

Perceptual and neuronal correspondence in primary visual cortex

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Recent findings from the study of primary visual cortex in humans and animals blur the distinction between early and late visual processing. Under some conditions, the activity of neurons in primary visual cortex appears as close or closer to perception than activity in 'higher' visual areas.

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Abbreviations

2-DG	2-deoxyglucose
FEF	frontal eye field
fMRI	functional magnetic resonance imaging
LGN	lateral geniculate nucleus
MST	medial superior temporal area
MT	middle temporal area
PET	positron emission tomography
rTMS	repetitive TMS
TE	temporal visual area
TMS	transcranial magnetic stimulation
V1	primary visual cortex
V2	second visual area

Introduction

Intricate block diagrams of the visual system, showing the primary visual cortex (V1) at the bottom of an inverted pyramid of areas [1,2], are almost ubiquitous in introductory textbooks and lectures. It is tempting to infer from these figures that serial processing extending into the parietal, temporal, and frontal lobes, approaches perception as the hierarchical ladder is climbed. However, recent research using neurophysiological recordings in animals and functional magnetic resonance imaging (fMRI) in humans makes it increasingly clear that this inference is overly simplistic. Although there is unquestionably some degree of serial processing from V1 to 'higher' cortical areas, in many situations, activity in early visual cortex is better correlated with, and may be more intimately involved in, perception than activity in later areas. Ultimately, words such as early and late, which imply temporally segregated processes, may be more misleading than helpful in understanding visual processing that takes place in a tightly interconnected assembly of areas. The analysis below examines facets of visual processing that are often taken as signs of higher level function in extrastriate cortex, but are also seen in V1. These include correlations of neural activity with perception, neural responses that are invariant across perceptually invariant stimulus regimes, selective visual attention, and mental imagery.

The timing of neuronal responses

In a relay race, each runner completes a segment before passing the baton to the next, until the last runner reaches the finish line. If visual processing were analogous to a relay, the first visual processing stage would perform a set of computations until they were complete and then pass the result to the second stage, the second would pass a result to the third stage and so on, with perception being the output of the last stage. However, there is considerable evidence inconsistent with strict serial processing in the visual system.

Response latencies do not always follow predictably from cortical hierarchies constructed from known pathways and rules of connectivity [1,2]. The clearest example of this is the dorsal visual stream, usually drawn as a pathway extending from V1 to the second visual area (V2) and the middle temporal area (MT), then onwards to the medial superior temporal area (MST) and the frontal eye field (FEF). In reality, response latencies at 'later' stages, such as MT, MST and FEF, differ little from latencies in V1 and V2 [3,4–7]. In the ventral stream, latencies increase more progressively, with average temporal visual area (TE) latencies being ~40 ms longer than those observed in V1 [3,6].

The importance of response latency for serial processing depends to some extent on the range of latencies within each area and the typical duration of responses. There is considerable scatter in the latencies within each cortical area — of the order of 60–80 ms in areas stretching from V1 to TE [3,6]. In V1, responses to the onset or offset of a stimulus typically evolve over hundreds of milliseconds, suggesting that computations are ongoing [8–10]. Even with very short stimulus presentations (i.e. <20 ms), responses in TE have a duration of hundreds of milliseconds [11–13].

Combining these data on response latency and scatter with those for response duration paints a complex picture of activity in the visual pathways. In the dorsal stream, areas reaching from V1 to MST and FEF are almost simultaneously activated and this coactivation lasts for ≥100 ms. In the ventral stream, there is an average delay of ~40 ms between V1 and TE; however, the latency scatter is so large that many V1 neurons will not begin firing until after many TE neurons have already begun firing. After the initial response latencies, visual areas stretching from the pole of the occipital lobe to the tip of the temporal lobe are coactive for fifty to hundreds of milliseconds.

