

High-Acuity Information Is Retained through the Cortical Visual Hierarchy of Primates

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Vision requires perception of both coarse layout and fine details of objects. In this issue of *Neuron*, Lu et al. (2018) describe a possible basis for the latter: neuronal clusters in area V4 coding high-acuity information, despite the tendency along the visual hierarchy to generate global representations of objects.

It need not be the case that when we appreciate the overall shape of an object, we are not able to also appreciate some significant detail of the same object. Think for example of an elegantly decorated piece of pottery, like the one shown in Figure 1A: while we enjoy the silhouette of the vase, we can also notice some fine figure painted on it. Likewise, while we appraise the overall shape of a macaque monkey face, we can nonetheless notice the color of its eyes' iris (Figure 1B). This indicates that our analysis of the visual world relies on the concurrent engagement of mechanisms supporting fine-scale and large-scale processing of the retinal image. Students of visual perception have long claimed that in fact vision incorporates both types of analysis—known as “local” and “global” processing—and have generally claimed that global processing precedes local processing in time (Figures 1C and 1D) (Hegdé, 2008).

If one then considers the hierarchical organization of the visual system, and especially of the so-called “What” ventral (occipito-temporal) visual pathway, one discovers that along subsequent stages of the hierarchy, processing actually appears to evolve from local to global in nature, or at least this is what has been traditionally assumed. The size of neuronal receptive fields increases as one moves up the hierarchy, allowing for more extended patterns to influence activity of the given neuron at increasingly high stages of the hierarchy (Kravitz et al., 2013); most importantly, as one ascends the hierarchy, one finds that individual neurons tend to become selective for lower spatial frequencies (Desimone and Schein, 1987)

and more complex stimulus configurations, and in some cases such selectivity appears to be matched to whole objects, such as faces, other body parts, or whole inanimate objects (Kravitz et al., 2013). If anything, then, it would appear that local processing occurs first, both in time and (anatomical) space, followed by global processing, unlike what is generally observed by measuring perception.

More directly relevant to the present discussion, as one again thinks of the visual (occipito-temporal) hierarchy—say from primary visual cortex, or area V1, to the different sectors of inferotemporal cortex—one would thus predict that details are lost at the service of building global shape representations. However, given that local details are not lost, and in fact they are readily available to our perceptual experience, it must be that the visual system can effectively access fine-grained representations of the visual input. How could this be achieved?

To some extent this might be achieved by means of changes in eye-gaze direction, such that, for example, when needed, a small detail of an image is swiftly brought onto the fovea, which enables high-resolution analysis of the targeted feature (Montagnini and Chelazzi, 2005), perhaps momentarily losing track of the global configuration. Somehow related to the previous point, it has also been claimed that (covert or implicit) attention mechanisms are available to emphasize either local or global processing at subsequent moments in time, thus giving alternative precedence to one or the other type of information contained in the visual image (Flevaris and Robertson, 2016). Yet a different possibility is

that, while higher stages of processing prevalently extract global form, and aim for building largely invariant object representations, the perceptual system can nonetheless access lower-level, high-resolution representations, so that global form and local detail can be (quasi) concurrently available for perceptual analysis. The latter solution could come about through a key property of the relevant networks, incorporating both feedforward and recurrent processing, effectively linking together—or “binding”—global and local information into a unitary representation of the given object (Hochstein and Ahissar, 2002). This being the state of affairs, the study by Lu and colleagues in this issue of *Neuron* (Lu et al., 2018) provides compelling evidence that invites a far-reaching change in perspective regarding this aspect of visual perception, namely the way in which local and global processing are orchestrated together in the primate brain.

Lu et al. (2018) explored spatial frequency (SF) encoding along the cortical visual hierarchy of the macaque brain, under the reasonable assumption that low spatial frequency analysis mainly supports coarse representations, whereas high spatial frequency analysis mainly supports the representation of fine detail. For this purpose, the research focused on parafoveal V1, V2, and especially V4 representations and discovered functional domains in V4 that, unlike nearby tissue, encoded high SFs, up to 12 cycles/degree. Incidentally, an early report of occasional V4 neurons that were selective for high SF was provided some years ago by Desimone and Schein (Desimone and Schein, 1987).



