Dispatch

Vision: Face-Centered Representations in the Brain

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A longstanding debate in the face recognition field concerns the format of face representations in the brain. New face research clarifies some of this mystery by revealing a face-centered format in a patient with a left splenium lesion of the corpus callosum who perceives the right side of faces as 'melted'.

The machinery that performs visual cognition humans is endowed with an unmatched range of capabilities supported by the most powerful of sensory systems. It routinely performs a variety of recognition tasks that all start with the projection of a stimulus onto the high-dimensional retinal input with ~150 million rods and cones. A large proportion of cortex reduces this input into lower-dimensional representations that serve the key functions of visual perception and cognition. This reduction takes place within an architecture made of two hemispheres exchanging information via the corpus callosum. A key challenge remains to understand the format of these lower-dimensional representations and their contents, both in the brain and its models. In this issue of *Current Biology*, Almeida *et al*. [1] address the challenge in a study of patient A.D., who experiences a sudden and systematic perceptual distortion of the right side of faces — the right half of a face appears 'melted', in a similar manner to the melted clock on Dali's famous painting — as a result of a left splenium lesion of his corpus callosum that hinders the exchange of information between the two hemispheres.

The two hemispheres of the brain perform specialized cognitive functions and exchange outcomes via the corpus callosum to produce a unified cognition. Sperry and colleagues [2] famously showed that disruptions of communication in split-brain patients induced a strikingly dissociated cognition and conscious awareness — in these patients, the corpus callosum was sectioned to disable communication of epilepsy from its site of origin in one hemisphere to the other hemisphere. In patient A.D., a sudden lesion to the left splenium of the corpus callosum produced a striking effect, specifically of the perception of faces — technically referred to as contra-lateral hemi-prospmetamorphosia — whereby the right side of faces are perceived as melted: out of proportion, drooping or swollen, and not fitting with the left side. Though not explicitly understood as a section of the corpus callosum, A.D.'s splenium lesion is nevertheless important for understanding cognition because it dissociates perception of the left and right sides of faces.

Almeida *et al*. [1] used this rare condition to adjudicate between three frames of reference as possible formats of A.D.'s face representations. A retino-centered format would represent the visual field, with A.D.'s perceptual distortions located only to the right side of his fixations. That is, a face projected to the left side of A.D.'s fixation would not appear distorted. A stimulus-centered format represents the image plane. Here, the right side of the two-dimensional image would be perceptually distorted, irrespective of whether the face within the image is right side up, or upside down. Finally, a face-centered format moves the reference frame to the three-dimensional space of the face itself. Perceived distortions would follow any rotation of the face, in the two-dimensional image plane or in three-dimensional depth. For example, a face rotated clockwise in the image plane would be perceived with a distortion on the right side of the face itself, irrespective of the rotation angle of the face (see Figure 1 in Almeida *et al*. [1]).

This reasoning motivated the experimental work of Almeida *et al*. [1], which provided clear support for the face-centered format. That is, perceptual distortions on the right side of the face persisted even when an image was projected in the left and right visual fields either as full or as left and right split-halves faces, or rotated in the two-dimensional image plane or in three-dimensional depth to reveal only the profile or three-quarter view. Finally, the absence of distortions with other visual categories confirmed the specificity of the hemi-prospmetamorphosia to faces. The distorted contents primarily involve the right eye, the right side of the nose and the right corner of the lip, each reported as melting downwards, with less pronounced effects for faces that were not upright. Interestingly, even though faces have a level of bilateral symmetry that should enable the reconstruction of a full face from only a few views [3], in the case of A.D., bilateral symmetry does not appear to facilitate reconstruction of the distorted right side from the preserved left side (compare with visual filling-in mechanisms [4]).

These results on A.D.'s hemi-prospmetamorphosia have far reaching implications for visual recognition research in the brain and its models (for example, deep networks), both for format of representations and their information contents. Starting with representation formats, we know that the left and right occipital cortices initially represent the contra-lateral hemifield with some overlap in areas V1 to V4 [5]. A face presented in the centre of the visual field is therefore representationally split on a vertical axis in the contra-lateral hemisphere (for example, with the left face side represented in the right hemisphere and vice versa). To integrate these split-half representations and produce a bilateral perception, A.D.'s hemispheres communicate via a lesioned corpus callosum. Almeida *et al*.'s [1] results suggest that the impaired architecture does construct a bilateral representation of the two face halves in the left and right pathways (see also [6]). Whether each comprises a face-centered distortion of the right face half remains an open question.

The functional role of such face representations in the left and right hemispheres is unclear, when we know that the right hemisphere typically serves stimulus categorization [7] and perception [8,9]. Left and right versions could represent the stimulus for the specialized cognitive functions of the left and right hemispheres. To shed light on this, studies aiming for a finer granularity of face representation could reveal a specialization of information contents represented in each ventral pathway to support the specialized functions of each hemisphere. Further research, including modelling, should address where, when and how the communicating visual pathways transform initial representations in the occipital cortices (with contra-lateralized, retino-centric and mid-line split properties) into ventral representations (with bilateral, scale invariant and face-centered properties), that achieve the perceptual invariances demonstrated by A.D..

Having discussed how a face-centered format of representation could rely on two communicating hemispheres, we now turn to the distorted contents of A.D.'s face perception. There is a longstanding debate in the literature about whether face information contents are represented as wholes, or as combinations of features (reviewed in [10]). A.D.'s perceptions of right-distorted faces suggest at least the constraint of a midline split of contents related to the mis-communicating hemispheres, which in turn challenges the idea of faces represented as wholes. Verbal reports from AD further indicate that the distortions primarily concern discrete features (for example, the right eye, the right corner of the mouth), though these reports could simply reflect a verbalization bias to name face properties rather than evidence for featural representation *per se*. Objective studies of A.D.'s distortions — for example, with added noise reverse correlation (reviewed in [11]) or generative models tailored to the reported shapes of the distortions — could further document their specificity, in terms of the types of shapes, precise locations in face-centered coordinates, and interactions with face features [12]. Such a study would objectively assess whether A.D.'s distortions globally affect the full right half of the face, or primarily its component features and if so, how.

A.D.'s case further raises the important question of the relationship between his distorted perception of faces and his memory of faces. To address this, one could task A.D. with predicting a face from memory when none is present in the input on any trial with only white noise templates shown as stimuli [13]. Following the experiment, reconstruction of the predicted face could reveal whether top-down cascading of the prediction from memory would incur right-sided distortions similar to the perception. An alternative would ask A.D. to report imagined faces, for example, at different rotations in depth, to analyse whether the top-down cascading of the visual prediction from memory into left and right V1-V4 activations [14,15] comprises (in left V1-V4) distortions, or not.

The new study of A.D.'s hemi-prospmetamorphosia with the ingenious designs of Almeida *et al*. [1] has revealed a face-centered format of face representation, involving an architecture split into two hemispheres, where initial contra-lateralized representations become later 'stitched up' into a unitary conscious perception that requires inter-hemispheric communication of information. These results suggest fundamental constrains on the architecture of recognition in the brain and its implementation in deep convolutional network models that should shape further research.

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