The implication is that the relay race analogy is entirely inappropriate, and visual processing may be more similar to the Tour de France, with members of a team (an array of visual areas) working simultaneously at different paces for the same team goal (perception). This point is underscored

by demonstrations of temporal asynchrony in the perception of different visual attributes [14,15]. With the exception of the earliest spikes in the ventral stream, there is no simple sequence of activated visual areas. Complex perceptual processes that occur in a couple of hundred milliseconds are routinely accompanied by coactivity in a large number of visual areas, including V1.

A recent study by Pascual-Leone and Walsh [16•] makes clever use of transcranial magnetic stimulation (TMS) and response timing to explore the role of V1 in motion perception. TMS stimulation of V1 can produce the perception of stationary phosphenes (i.e. perceived light in the absence of retinal stimulation) and TMS of MT can produce the perception of moving phosphenes. In this experiment, TMS stimulation of MT was done at the threshold intensity needed to evoke phosphenes, but the V1 TMS was below threshold. If TMS was applied to V1 before MT, moving phosphenes were perceived the same as if no V1 TMS had been administered. However, when MT was stimulated 5–45 ms before V1, subjects either perceived no phosphenes at all, or they saw phosphenes that appeared stationary rather than moving. In other words, despite the MT activation, disturbing V1 activity at a later time abolished the motion percept. Thus it appears that, at least in this unusual situation with external brain stimulation, V1 activation is critical for the perception of motion.

Perceptual correlates in V1

The analysis of response times across visual areas suggests that V1 is a possible substrate for perception, in that V1 is part of an assembly of areas that are coactive when perception occurs. Indeed, correlations between V1 activity and perception have been reported in diverse domains spanning low-level to high-level vision. V1 has several unique properties that a perceptual system evolved for behavioral expediency might exploit: it is the first cortical area to receive afferents from the lateral geniculate nucleus (LGN), it is the largest visual cortical area, it has the highest resolution retinotopic map, it has the smallest receptive fields, and it has independent input from the two eyes.

Examples of correlations between V1 activity and ‘low-level’ perception include acuity, contrast sensitivity, and orientation sensitivity. In both humans and monkeys, the magnification factor for V1 accurately predicts visual acuity at different eccentricities across the visual field [17–19]. Less is known about magnification in extrastriate cortex, but the data available suggest that acuity may not scale with magnification in any area beyond V1. Thus, high acuity vision may rely on signals available only in V1.

Neurons in striate cortex are particularly sensitive to contrast [20,21] and their responses have been linked to human contrast detection thresholds [22,23]. Recently, Boynton *et al.* [24] reported that across a range of baseline contrasts, human observers detected contrast increments

when fMRI activity recorded in V1 increased above a threshold amount. In the case of orientation, accurate predictions about human perception and discrimination can be made from the distributed pattern of activity within V1 [25–27].

Neuronal behaviors with parallels in higher level visual processes have also been reported in V1. The response of a V1 neuron to stimuli within its receptive field can be powerfully modulated by stimuli outside it [28]. Knierim and Van Essen [8] found that these surround interactions produce neural responses consistent with the perceptual pop-out of a stimulus from its background. Other studies have reported delayed V1 responses consistent with figure-ground segregation [9,10], although a more recent study has questioned this conclusion [29]. The perception of lightness — another element of mid-level vision — also has neuronal correlates in V1 (of cat). Not only is the average V1 response correlated with perceived lightness, the response is also immune to changes in illumination (i.e. it is lightness constant) [30–32]. The finding of this form of response invariance in V1 is of interest, in part, because other forms of response invariance, such as insensitivity to size or three-dimensional orientation observed in the inferotemporal area, are sometimes taken as indications of higher level processing [33–36].

In human perception [37,38] and monkey V1 complex-cell responses [37], sensitivity to contrast depends similarly on the presence and organization of secondary stimuli near a target. Perceptually, arrangements of separated line segments can lead to powerful grouping and integration into a single continuous contour. The facilitation observed in neurons when line segments are collinear but separated by a gap, might play a role in contour integration. Of particular interest in the study by Kapadia *et al.* [37] was the finding that the perceptual and physiological interactions (in V1) showed a similar dependence on the spatial scale and the difference in orientation between the target and secondary stimuli. Although the similarity between interactions observed in V1 and perception might be coincidental, the diverse magnification factors and interaction ranges present in various visual cortical areas would be unlikely to lead to such a correlation for many other areas.

