

Intermediate level cortical areas and the multiple roles of area V4.

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Conflict of Interest Statement

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Abstract

Despite advances in deep neural networks for object recognition, the function of the mid-level stages of visual processing in the mammalian cortex evades a simple description. This review focuses on the status of cortical area V4 to present evidence for a diversity of roles for mid-level visual areas. Some properties of V4 neurons resemble the static nature of mid-layers of neural networks when training has been completed. However, V4 also gates information flow to higher cortical areas in a dynamic way, reflecting the influences of attention, context, and reward. The most recent evidence suggests a role for mid-level cortical areas in the selective generation of responses to specific sensory inputs. The finding of signals relating to response selection in cortical areas whose role was thought to be fundamentally concerned with sensory representations will require a different approach to evaluating the roles of these areas in cognition. (146 words)

Introduction

The ventral visual areas of the macaque brain and their equivalents in human cortex form a sequence of visual areas, often considered to be fundamentally hierarchical in organization [1]. They are conceptualised as a sequence of processing stages for visual recognition, with high-resolution representations of retinal inputs in the primary visual cortex, V1, ending with representations of perceptual-like qualities deep in the inferotemporal cortex, where neurons often require specific, complex and integral visual objects to generate strong responses [2]. This brief overview is concerned with what happens in between those extremes. It is in intermediate-level cortical areas where the important computational steps towards visual recognition are taken [3-5].

Figure 1 shows that visual cortical area V4 is one of these intermediate stages, lying at a secondary/tertiary level of processing from V1, the primary visual cortex. V4 receives some input directly from V1 and a greater portion indirectly via V2 [6, 7], although the input from V1 arises only from the foveal representation. V4 sends forward anatomical projections to posterior regions of inferotemporal cortex, notably TEO, and onward further down the temporal lobe to cortical areas that are known to be critical for object recognition [1].

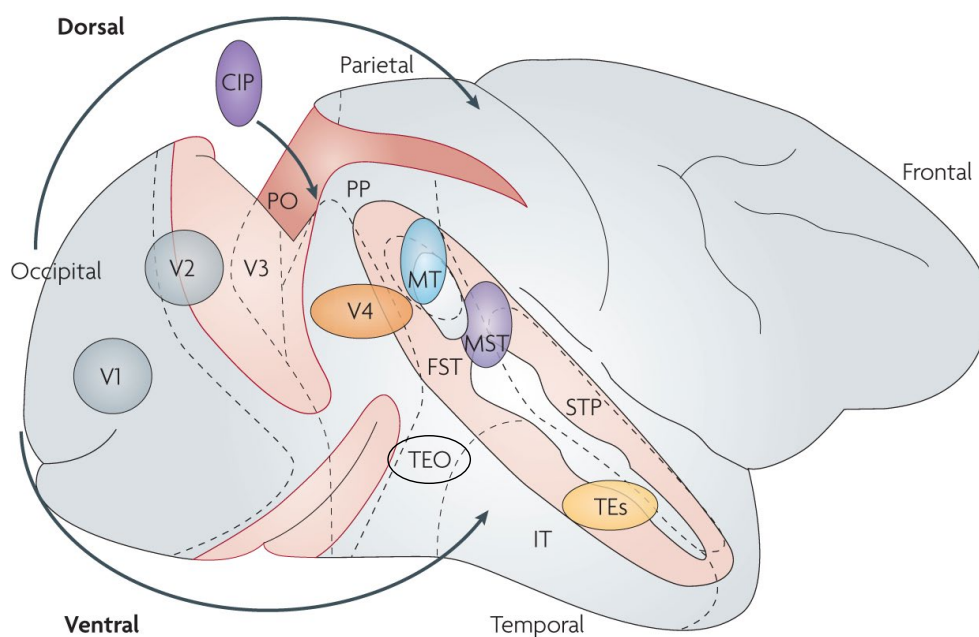


Figure 1: Location of visual area V4 as a mid-level cortical area. Lateral view of right hemisphere of macaque monkey cerebral cortex. Cortical processing for pattern and object recognition begins in V1, transferring through V2, V4, TEO and further along ventral pathway to areas such as TEs in anterior inferotemporal (IT) cortex. Adapted from [8].

