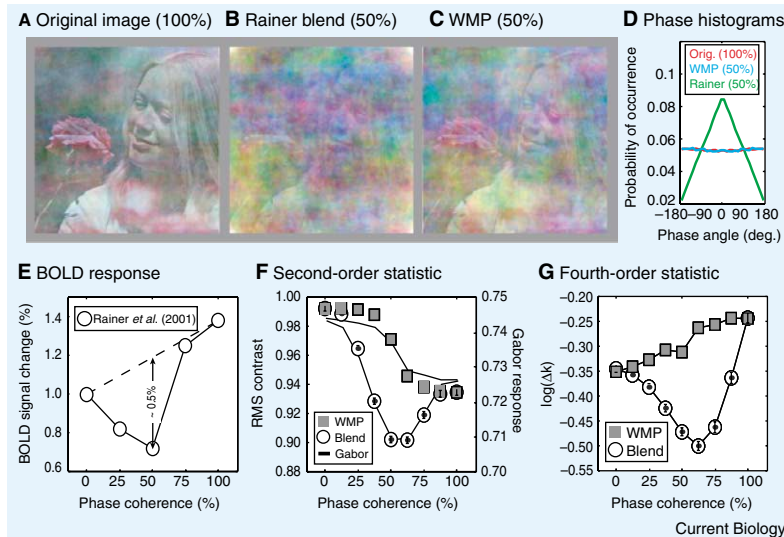


Figure 1.

(A) An image from Rainer *et al.* [4]. (B) A 50% image–noise blend similar to the ones used by the authors. Note the bright blobs in the corners of the image and the lower contrast of the face compared to (C), a 50% weighted mean phase (WMP) image. (D) Phase histograms show that Rainer *et al.*'s [4] phase-blending technique leads to an over-representation of 0° phase. Although the global power spectrum is conserved, when the FFT is back-transformed the 0° components add at the corners of the image (where all frequencies are aligned) reducing the availability of contrast energy elsewhere in the image. (E) Data from Rainer *et al.* [4]; cortical activity is reduced for intermediate levels of phase coherence. (F) RMS contrast of images blended using the Rainer technique (open circles) also shows a non-monotonic dependence on phase coherence. An alternative method using the WMP (filled squares), does not. The response of Rainer *et al.*'s Gabor model (solid line) is largely determined by simple contrast change. (G) A statistical measure of image *sparseness* (sample-corrected kurtosis) estimated from the Rainer stimuli shows a substantial non-monotonicity with degree of phase coherence and, like the BOLD data, is higher for full-coherence images than pure noise.

original data and the expected activity if BOLD level were a monotonic — here, linear — function of phase coherence. Clearly the 50% phase coherence level produces the largest drop in BOLD activity (~0.5%) and a drop in RMS contrast of around 10% (Figure 1F). The effect of RMS contrast on fMRI BOLD has been considered by Achtmann *et al.* [10] who measured V1 response to phase scrambled and intact two-dimensional circumferential gratings. In that study a 10% reduction in RMS contrast of their phase-scrambled stimuli reduced activity by around 0.45% which is not far from the 0.5% drop observed by Rainer *et al.*. Although the stimuli used in these two studies were different, Achtmann *et al.*'s were similar to natural images inasmuch as they were spatially broad-band two-dimensional patterns that contained edges at all orientations. Furthermore, even if contrast reduction is not solely

responsible for observed BOLD, it could interact with changes in other image statistics. Figure 1G shows the phase-only kurtosis for the stimulus set. This statistic is computed relative to the expected kurtosis from phase-scrambled versions of the stimulus [9,11] and effectively corrects for the fact that normal kurtosis — the fourth moment of the grey levels — is dominated by the high-spatial frequency content of images. This statistic, important for human detection of changes to image phase structure [9], also shows a strongly non-monotonic dependence on the level of phase coherence and, like the BOLD signal, is also higher for pure images than for pure noise.

In summary, we do not seek to derive a general predictor of cortical activation but merely observe that the phase-blending procedure used in Rainer *et al.* [4] leads to non-monotonicities in two simple statistics that are

already known to be linked to the human perception of structure in images: contrast and kurtosis. It is an unfortunate consequence of this that one cannot definitively conclude which image attribute determines cortical activity: contrast, sparseness, or a trade-off between the two.

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