Neurons have also been recorded in V1/V2 that respond in a manner correlated with perception during binocular rivalry [39]. Although the percentage of cells with such responses in V1/V2 is lower than in later visual areas [39,40], the total number of cells that follow shifts in rival percepts may actually be higher in early cortex because of the large size of V1 and V2.

Area V1 is the first locus at which afferents from the two eyes converge and is the last area at which the responses of some cells can be unambiguously linked to the eye seeing a stimulus. There is a form of depth perception termed *da Vinci stereopsis* [41], in which depth is inferred from

monocular visual input resulting from the occlusion of one object by another. This form of stereopsis appears to require eye of origin information, which is explicit in V1 but may not be available in other areas. In another study related to depth perception, Sugita [42] recorded the response of V1 neurons to a stimulus consisting of two line segments on opposite sides and outside a receptive field. The cells did not respond if nothing filled the gap between them or if a visible patch was given a disparity putting it behind the segments (a situation inconsistent with the segments being a single line covered by an occluder). However, if the patch was given a disparity placing it in front of the segments — a situation consistent with occlusion of a long line — some cells were excited. Thus, the responses of these neurons were consistent with perceptual amodal completion of the line.

Imagery

Mental imagery is visual perception in the absence of retinal stimulation, sometimes called ‘seeing with the mind’s eye’. Although people can tell the difference between imagery and normal visual perception, imagery might be helpful for distinguishing brain areas required for perception from those involved in simply relaying signals from the eyes (because retinal input is not needed for imagery). It is generally agreed that forming mental images activates extrastriate visual areas; however, there is disagreement about whether primary visual cortex is involved [43–45]. Evidence from humans with brain lesions is consistent with early visual cortex playing a role in visual imagery, though this role may be different or less than during normal visual perception [46–48].

Early work by Kosslyn *et al.* [49] suggested that, at least in some situations, imagery involves the formation of an internal, spatially accurate representation of an image. In positron emission tomography (PET) and fMRI brain imaging studies, several mental imagery tasks have been reported to activate early retinotopic visual areas [50–52]. For example, Kosslyn *et al.* [53] asked subjects to make comparisons between mental images of gratings they had previously seen in different visual quadrants. During the imagery task, area 17 was activated in PET recordings, and repetitive TMS (rTMS) over area 17 increased reaction times for both the normal perception of the gratings and the imagery task. If, as the authors claim, the rTMS did not affect other visual areas, the experiment implies that activity in area 17 is normally used to perform the imagery task, rather than being an epiphenomenon.

Interactions between imagined stimuli and real stimuli have properties suggestive of area 17 involvement. Polat and Sagi [38,54] previously showed that if a small patch of grating (a ‘Gabor target’) is flanked by other gratings, at certain separations in the flanking, the flanking stimuli decrease the contrast threshold for the central target. Ishai and Sagi [55] repeated this experiment and conducted a variation in which subjects simply imagined the presence

of the flanking stimuli with actual presentation of the central target. In this imagery condition, the imagined flanking stimuli decreased the contrast threshold for the central stimulus, when they were imagined at a distance similar to that which gave a threshold decrease with real visible flanking stimuli. Other properties of this odd interaction with imagined stimuli suggested that the interaction occurred very early in visual cortex. First, the imagery interaction was orientation specific. In other words, just as in the real version of the experiment, the orientations of the central target and flanks had to be the same. Second, the imagery effect was monocular — there was no reduction in contrast threshold when the flanking stimuli were memorized by exposure to one eye, but the central target was exposed to the other eye during imagery testing. The combination of orientation selectivity and monocularly suggests that the imagined stimuli and the interactions occurred in area 17.