How to evaluate mid-level cortical areas: information penetrance and fidelity

Mid-level areas such as V4 are the subject of intense interest [9] because it is in these areas that critical steps from sensation to cognition are achieved. Not everything that is received by a mid-level area is relevant or useful enough to be passed on to higher visual processing areas. Equally, it is important to pass on critical information as reliably as possible. These two requirements can be captured by the terms penetrance and fidelity. Penetrance is borrowed from genetics, where it describes the phenomenon that possession of the variant copy of the gene does not always lead to the variant phenotype. Other factors shape the role of the gene products before they are expressed as a phenotype. In terms of neural processing, penetrance refers to a selective-gating role for mid-level cortical areas.

Fidelity means the capacity to perform a faithful transmission of any information that is needed for current perceptual tasks. Fidelity is reduced by noisy transmission, where valuable signal is masked by ongoing noise, but it is also reduced by distortions or competing biological signals. In terms of spike generation by single neurons, fidelity incorporates both reliability and temporal precision of spiking responses [10].

These concepts can be formalized a little further using information theory. Suppose that we have a collection of images that depict different objects that we wish to use to train a deep learning network to identify and label the objects [3, 5, 11]. These images are passed through a sequence of processing stages. For any processing stage, we can ask two questions from an information theoretical point of view: (1) Is the information needed to identify the object present? (2) Is the information needed to reconstruct the current image available? For each calculation, we can use the standard mutual information calculation $I = H_{\text{total}} - H_{\text{ex}}$ where H_{total} is the entropy of neural responses across repeated presentations of all stimuli (object or image) in the set and H_{ex} is the entropy of neural responses across repeated presentations of the single example stimulus. Entropy of neural responses is defined in the standard way $H = -\sum p(s) \log_2 p(s)$. This gives two quantities: I_{Object} information about the displayed object and I_{Image} information about the details of the image on display. There is a question over the baseline set for images, which could include all possible grey-level combinations or could address the smaller set of images that conform to natural image statistics. It does not much matter for the current purposes as we are interested chiefly in the change in I_{Object} and I_{Image} from one processing stage to the next.

Transferring this to the visual cortical areas of the ventral processing stream, early cortical areas such as V1 should have both high I_{Object} and I_{Image} . The representation in V1 must contain useful information about the object, I_{Object} , otherwise higher cortical areas could not perform the identification task, but V1 also contains a good deal of information about grey levels and colour, I_{Image} , that would be necessary to reconstruct the image itself. Later cortical areas maintain high I_{Object} but gradually lose information about the details of the image. In this regard, the functional role of intermediate cortical areas is to maintain fidelity by transferring signals without losses of I_{Object} , whilst apply selective penetrance, which means successfully decreasing I_{Image} . At the same time, the higher cortical areas should achieve a more compact representation of the different objects, which will result in the distribution of neural responses having a few strongly responding neurons and many weakly responding neurons: in statistical terms, the distribution of responses should become more kurtotic [12]. Further testing of this idea in several visual areas would be welcome.

Topography and Projections

In common with most sensory areas, V4 shows a topographic organization with respect to the primary sensory receptors [13, 14]. However, from the earliest investigations [14], it has been clear that this topography is irregular, reflecting zones of functional specialization within this area [15]. More recent mapping studies, using high-resolution fMRI, have further refined the assignment of critical boundaries, such as the vertical and horizontal meridians. The studies have pointed to additional retinotopic structures around the borders and within the domain of the originally defined V4 [16, 17]. Anatomical tracing has presented evidence that compartments of V4 are functionally related to the thin-stripe and inter-stripe compartments of V2 identified by cytochrome oxidase staining [18].

