Author response to:
"Decoding Face Exemplars from fMRI Responses: What Works, What Doesn't?" by J. Carlin (2015)

fMRI MVPA can decode some variables better than others, and clustering is a likely culprit

Julien Dubois[1], Archy O. de Berker[2], Doris Y. Tsao[1]
[1] Division of Biology, California Institute of Technology, Pasadena, California 91125; and [2] Pembroke College, University of Cambridge, Cambridge CB21RF, United Kingdom

In our recent study in The Journal of Neuroscience (Dubois, de Berker, & Tsao, 2015), we compared the amount of information about face identity and face viewpoint that can be retrieved from populations of single units and from functional magnetic resonance imaging (fMRI) voxel patterns with a simple linear classifier in the macaque monkey. Based on our decoding results and on further probing of properties of the single-unit representations, we concluded that multi-voxel pattern analysis (MVPA) of fMRI data was not able to extract information from underlying single-unit populations that were poorly clustered with respect to their selectivity within the dimension of interest. Carlin (2015) challenges our conclusion, arguing instead that poor functional signal-to-noise ratio (fSNR) can account for our results. We welcome the opportunity to clarify the arguments that led us to discard the fSNR account, and address Carlin (2015)'s arguments point-by-point below.

Carlin (2015) first points out that identity can be decoded above chance in ML/MF despite the low identity clustering for neurons in this region. While this may appear to weigh against the clustering explanation and in favor of an fSNR account (as Carlin (2015) rightly notes, ML/MF has the highest fSNR in the fMRI data), the complication here is that fMRI is not actually picking up identity information, but a low-level confound. The output of the classifier for ML/MF (Fig. 6) is very similar to the output for V1 (Fig. 8): above chance performance is driven by ID5, who was bald and generally brighter than the other identities. What may be confusing is that this confound did not artificially inflate identity clustering in ML/MF (Fig. 7): this is because clustering was established on the basis of all 25 identities in the face views image set (Freiwald & Tsao, 2010), hence drowning the influence of ID5 and more closely reflecting identity clustering than low-level confounds.

Carlin (2015)'s second argument is that, if clustering is the sole determinant of successful fMRI decoding, then we should get a similarly successful readout of the underlying neural population information for viewpoint and identity in a patch that has similar clustering for these two dimensions. Carlin (2015) points to AM as having this property, and then argues that since identity is not read out well whereas viewpoint is, clustering cannot be the single explanation. But viewpoint and identity clustering in AM are not identical: by our proxy measure, viewpoint clustering appears ~50% higher than identity clustering in AM (Fig. 7). What is definitely equal in both conditions is the fSNR, and thus the striking discrepancy between viewpoint and identity information retrieval in AM (where identity decoding is in fact substantially *better* than viewpoint decoding in the single-unit population) cannot be due to fSNR. This observation led us to look for alternate explanations, and clustering turned out to be one likely candidate.

A more pertinent observation that Carlin (2015) makes is that M6, who had the highest SNR in AM (Suppl. Fig. 7), also showed the best fMRI decoding accuracy for viewpoint and for identity in AM (the latter reaching significance at α=0.05). Though the difference in fSNR between M6's AM and M7/M8's AM is not huge (~0.75 vs. ~0.6), this is worth pondering. However, we note that the detailed pattern of identity classification for M6's AM (Suppl. Fig. 6) shows that ID5 is the sole driver of above chance performance. It can hardly be argued that this is a successful readout of the information in underlying units.

Carlin (2015) finally states that "macaques exhibit particularly severe ventral temporal dropout with conventional fMRI methods." fMRI of the ventral temporal lobe is notoriously challenging: air

spaces within the temporal bone lead to strong susceptibility-related field gradients. However, this technical issue is not "particularly severe" in the macaque, as compared to humans, as Dubois et al. (2015) are not using "conventional methods." The MION contrast agent we used improves SNR by a factor of 3 at 3T, compared to BOLD (Vanduffel et al., 2001). In addition, MION allows shorter TEs (17 ms in Dubois et al. (2015) compared to 30-40 ms in typical human BOLD fMRI) which reduces dropout. Finally, smaller voxel size (1 mm isotropic in Dubois et al. (2015) who use an AC88 gradient insert, compared to 2-3 mm isotropic in typical human BOLD fMRI) limits the effects of in-plane dephasing and again reduces dropout. We therefore argue that signal dropout in Dubois et al. (2015) is likely to be less severe than in the human fMRI studies cited by Carlin (2015) (see also Tsao, Moeller, & Freiwald, 2008). We welcome Carlin (2015)'s emphasis on the technical difficulties of imaging ventral temporal cortices, and would advise future experimenters to take a look at the raw data and quantify fSNR, especially in the areas where they have significant findings.

Our study does not claim to be the final word on what fMRI MVPA can achieve. We demonstrated a discrepancy between the ability of fMRI MVPA to retrieve information about two dimensions of interest (face identity and face viewpoint) compared to single unit populations; we ruled out several explanations for this discrepancy (including fSNR), and identified clustering of like-tuned units as the most viable explanation (amongst the ones we considered). We do not stand by a "strict clustering account" for explaining what can and can't be decoded using fMRI MVPA; obviously other factors are involved, such as sharpness of tuning of clustered neurons. It is possible that technical advances improving resolution and fSNR will lead to successful identity decoding in the anterior temporal lobes of the macaque in the future – our study simply demonstrates that the less clustered the representation, the more elusive it becomes for fMRI, even with MVPA. We discuss at length in (Dubois et al., 2015) the limitations of our study, as well as possible reasons why some human fMRI studies may have achieved significant identity decoding where we did not in the macaque.

With respect to Carlin (2015)'s final words: all results, significant and null, should be interpreted with caution. Significant results are much easier to argue for within the statistical framework most widely used and understood by the community; whether this framework is the best one to advance science is a subject of intense current debate (e.g., Ioannidis, 2005; Button et al., 2013; Halsey, Curran-Everett, Vowler, & Drummond, 2015).

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