After years of controversy, there is no consensus about the involvement of V1 in mental imagery. On the basis of the inability of some experiments to demonstrate V1 activation, caution is warranted [44,45]. However, an intriguing possibility is that V1 is only active during some types of imagery tasks for which it is required. For example, Thompson *et al.* [52] have proposed that activation of early cortex by imagery is related to the spatial demands of the task rather than to the spatial properties of the stimuli. If true, this would mean that imagery, and perhaps perception in general, might access information in V1 only as needed.

Selective visual attention

Voluntary and automatic shifts of visual attention are often thought to be intimately involved in conscious perception, because they represent an active selection process in which a subset of the visual input is scrutinized. In most early [56–58] and some more recent [59] physiological studies, attentional modulation of neural activity was observed in ‘higher’ visual cortical areas, but not in striate cortex. However, other recent experiments have found attentional effects even in primary visual cortex [60–62].

Haenny and Schiller [63] recorded from neurons in visual areas V1 and V4 while monkeys performed a visual matching task and found that their responses were enhanced by attention in about one-third of V1 and two-thirds of V4 cells. However, Motter [60] found rather similar effects of attention in V1, V2 and V4 with monkeys trained to make orientation discriminations either within or outside the receptive field of a neuron. In each cortical area, roughly one-third of the neurons gave a different response to a stimulus in the receptive field when it was attended and not attended. The most common response difference was a larger response when attention was directed to the receptive field than when it was directed elsewhere. Attentional effects have also been observed in multi-unit recordings from primary visual cortex with animals trained on a curve-tracing task [61]. Ito and Gilbert [62] observed small

effects of attention on responses of V1 neurons to stimuli in their receptive fields, and also a larger attentional modulation of contextual influences. In this latter effect, the facilitatory influence of a line outside a receptive field on the response to another line in the receptive field was enhanced by attention to the receptive field.

To visualize the influence of attention, Vanduffel *et al.* [64•] had monkeys perform two tasks that used identical stimuli but required different levels of attention. The difference in brain activation was imaged by double labeling with 2-deoxyglucose (2-DG). Attention-dependent differences in 2-DG labeling were observed in both V1 and the LGN. Of particular interest was the observation that the primary effect of attention was suppression of unattended areas rather than facilitation of the attended area. These findings suggest that attention involves a very early filtering operation, though they are not easily reconciled with the earlier electrophysiological results.

In contrast to the mixed data from electrophysiological studies, the influence of attention on visual responses in primary visual cortex has been routinely observed in brain imaging studies of humans [65–70,71•,72–74]. In general, these studies report an increase in brain activity at the attended location. In addition, Tootell *et al.* [65] observed less brain activity at unattended locations. Tootell *et al.*'s finding is consistent with the earlier observations using 2-DG, mentioned above. Kastner *et al.* [75] also saw suppressive effects of attention in V2, V4 and TE, but not V1. The lack of an effect in V1 may have been a consequence of the relatively large size and distance of the stimulus elements in this experiment. Attentional modulation in V1 and extrastriate cortex was visualized by Brefczynski and DeYoe [69] and, at the resolution of fMRI, it appears to be as spatially precise as visual activation — the enhanced activity associated with attention to one stimulus surrounded by others occurs at the same topographic location as visual activation by the stimulus in isolation.

Two factors appear to play important roles in whether modulation by attention is observed in V1. First, the behavioral task must be sufficiently attention demanding. For example, using fMRI, Somers *et al.* [67] found large attention effects in V1 — comparable to those seen in V4. This may have been a consequence of the difficult RSVP (rapid serial visual presentation) task subjects performed. Similarly, the relatively large single-cell effects that Motter observed in V1 [60] may have been associated with the peripheral orientation discrimination task the animals were trained to perform. Martinez *et al.* [68] attributed the V1 effect they observed to the requirement that subjects focus attention in a small area amidst clutter. Using a difficult pattern detection task, Ress *et al.* [76•] found a proportional relationship between task difficulty and V1 activity. Gandhi *et al.* [66] required subjects to perform a speed discrimination at threshold and the observed attentional modulation in V1 was comparable to that in MT+ (a human

motion-sensitive area probably homologous to cortical areas in the vicinity of MT in the macaque). These difficult tasks are in marked contrast to the simple saccade paradigms used in early physiological studies.

