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Perceptual Learning: Is V1 up to the Task?

Dispatch

Alexander Thiele

Our ability to make fine visual discriminations improves with practice, and so at some level so must our visual system. A new paper reports that the receptive field structure of a neuron can be fine-tuned for different visual tasks. These findings raise important questions about the circuitry and mechanisms that underly perceptual learning.

My friend Thomas is an artist, but whenever we look at the same things he illuminates an important problem in visual neuroscience. He sees things differently from me. In bland walls he sees the plaster's structure nicely contrasting the weathered chromium green of a nearby car. His pictures of boring environments thus make great paintings and photographs. Thomas' exceptional visual abilities have been honed by his years of training and practice as an artist. But those abilities must be supported by real differences in his brain. Where do these differences reside? And what are they? Are they permanent, or do they switch in and out depending on what he is trying to see? For a long time it has been known how the brain, and in particular the visual system, is shaped during early development (for example [1]). How learning affects organization of visual cortical areas during later stages in life is far less well understood, but a variety of recent studies have started to shed light on these issues.

Improvement with practice at discrimination tasks is referred to as perceptual learning. The enhanced abilities produced by visual perceptual learning are often restricted to the exact stimuli and the exact location in the visual field used for training. This suggests that learning happens in early visual areas [2], but the associated changes remain debated [3–6]. However, changes do occur as early as the primary visual cortex (V1). When animals were trained in difficult orientation discriminations, neurons in V1 that were ideally suited to help solving the task were found to show an increased ability to signal small orientation differences after learning [3].

A new paper by Li *et al.* [7] also demonstrates that, following a prolonged learning period, receptive field properties in area V1 vary depending on task demands. It has previously been shown that V1 neurons can alter their activity to stimuli presented in the receptive field depending on whether the stimulus is behaviorally relevant (for example [8–10]), and it was suggested that these effects reflect attention to relevant locations, objects or features. Li *et al.* [7] have now shown that neuronal activity in V1 can be selectively modulated by behaviorally relevant stimulus elements *surrounding* the receptive field.

In this new study [7], monkeys had to solve a vernier task where three lines were either collinear or non-collinear, or they had to solve a bisection task where the three lines of interest were parallel, with varying offsets between the center and the two side flanking lines (see Figure 1A for an example). After the animals had become experts in the task, the authors measured how the responses of neurons were affected by the stimulus elements used in the vernier and the bisection task. The central part of the stimulus was presented in the receptive field center and the end flanks and side flanks used for the bisection and vernier tasks surrounded the receptive field. Which task to perform was indicated by a combination of color and contrast cues (Figure 1A).

Li *et al.* [7] found that neurons changed their responses in a task-dependent manner: a large proportion of neurons carried more information about the end-flanks when the monkey performed the vernier task, and more information about the side flanks when the monkey performed the bisection task. This is an interesting finding, because it suggests that receptive field properties in V1 are adaptive, and can change according to task demands. Somewhat surprisingly, the authors did not find an obvious relationship between the side and end-flank offset tuning, apart from the fact that end flanks generally were more effective in modulating the tuning when monkeys performed the vernier task, while side flanks were more effective in modulating the tuning when monkeys performed the bisection task (although there were some notable exceptions to this).

Li *et al.* [7] further investigated whether these task-dependent changes would occur even when the monkeys performed the tasks in a location remote from the receptive field, while the neuron was probed with the same stimuli as before. This approach allowed them to investigate to some extent what effect spatial attention has on the neuronal activity. Additionally, it probed whether performing the task affects neuronal processing globally, or whether it is restricted to the location of relevance. The authors found, in line with previous reports (for example [10,11]), that spatial attention affects neuronal processing in primary visual cortex, and that the task-related modulations vanish when the task is performed at a visual location distant to the receptive fields of the neurons under study. They argue that task relevance appears to affect tuning properties of neurons locally, going beyond those changes generally ascribed to attention.

These results are intriguing and raise a variety of interesting and challenging questions. Is spatial attention really unable to explain the results? Are the results a reflection of specialized receptive field properties that emerged while monkeys learned the

Henry Wellcome Building, University of Newcastle upon Tyne, Newcastle NE2 4HH, UK. E-mail: alex.thiele@ncl.ac.uk