Like other visual sensory areas of the neocortex, V4 has a system of long-range intracortical connections that are revealed by tracing with biocytin or horse-radish peroxidase [19], as well as a honeycomb structure in layer 2/3, which has a shorter-range repeat structure [20]. The forward projections of V4 are primarily to the posterior inferotemporal cortex, to the area designated as TEO [6], from which there is onward projection into anterior inferotemporal cortex. There is also evidence of compartmentalization in the organization of these projection neurons.

Visual Encoding in V4.

Functionally, lesion evidence points to a role for V4 in fine-grain spatial recognition, including the learning of new discriminations [21-23]. However, the earliest evidence from physiological recordings pointed to a specialized role of V4 in colour processing and recognition. It is unclear whether all of the colour and spatial processing can be neatly assigned to different distinct compartments of V4 although there is no doubt that such compartments exist [15]. An early extensive set of recordings demonstrated that information-theoretic analysis of neuronal firing shows that many single V4 neurons carry signals about both spatial pattern and colour [24].

A recent study [25] has shown how the specialization of compartments in V4 may lead to the accurate transmission of fine spatial detail. Direct measurements in the foveal region of V1 show that single neurons in that cortical region signal fine spatial detail about high spatial frequencies right up to the acuity limit [26]. Using both optical imaging and single neuron recording, the new work shows that there are specialized compartments for high spatial frequencies in V4. These appear to reflect the variability in the retinotopic mapping within V4, resulting in islands of cortex with a wide range of tuning for spatial frequency, including neurons suitable for high acuity pattern recognition. Such neural receptive fields are presumably those that are most susceptible to visual crowding effects [27].

These recent findings may map nicely onto earlier anatomical work that suggests a segregation of visual processing according to visual field location within V4 [28]. Anatomical tracing suggests not just a segregation of regions of V4 according to location in the visual field, but a different functional pattern of cortical [28] and subcortical [29] connections for the foveal and peripheral parts of V4, with certain brain locations exclusively connecting with only the foveal or only the peripheral portion of V4.

V4 neurons encode information about the content of natural image sets with as much accuracy and fidelity as neurons deeper in the ventral visual pathway in the inferotemporal (IT) cortex [4]. The same study showed that V4 neurons are less able to generalize across spatial location than IT neurons, whilst V4 neurons are less disrupted than IT neurons by scrambling of image content, consistent with the long-held view that some IT neurons signal the presence of certain types of visual object [2].

More recent analyses have shown close correspondence between the selectivity of V4 neurons and units of the convolutional network model AlexNet [30] for 2-D shape stimuli with variation of angular position and curvature. These neural networks have a hierarchical set of neural processing layers, rather like the ventral stream pathway. The networks are trained at the top level to learn how to assign object labels (“bus”, “cat”) to pictures of the objects. The weights of all the network connections (equivalent to synaptic strength for a biological neuron) are adjusted all the way back down through all layers as learning proceeds. When the weights are stable, the network can be tested for performance with a new set of pictures and the responses of each of the intermediate layers can be investigated. The repertoire of the neural nets is still limited and, for comparisons with primate vision, the lack of binocularity is a limitation but see [31].

Subjecting the responses of Alexnet units to the same testing and analysis procedures that have been used to characterize real V4 neurons shows that Alexnet does not just match biological performance on image identification tasks. Interesting, it is also found that many of the internal units of Alexnet have selectivity for curvature and object boundaries similar to the single neurons recorded in V4 [11]. This similarity emerges from the training regime of the neural net, rather than being designed into the network architecture.

There are limits to the perceptual-like qualities of neuronal firing in mid-level areas, like V4. Perceptual reversals under binocular rivalry are evident more robustly in temporal areas that receive input connections from early and mid-level visual areas, such as V4, rather than in those areas themselves [32]. Similarly, in a challenging image identification task, later inferotemporal areas show delays in neuronal discrimination that parallel the delays in behavioural discrimination, but those delays are not observed in the responses of area V4 [33]. Beyond the inferotemporal stream, neurons in pre-frontal cortex show greater sensitivity to partially occluded objects than neurons in V4 [34].



