

Do we need another neural correlate of contour integration?

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Abstract. Gilad and colleagues use an elegant combination of voltage-sensitive dyes and high temporal and spatial resolution optical imaging to visualize a differential response to collinear contour elements in monkey V1. This result adds to the literature on the neural correlates of contour integration, but does not yet tackle (or seek to tackle) the question as to whether contour integration is mediated by lateral connections within an area (e.g., V1), through pooling of feedforward connections, or feedback mechanisms. Moreover, while Gilad et al. find that their differential response is correlated with the behavioral performance of each monkey, there are reasons to suspect that the correlation they observe is a consequence of processing in higher regions, and that the differential V1 response may not play a critical role in integrating contour elements, or in generating the monkey's response. Moreover, this differential V1 response was not observed in a monkey who was not trained on the task, a result that can only be reconciled, if one assumes that the monkey could not see the contour prior to training. If valid, this could raise doubts as to whether the study of contour integration really provides insights into the processes by which normal visual perception is achieved.

Keywords: contour integration, neural correlate, perception, lateral connections, pooling, feedback.

Since Hubel and Wiesel (1959) discovered orientation-sensitive cells in V1, visual neuroscience has not yet progressed to any kind of consensus as to how those orientation-sensitive responses are combined into contours that extend beyond the receptive field of each cell. More specifically, we have yet to answer whether this integration is mediated by lateral connections within an area (e.g., V1), through pooling in higher brain areas with larger receptive fields, or recurrent processing between areas?

Gilad, Meirovithz, and Slovín (2013) show that high-resolution optical imaging and voltage-sensitive dyes could provide important insights into this. Exploiting their high spatial resolution, they are able to demonstrate that elements arranged into a contour show a different response compared to background elements. Gilad et al. study the time course of responses in V1 to an image composed of an array of local oriented image patches (Gabor), some of which are oriented in alignment with each other so as to form an extended contour. Exploiting their high temporal resolution, they show that the initial response in V1 shows an increase in activation at the location of each (Gabor) image element. At a later time point however, there is a clear differential response at the retinotopic position where the elements are located on the contour in comparison to the locations associated with elements in the background. This differential response largely seems to reflect a suppression of the background elements. In the authors' words, this technique enabled them to "visualize in single trials a salient continuous contour 'popping out' from a suppressed background."

However, while offering a methodologically elegant visualization, neither this result, nor any of the numerous contour integration studies coming before it (Bauer & Heinze, 2002; Kapadia, Ito, Gilbert, & Westheimer, 1995; Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003; Li, Piëch, & Gilbert, 2006; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998) can answer whether contour integration occurs through pooling, lateral connections, or requires feedback. As discussed by the authors, the late nature of the differential response raises the possibility that it may result from a feedback signal from higher areas, such as an attentional enhancement of the contour relative to the background. If so, this signal could originate in neurons that detected the contour simply by pooling responses with larger receptive fields at higher stages of the visual system (e.g., V2-LOC). In principle, however, it is also possible that slower, unmyelinated lateral connections within V1 could also result in a differential response that only emerges at a later time.

But it should be noted that previous behavioral work questions the idea that early facilitation effects caused by flanking elements (and lateral interactions) are uniquely responsible for contour detection (Hess, Dakin & Field, 1998; Huang, Hess & Dakin, 2006; Williams & Hess 1998).

The authors conclude that the opposing responses “in the contour and background in V1 may underlie perceptual grouping in V1.” In support of the active functional role that this differential signal in V1 could play in achieving the perceptual grouping in this task, the authors demonstrate that the differential response in V1 is closely correlated with the monkeys’ actual behavioral performance. The interpretation of this correlation is however contingent upon whether the detection of the contour actually resulted from lateral interactions, or from pooling in higher areas with larger receptive fields. If pooling at higher areas was required, then it is possible that the correlation with behavior actually reflects a stronger feedback signal based on the success of higher areas. Therefore, we cannot know if the differential response in V1 is merely a consequence of feedback from higher areas that in fact perform the task or whether this neural correlate in V1 was really critical to the perception of the contour, and the performance of the task. In fact, these possibilities are not mutually exclusive: circuits in V1 may be required for the perceptual grouping process itself, but the feedback signal may be required in order to select the contour such that it can guide behavior. As the results stand however, we cannot know if the differential signal in V1 played a critical role in the monkeys’ performance, or was a consequence of successful performance at higher stages of their visual system and resulted from feedback that didn’t actually play a functional role.