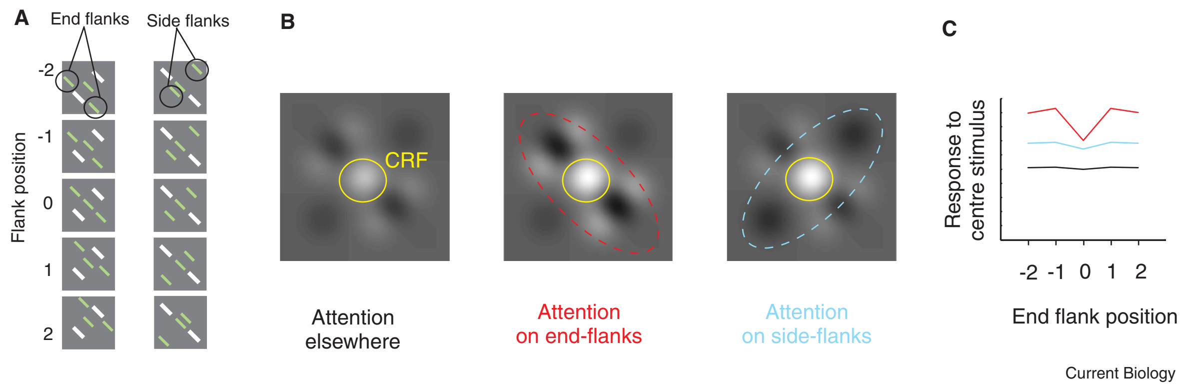

Figure 1. Changes in receptive field properties of V1 neurons associated with perceptual learning.
(A) Part of the stimulus set used by Li *et al.* [7]. Color of the bars signaled which task to perform (vernier task left, bisection task right). The end and side flanks flanks could occur in five positions with different offsets relative to the central bar. The latter was always placed in the classical receptive field (CRF). (B) Three 'activation maps' of hypothetical center surround organization. The yellow circle indicates the location of the classical receptive field. Bright areas show regions from which the neuron can be excited, black areas show regions from which the neurons can be suppressed. When attention is directed away from the receptive field the overall efficacy of center and surround mechanisms is relatively weak, resulting in a relatively little modulation as the end flanks are presented in different location (black tuning curve in C). The CRF and surround within the red dotted ellipse influence is increased when attention is directed toward the end-flanks in order to solve the vernier task. This results in overall increased activity, and substantial modulation as the end-flank position is altered (red curve in C). If attention is directed toward solving the bisection task, the end flanks will be less effective in modulating the center response, resulting in a relatively flat elevated tuning curve (blue curve in C).

task? Would they be found in a naïve monkey? If the properties arise through learning, how do these changes come about? What are the sources that govern these changes?

Let us return to the spatial attention hypothesis. The effect of spatial attention on neuronal activity is generally similar to increasing the signal strength at the attended location [12]. Neurons in V1 have a center-surround organization, such that stimuli placed at various locations surrounding a receptive field can modulate the response to stimuli presented in the center of the receptive field, while they do not elicit responses on their own [13]. Spatial attention might be able to selectively modulate these center-surround influences, as outlined in Figure 1B. While animals performed the vernier task, the receptive field surrounds representing the end-flank positions may have become more influential in modulating the neuronal response. This simple model predicts that attention increases firing rates at the attended location, and that end-flanks are more effective in modulating the neuronal response when animals perform the vernier task (Figure 1C).

The example shown in Figure 1B and C is just one arbitrary possibility of center-surround organization. Receptive field surrounds of a neuron can be asymmetric and fairly complex in nature — a stimulus placed in one location of the surround can have a suppressive effect on the response to a stimulus presented in the center, while it may be ineffective or even facilitating if it is placed in a different part of the surround [14]. These differences in center-surround organization could lead to a whole family of task-dependent tuning curves. The tuning changes seen by Li *et al.* [7] might thus reflect the underlying structure of center-surround organization highlighted by allocation of spatial attention. The tuning functions of V4 neurons show similar behavior: they change their tuning as a function of allocation of attention to different areas surrounding the receptive field [15]. If attention can selectively modulate surround influences, then it might change receptive field filter properties such that neurons can transmit information differently for a wide variety of tasks.

But what are the sources for these modulations? The task-related effects are almost certainly mediated by top-down influences. These top-down signals may arise in the parietal cortex and/or the frontal eye field (among others). Elegant studies have recently demonstrated that top-down projections from the frontal eye field to visual area V4 can enhance stimulus-related activity [16], and electrical stimulation of the frontal eye fields can increase an animals' contrast sensitivity [17]. Another, not necessarily exclusive, possibility is that activation of neuromodulatory systems could contribute to the results described by Li *et al.* [7]. The cholinergic system is likely to be involved in attentional processes [18,19], and slice studies have demonstrated that high level of acetylcholine alter the synaptic efficacy of feed-forward and lateral intracortical connections [20]. In our laboratory, were have observed that spatial attention and the application of acetylcholine have very similar effects on spatial integration in V1 (unpublished results). Thus, task-related alterations of the efficacy of feed-forward and lateral connections through (co-)activation of the neuromodulatory system might also lead to tuning changes similar to those described by Li *et al.* [7].

Although a lot of progress has been made in understanding the underlying mechanisms of attention, perception and selection, it will still be a while before we fully understand why my friend's visual world is so different from mine.

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