Figure 2: a photo image and its representation in the early layer of Alexnet [30]. Deeper layers of Alexnet have patterns of activation that are hard to relate to the original image when viewing the activations as images using the human eye. Alexnet eventually labels this image as an “Apiary”, which can be understood perhaps in relation to the silhouette of the tree outline in the background.

3-D signalling.

To a large degree separate from experimental studies of spatial pattern and texture discrimination in V4 neurons, the selectivity of V4 neurons to binocular depth cues has also been tested. Signalling in V4 is biased towards near disparities, in front of the fixation plane [35], but extends also to a specific sensitivity for the orientation of line contours [36] rotated out of the fixation plane in 3D space. As for processing of other image information, V4 signals for binocular depth are a step closer to perceptual-like qualities. For example, V4 neurons are specifically sensitive to the relative depth between a central patch of dot features and a surround annulus [37]. A specific sensitivity for relative depth better matches human and monkey psychophysics [38] but is not observed in V1 [39].

A separate form of depth-related signalling in V4 arises from responses to overlapping and occluding surfaces in the visual scene. These surfaces have an ordinal relationship to one another, such that a particular surface A is in front of surface B, without any specification of the size of the change in depth between the surfaces. A single edge contour in the visual stimulus, marking a local edge transition from bright to dark, may be surface transition from near to far or from far to near, depending on the context of other edge contours in the neighbourhood. A comprehensive study of neurons in V1, V2 and V4 showed increasing sensitivity to the surface context within V4 in comparison with earlier areas [40], although there is also a substantial difference between V2 and V1. This kind of signalling related to the perceptual assignment of contours to surface structure in the visual scene has recently been studied at the level of population-encoding in V4 using illusory contours [41].

Dynamic gating in intermediate cortical areas and the effects of attention

In practice, intelligent visual systems need to vary the penetrance of information flow through intermediate cortical areas, so that the visual system can make dynamic changes in the discarding of irrelevant, even conflicting, neuronal signals that are not relevant to the current perceptual states. The plural “states” is used because there will always be multiple tasks that are being performed. Even at the highest levels of focussed attention on a particular task, there must remain a sensitivity to external events that might change the need for a task or its urgency or relevance.

For V4, lesion evidence indicates a deficit in the allocation of attention to fine discriminations [42], although the impact of lesions on spatial texture discriminations is not wholly explained by attentional effects [43]. Attentional effects have been extensively studied at the single neuron level in V4, where it has almost become the paradigm case for the study of cognitive influences on sensory processing. Normally, the behavioural task provides a cue to direct attention to spatial locations or stimulus features, followed by a judgment on the stimulus presented. The cue is only probabilistically valid, so that there are trials upon which the cue directs attention away from the feature of interest. The outcome is an enhancement of neuronal firing in response to the stimulus when attention is allocated to its location or features. An intense debate has been conducted on the question of whether attentional effects in V4 are best explained by a gain control with no elevation of baseline firing [44]

Duncan and Desimone articulated the biased competition model of attention as essentially a classic information capacity limit, in which there is a competition among stimuli as to which will get through the gate [45]. Past experience is embedded in this model by proposing that memories will bias this competition, such that memories behave much like external stimulus cues. These interactions set the competition between one stimulus and another, so they control stimulus-stimulus (S-S) competition. Within area V4 this framework can be applied to both spatial and feature attention. This model also has been applied to a variety of neuronal signals: attentional modulation of baseline firing rates, which has been controversial [46, 47]; gain-related changes in neuronal responses to stimulus presentation [48], universally confirmed; and distinct modes of neuronal signalling such as gamma-band oscillations [49, 50] and the correlation structure of neuronal firing in populations [51].

Beyond gating of stimuli: sensitivity to responses and outcomes.

