Forward models of repetition suppression depend critically on assumptions of noise and granularity

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We reran Alink et al.’s simulations after correcting this error. The “winning” model reported for the gratings dataset no longer captured three of the six data-features it was intended to reproduce (Fig. 1). In fact, none of the 25 local-scaling models identified in their Supplementary Table 1 matched the totality of the empirically observed data features. Thus, while Alink et al. state that one model fits better than the rest, our simulations challenge this conclusion.

We wondered if, after correcting the noise distribution, a different combination of model parameters might match the empirical observations, and if so, whether such a combination would still favor local scaling. We found none of the 648 local-scaling models defined by the search grid matched the six empirically observed data-features. Moreover, when we explored higher SNR regimes, local-sharpening models showed repetition suppression effects that, like the local-scaling model, also matched the six empirically observed data-features. Nevertheless, our simulations challenge this conclusion.

Having shown that assumptions about the noise affect the output of Alink et al.’s model, we wondered if the models are also dependent on assumptions regarding the strength of the signal. We explored the impact of two key parameters of Alink et al.’s model: tuning bandwidth ($\sigma_{\text{Tuning}}$) and granularity...
A link et al. asserted that changing the number of orientation-tuned sub-populations (or clusters, or granules) assumed to be sampled within each fMRI voxel “does not have a qualitative effect on the simulation results.” This statement is inconsistent with previous work\textsuperscript{13} that manipulated this parameter to change the granularity of simulated brain patterns. This work revealed that pattern correlations are indeed sensitive to such changes—as well as changes in other properties that influence SNR, such as tuning bandwidth. We found that doubling the number of orientation-tuned sub-populations sampled per voxel inverted the direction of the CP data feature of the winning parameter combination for the grating dataset (Supplementary Fig. 1). This result contradicts the claim that the assumed level of granularity does not affect the qualitative pattern of results produced by A link et al.’s model. The level of the granularity-controlling parameter $G$ critically affects the nature of the signal component. It determines the extent to which the data are genuinely multivariate, rather than

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**Fig. 1 Noise parameters influence feed-forward models of fMRI-pattern correlations.** Top row: pattern of results reported by A link et al. for the winning parameter combination $[\sigma = 0.8, \beta = 0.4, \sigma = 0.4]$ for the grating dataset (cf. Supplementary Fig. 4 in A link et al.). The direction (increase or decrease when comparing initial and repeated responses) of the six empirically observed data-features (cf. Figure 3 in A link et al.) is only observed when uniformly distributed noise in the interval $[0, 0.1]$ is added to the simulated brain patterns. Bottom row: the qualitative pattern of results observed for the winning parameter combination shown in the top row changed substantially when adding zero-mean Gaussian noise with a standard deviation of 0.1 instead of uniformly distributed noise. Of particular interest, the data-features BC, CP, and AMS are (shown within a red box) no longer qualitatively consistent with the empirical observations. Compare the corresponding slopes of lines in the top and bottom rows. Init initial presentation, rep repeated presentation, MAM mean amplitude modulation, WC within-class correlation, BC between-class correlation, CP “classification performance” (CP = WC – BC), AMS amplitude modulation by selectivity, AMA amplitude modulation by amplitude. Solid bars indicate mean of each condition and error bars 95% confidence intervals given the (simulated) between-participant variability. Diagonal lines indicate the slope of linear contrasts across conditions, and dashed lines indicate 95% confidence interval of the slope. See A link et al. for methodological details and proposed interpretation of error bars and p values above each subpanel. In our view, given that arbitrary modeling choices determine the across-subject variability produced by the model, the reported error bars and accompanying p values have therefore little, if any, statistical meaning.
reflecting a single underlying dimension, such as signal strength.

We have identified an error in a recent fMRI modeling paper, from which we draw general conclusions relevant to a broad class of models. Signal strength and measurement noise influence both simulated and empirically observed correlations between brain activation patterns. These factors profoundly impact the interpretation of forward models in brain imaging. The results reported by Alink et al. hinge on assumptions neither explored nor discussed in their manuscript. Their models were not constrained by empirical estimates of key parameters determining signal and noise strength. Nor did they demonstrate robustness of their conclusions to a plausible range of noise parameters. Hence, while the instantiated forward models are useful for exploring the regimes and constraints that relate neural population responses and BOLD (blood-oxygen-level-dependent imaging) responses, they do not demonstrate that repetition suppression is best modeled by local neural scaling. Similar considerations extend more generally to the evaluation of neurobiologically minded interpretations of standard multivoxel pattern analyses.

**Fig. 2 Noise amplitude and signal strength influence empirically observed fMRI-pattern correlations.** a fMRI patterns formed by concatenating responses across voxels for each of two experimental conditions—here, visual gratings oriented either 45° or 90° from the horizontal. The strength of the signal component distinguishing the brain responses associated with these two gratings can be quantified as the Euclidean distance between these two spatially distributed brain response patterns, treated as vectors, and denoted here as \( \vec{v} \) and \( \vec{w} \). The full range of simulated granularity levels is \([1, 512]\) (\(2^n\)), with \(n = 0, 1, ..., 9\) granules per voxel. A dramatic effect of granularity on signal strength can be noted along the \(y\)-axis. If granularity were irrelevant, the observed monotonically decreasing curve would be instead a flat line. Given that pairwise correlations are known to be determined by noise amplitude as well as signal strength, this simulation demonstrates that the validity of inferences regarding neural coding based on fMRI-pattern correlations depend on granularity assumptions as well as noise parameters.

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

**Data availability**
The fMRI response data relevant to this article was made available by Alink et al. and can be downloaded from the Open Science Foundation project [https://osf.io/4f28y/].

**Code availability**
The code necessary to replicate Figs. 1 and 2 in our letter is based on code made available by Alink et al. from the Open Science Foundation project [https://osf.io/4f28y/]. Our modified functions can be downloaded from https://github.com/toporam/code-Ramirez-Merriam.git.

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Author contributions

Writing of the paper was performed collaboratively by F.M.R. and E.P.M. F.M.R. identified the errors in the code used by Alink et al.1 and noted their implications. The model simulations reported here were conceived and performed by F.M.R., using as basis the code made publicly available by Alink et al.1.

Competing interests

The authors declare no competing interests.

Additional information

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