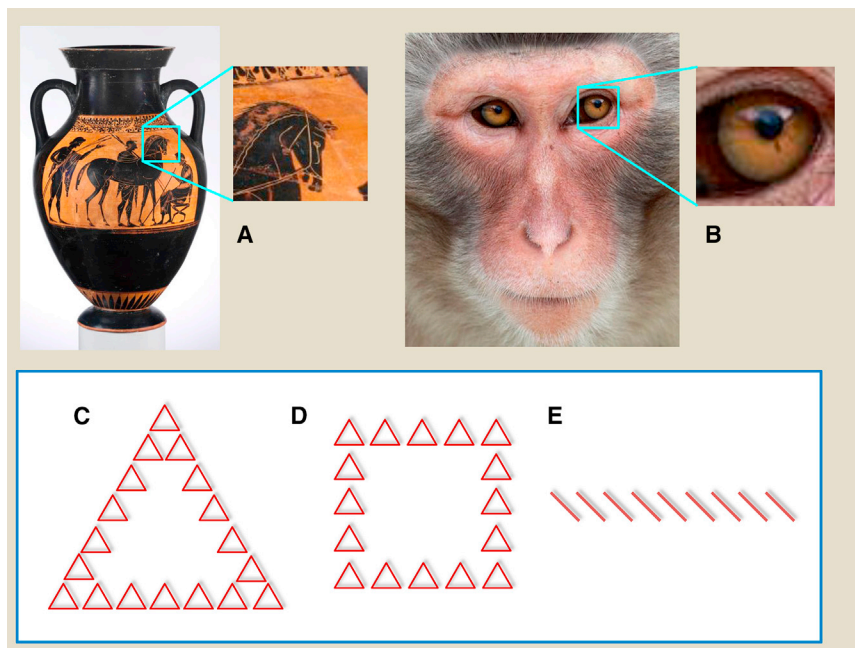


Figure 1. Examples of Hierarchical Stimuli Allowing Local and Global Processing

(A) A piece of fine painted pottery from ancient Greece. While appreciating the silhouette of the vase, one can also notice a small figure painted on it. Photo credit: MET Museum, Lysippides Painter, via Wikimedia Commons ([https://commons.wikimedia.org/wiki/File%3ATerracotta_amphora_\(jar\)_MET_DP138645.jpg](https://commons.wikimedia.org/wiki/File%3ATerracotta_amphora_(jar)_MET_DP138645.jpg)). (B) The face of a macaque monkey (*Macaca Fuscata*). As before, one can appraise the overall shape of the face, but also notice the color of one eye's iris. Photo credit: Alfonsopazphoto (Own work Animais Fotos), via Wikimedia Commons (https://commons.wikimedia.org/wiki/File%3AWildlife_primate_monkey-of-japan_macaca-fuscata_closeup_31-05-2010.jpg). (C and D) Two local-global stimuli of the kind used in perceptual studies. In (C), a global triangle is made of local triangles (congruent); in (D), a global square is made of local triangles (incongruent). (E) A local-global, compound stimulus of the kind used by Lu et al. (2018). A horizontal global segment is made of left-tilted local segments (incongruent).

As a first step, the authors of the present study assessed population SF selectivity simultaneously across parafoveal V1, V2, and dorsal V4 representations by means of intrinsic-signal optical imaging in rhesus macaques (*Macaca mulatta*). As expected, this approach revealed a monotonic decrease of optimal SF from V1 to V2 and then V4, and also a decrease of optimal SF with retinal eccentricity in all three areas. Next, SF selectivity was neatly assessed within the distinct functional compartments of areas V1 and V2: the blobs and interblobs in V1 and, respectively, the thin and thick dark stripes and the pale stripes in V2. The approach revealed higher optimal SF for inter-blobs compared to blobs, but highly comparable values across all three V2 compartments. Moreover, as expected, a decrease in optimal SF with retinal eccentricity was confirmed for all five compartments. In spite of the overall pattern, closer inspection of the population activ-

ity revealed local domains within parafoveal V4 where responses could be obtained with higher SFs, up to 8 cycles/degree and above. Importantly, such domains were observed at eccentricities in the retinotopic map where lower SF selectivity was to be expected based on global responses, thus violating the dominant inverse relation between SF preference and retinal eccentricity (De Valois et al., 1982). Instead, the SF selectivity of these domains was similar, if not higher, to that of V1 and V2 responses at equivalent eccentricities.