An alternative to the S-S framework is that V4 may exert a degree of control over stimulus-response (S-R) relationships. Within the S-S framework, information that arrives in V4 and passes out to higher-order areas undergoes a selection process that is driven by a competitive interactions between the neural representations of two or more stimuli, as in the Duncan, Desimone framework. There is, however, evidence that there are signals in V4 that are linked to the selection of particular responses in response to a given stimulus. One line of evidence for these S-R links comes from an experiment, in which neurons were recorded in V4 whilst animals attended to coloured, oriented bars [52]. For any particular trial, the animal was cued to attend to either colour or orientation. During training, specific colour, such as red, were associated with one response alternative (LEFT), whilst another colour, such as blue, signalled the other response (RIGHT). There was a similar association of vertical and horizontal orientations with LEFT and RIGHT respectively. For a red vertical

bar, the animal should always choose LEFT, whether responding to colour or orientation. However, a mixed stimulus, such as a blue vertical or red horizontal bar requires a different response depending on the delivered attention cue. This experimental procedure dissociates the S-S interactions from the S-R interactions and revealed that V4 neurons encode the trial-relevant response to a mixed stimulus in the time-points approaching the moment for the behavioural response.

By boosting a signal to a group of neurons that code for a stimulus that is associated with a particular response, there is an increased likelihood of producing that response when the stimulus is presented. In this model, the increased signal in the sensory neurons arises because top-down sources that favour a particular response permeate a wide set of neurons that are associated with making that response choice. An obvious candidate for a wide-ranging signal relating to a choice of response is the immediate past history of reward, a signal which both human and animal subjects are known to track accurately and has recently been shown to enter V4 [53] and the mid-level cortical area V5/MT [54] during perceptual decision making.

Both S-S and S-R influences may be at work in V4. A further example of the role of V4 in controlling selective penetrance of information in both S-S and S-R frameworks is provided by the recent demonstration that during performance of an orientation discrimination task, upper layer signalling in V4 is more closely related to the sensory attributes whereas lower layer signalling is more closely related to response choice [55]. In both these experiments [52, 55], V4 neurons appear to alter their response according to the behavioural category with which the sensory feature is associated. This is consistent with a role for S-R links rather than purely perceptual S-S links. However, it appears that there may be some separation of the ways in which boosting of S-R and S-S links occurs, given the evidence for laminar segregation of these signals [55].

Conclusions.

V4 is a widely studied example of a mid-level cortical area, thought to lie at a strategic position in the ventral stream pathway that is primarily concerned with object and pattern recognition. One stream of evidence has pointed to the role of V4 as generating selectivity for more elaborate and abstracted features, compared with the oriented lines, edges and spatial frequency wavelets that describe V1 responses. This more elaborate selectivity, for properties such as curvature and corner configuration, is nonetheless still delivered by static properties of the neurons, trained into the visual connectivity during neural development or long-term adult plasticity. A different stream of evidence indicates a more dynamic role, which information transfer through the mid-level area is shaped by task requirements. Changes in these requirements exert short-term changes in the information content of signals leaving V4, adapting these signals to both the configuration of stimuli in the visual scene and the behavioural choices that the animal will make in response to those stimuli. It is argued here that these two seemingly different activities of V4 are fundamentally driven by the same information-processing requirements, which are to allow certain signals to permeate through, whilst maintaining a set of options for rapid release of temporarily rejected signals in the event that the task requirement or the state of the world changes.

Future studies of mid-level areas need to focus further on the transformations from dense to sparse coding that are implied by the transition from an image-like representation of the visual input in early cortical areas over to a perceptual-like representation of visual objects deep in the inferotemporal cortex. The extent to which mid-level cortical areas arrange selective and sometimes variable penetrance of information through to these higher areas is key to their role. Yet, we learn from inspecting the patterns of activity within artificial neural networks that it is hard to conceptualize in any easy way exactly what are the functional operations of mid-level processing areas. Approaches that employ simultaneous recordings of neuronal populations from multiple areas within a framework that considers the information transfer appear to be the most profitable avenue to explore.

Declaration of Interest

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