The possible noncritical status of this differential V1 response in performing the task is suggested not only by its long latency but also by the fact that a nontrained monkey (reported in supplementary materials) does not show this response differentiation in V1. These results are consistent with those of an earlier study that also showed a late enhancement of firing in single neurons whose receptive fields fell on the contour; but only after training on the contour detection task (Li, Piëch, & Gilbert, 2006). Indeed, in this previous study, this effect also disappeared under anesthesia (Li et al). Therefore, one can only maintain that these signals are truly involved in contour integration per se, if one assumes that without training a monkey simply does not see the contour. This is of course possible, but it is quite a big assumption. Indeed, if one assumes that the function of contour integration is to help us distinguish objects in the cluttered natural environment, it is perhaps questionable whether this function can only emerge after substantial training has occurred. If the type of contour integration studied here is not a part of the normal repertoire of perceptual functions with which monkeys normally solve their everyday perceptual challenges, then this also raises the question as to whether it should really be a focus of research in visual neuroscience.

In fairness however, it could be that training is required, not because contour integration (as studied by Gilad et al.) plays no role in the monkeys’ normal vision, but because it is a more demanding form of integration than the monkey would normally encounter. Even in that case however, one still has to consider the possibility that the signals in V1 do not reflect the bottom-up perceptual role of the visual system in grouping the contour, but rather reflect some higher level signal that the system has to use to help solve this more demanding task. For example, we know that neurons in the frontal lobe become tuned to visual stimuli as they become task relevant (Freedman, Riesenhuber, Poggio, & Miller, 2001). Furthermore, we know that high-level signals, such as holding an item in working memory, can be fed back to V1 (Harrison & Tong 2009). Thus, the demanding nature of the task (evidenced by the requirement of training), may recruit additional neural resources (even in the frontal lobe) in performing the task, and, as argued earlier, it maybe performance at those higher levels that causes a feedback signal to V1, which results in a V1 signal that is a consequence of successful performance at higher levels, not a cause of it.

Thus, reflecting critically we cannot rule out the idea that this neural signal in V1 is actually epiphenomenal to the actual perception of grouping and the generation of the monkey’s response. Future research must address this question by focusing more directly on the computational questions (pooling, lateral interactions, and feedback) and the actual functional status of any neural correlates, particularly in relation to known time delays across lateral interactions, between areas and the actual time required for the monkey to generate its response. We need to use the time course of the flow of activations within and between different areas of the brain to help inform our understanding of the functional status of different neural signals. More specifically, we could ask, could the current signal in V1 even be communicated in time for it to reach the motor cortex responsible for controlling the monkeys’ behavior if an immediate response was required? We also need to be more concrete about the

speed of lateral connections within V1, and whether the spacing between the stimuli being presented would make it possible for lateral connections to have had an influence over the time course described. Indeed, this could be built upon further by testing whether the spacing between presented elements influences the speed of the differential neural response in V1, and whether this timing could be predicted based on lateral interactions. The critical role of the timing of the response in V1 could also be tested with other techniques such as transcranial magnetic stimulation (TMS). Using a similar design as Wokke, Vandenbroucke, Scholte, and Lamme (2013), if V1 was inhibited in the late phase (by TMS), would behavioral performance drop? Critically, such manipulations could also be performed using an experimental task that taps contour integration incidentally (e.g., through priming) to rule out that these signals stem trivially from learning of the behavioral relevance of the embedded contours.

In combination with such considerations and different manipulations, voltage-sensitive dye imaging is a very promising technique that could answer a big debate whether pooling across different areas or lateral connections underlies contour integration. Indeed, it could also provide a powerful tool in texture segmentation debates. But for these debates to make progress we need to focus on the computational questions that need to be addressed, and whether the underlying neural architecture (and, in particular, the timing of neural communication) can implement such computations.

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