The initial finding was backed-up by electrophysiological laminar recordings in area V4 in order to characterize SF selectivity at a finer scale, again targeting the central visual field representation. The data showed a triadic relation, namely, that: (1) RF size increased with eccentricity; (2) in general, larger RFs were associated with a preference for lower SF; and finally, (3) optimal SF decreased with ec-

centricity. Most importantly, the evidence confirmed the existence of discrete clusters of neurons that were selective for relatively high SFs, 8 cycles/degree, and more. Note that nearby clusters, also corresponding to retinal eccentricities within 5 degrees of visual angle, were selective for much lower SFs, between 0.1 and 1.5 cycles/degree. The laminar recording technique further revealed consistency in SF selectivity across layers, attesting to the columnar organization of the high (and low) SF-selective clusters.

It has been reported that V4 processes more complex visual features compared to V1 and V2, emphasizing global contour and surface information (Kravitz et al., 2013). Strikingly, when local-global compound stimuli of the kind shown in Figure 1E were used for optical imaging experiments, high SF-selective clusters in V4 mainly encoded the orientation of the local elements, whereas global orientation was predominantly encoded by nearby clusters with standard, low SF selectivity. This implies that, when considering the two neuronal populations together, both global and local information is available and can be conveyed to later stages of the system. Once again, consistent results were obtained with electrophysiological recordings.

As already noted, perception is known to normally proceed from the global to the local level (Hegdé, 2008). In an attempt to link this aspect of perception to the underlying neural mechanisms, as a final step, Lu et al. (2018) looked at the latency of neuronal responses. To this aim, response latency was measured electrophysiologically for neurons in high versus low SF-preferring clusters. A latency difference of around 10 ms was consistently found between the two types of clusters, with earlier responses for the low SF-selective neurons and delayed responses for the high SF-selective neurons, and the pattern was confirmed across all cortical layers. Therefore, the timing of neuronal activation in the two different domains of area V4 appears to mimic rather closely the temporal progression from global to local analysis, as measured in perception.

Overall, the reported data suggest that area V4 may be able to confer both global-form and local-detail (high-acuity) information to later sectors of the

occipito-temporal cortical visual system, and perhaps to subcortical structures. The causal role in perception of neuronal activity in the high SF-selective domains in area V4 will have to be determined with future investigations. Meanwhile, we can offer some speculations as to its functional significance and suggest future directions for research in this domain.

For example, there is one special case where parafoveal high-acuity information might play a critical role in human perception, and this is the phenomenon in reading known as “preview benefit,” or the early acquisition of information about the word(s) that will be foveated next while reading a text (Schotter et al., 2012). This function can undoubtedly benefit from a system that is capable of supporting high-resolution analysis of stimuli falling in the near periphery of the visual field. Additionally, it will be of special interest to assess in future studies of area V4 whether high versus low SF-selective clusters are differentially modulated in accordance with covert attention being directed to the local versus global level of hierarchical visual stimuli (Flevaris and Robertson, 2016).

Furthermore, given the latency difference in neuronal activity related to global versus local processing in different SF-se-

lective clusters, as reported by Lu et al. (2018), further investigations on the temporal dynamics of V4 single-cell spiking activity in response to sustained visual stimulation might be especially informative. In fact, the possibility might exist that selectivity for high SFs increases over time post-stimulus onset, not only for single V4 neurons within high SF-selective clusters, but perhaps also for at least some neurons within low SF-selective clusters, such that high SF information (fine details) might become more broadly available within the general V4 population after substantial processing time (see Sani et al., 2013, for a compatible finding on luminance contrast coding in macaque area V4), thus establishing an even closer parallel to what occurs at the perceptual level. Finally, it will be very exciting to uncover the pattern of anatomical and functional connectivity that gives rise to fine-scale information being retained at the level of parafoveal V4, if not even at later stages—a possibility that should be immediately investigated.

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