In addition to task difficulty, the second factor that determines whether attention modulates V1 activity is the visual attribute that must be scrutinized. For example, with grating stimuli, Huk and Heeger [71•] instructed subjects to alternately perform threshold contrast and speed discriminations. With identical stimuli, area V1 was more modulated by performance of the contrast discrimination task, whereas MT+ was more modulated by performance of the speed task. Similarly, larger signals were seen in V1 by Watanabe *et al.* [72,73] when subjects attended to simple translational motion than when they attended to radial motion or the motion of one object amidst others, a task known to significantly influence MT [77].

Conclusions

Areas spread widely across the cerebral cortex are involved in visual behaviors, but not all are involved in perception *per se*. For example, extensive bilateral temporal lobe damage can profoundly degrade visual recognition and memory, but perception remains largely intact. This is seen in the Klüver-Bucy syndrome [78] and the classic case of patient HM's amnesia [79]. Likewise, prefrontal lobe lesions alter emotion, affect, working memory, and other attributes, but perception generally stays good [80,81].

In contrast to the effects of temporal or frontal lesions, it has been known since the nineteenth century that damage to the occipital lobe can render humans blind. Moreover, there is evidence that visual perception involves the activation of multiple occipital areas performing different duties. Examples include reports of achromatopsia [82] and akinetopsia [83], which result from different extrastriate lesions that otherwise leave perception normal. In these syndromes, extrastriate lesions seriously degrade color or motion perception, but most other aspects of visual perception remain reasonably normal. V1 might be responsible for some of the residual perception following the extrastriate lesions.

The latency and duration of V1 responses allow for the possibility that this area is involved in perceptual events that take 50 to hundreds of milliseconds. And in this broad time window, both early and late correlations of V1 activity with perception have been reported. Moreover, visual attention is frequently reported to modulate V1 activity, suggesting that V1 participates in selective processing rather than fixed filtering operations. The protracted and evolving responses observed in V1 might also be indications of dynamic processing.

The implication from studies of visual imagery and selective attention is that information uniquely available in V1 may be accessed on an as-needed basis. Tasks requiring high

acuity, or fine orientation or contrast discrimination may draw on V1, whereas less attention-demanding tasks, and judgments involving other visual aspects such as pattern motion, may not. The need for flexibility in visual processing and cooperativity between early and late visual areas is suggested by numerous perceptual phenomena. For example, there are interactions between brightness perception, depth perception, and grouping that appear to call for both bottom-up and top-down flow of information [84]. Similarly, the segregation of a figure from its background may require recognition of what the object is. In the classic picture of a barely discernible Dalmatian dog on a spotted background, it is difficult to imagine segregating the spots into a dog and background without the top-down imposition of information about dogs.

Though it seems doubtful that activity in primary visual cortex is always closely linked to perception, accumulating evidence suggests that V1 may sometimes play a direct role. In some behavioral situations, V1 may provide the most useful (or only) information. The cases cited above provide examples of correlations between visual perception and V1 activity. Although exhaustive recordings might be needed to prove that such correlations are not seen in any other areas, the correlations observed to date have properties, such as dependence on magnification factor or monocularly, that are not obviously present in any area beyond V1. A simple argument against V1's involvement in perception is that the activity of neurons in this area does not always correlate with perception. Although this is surely true, it is probably also true of all other visual cortical areas. Perception appears to rely on a division of labor across areas and dynamic interactions between them. The suggestion that perception is based on the flexible involvement of multiple tightly interconnected areas (including V1) is reminiscent of Hebb's concept of cell assemblies [85] and is related to processing theories relying heavily on feedback [7,86–88].

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