

## TOPICAL REVIEW

# Perceptual learning and adult cortical plasticity

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The visual cortex retains the capacity for experience-dependent changes, or plasticity, of cortical function and cortical circuitry, throughout life. These changes constitute the mechanism of perceptual learning in normal visual experience and in recovery of function after CNS damage. Such plasticity can be seen at multiple stages in the visual pathway, including primary visual cortex. The manifestation of the functional changes associated with perceptual learning involve both long term modification of cortical circuits during the course of learning, and short term dynamics in the functional properties of cortical neurons. These dynamics are subject to top-down influences of attention, expectation and perceptual task. As a consequence, each cortical area is an adaptive processor, altering its function in accordance to immediate perceptual demands.

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Experience plays an important role in the brain mechanisms of visual processing. This is true not only for the recall and identification of objects, but for intermediate level processes of contour integration and surface segmentation. The lasting experience-dependent changes in the functional properties of neurons and in the circuits underlying these changes is known as plasticity. The cortical areas involved in experience-dependent plasticity include not only temporal lobe areas involved in the representation of objects but all visual cortical areas, even primary visual cortex (V1). Learning is divided into declarative memory, the conscious recall of people, places and events, and implicit memory, the unconscious acquisition of habits and skills with practice. Perceptual learning is a form of implicit memory, involving improvement in sensory discrimination or detection by repeated exposure to sensory stimuli. Whereas declarative memory is localized to the temporal lobe, perceptual learning involves functional changes that are widespread throughout the cortex, and affects cortical function throughout life. The findings leading to this idea were unexpected. Torsten Wiesel and David Hubel had shown that properties of cortical neurons, like ocular dominance, could be affected by experience only during a critical period early in postnatal life. But evidence has accumulated that many other properties are subject to experience even in adulthood, and the mutability of these properties can account for the psychophysical changes occurring during perceptual learning, as well as functionally adaptive changes following CNS lesions.

A key to understanding the nature of experience-dependent changes in the visual cortex is the higher order, context-dependent properties of visual cortical neurons. The basic property of orientation selectivity discovered by Hubel and Wiesel is a framework upon which one can understand their selectivity for more complex features. If one uses a simple stimulus such as an oriented line as a visual stimulus to map a neuron's receptive field (RF), the measured extent of the RF is quite small. However, the discovery of long range horizontal connections in visual cortex suggested that neurons receive input from a much larger area of visual space than expected from RF maps derived from simple visual stimuli. These long range connections endow neurons with selectivity for more complex features than predicted from their response to a single line stimulus placed in and around their RFs. Their responses are context dependent, and the contextual influences play a role in contour integration as well as in sensitivity to the configuration of complex stimuli. The contextual influences are subject to visual experience, such that training on a visual discrimination task alters the neuronal tuning to the attribute involved in making the discrimination.

So far we have expanded the characterization of V1 from a fixed filter selective for simple line stimuli to an area coding for more complex visual features and changing its function according to visual experience. A third important insight into its function comes from experiments in behaving animals, which show top-down influences on neuronal stimulus selectivity. The responses

of cortical neurons are dependent on attention, perceptual task and object expectation. These cognitive influences act most strongly on the contextual influences referred to above. Therefore, the three influences on the stimulus selectivity of V1 neurons, context, visual experience and task, are intimately related and mutually interactive.

### Perceptual learning and contour integration

Both anatomical and physiological evidence shows that even in V1, neurons integrate information over relatively large parts of the visual field, much larger than what one would expect by RF maps obtained with single short line stimuli. Cortical pyramidal cells have axonal arbors that extend for distances up to 8 mm parallel to the cortical surface (Gilbert & Wiesel, 1979; Rockland & Lund, 1982; Gilbert & Wiesel, 1983; Stettler *et al.* 2002). This means that their targets are capable of integrating information over an area of visual space much larger than their RFs as measured by a single line stimulus. We can see this lateral connectivity by combining labelling of the long range horizontal connections with electrophysiological visuotopic maps and optical imaging. As shown in Fig. 1, although neurons in the superficial layers of parafoveal areas of the cortical map ( $\sim 4$  deg eccentricity) have RFs  $\sim 0.5$  deg in diameter, the horizontal connections at this eccentricity extend for  $\sim 4$  deg, nearly an order of magnitude greater in linear dimension. The horizontal connections also show a specific relationship with the cortical orientation columns. The collaterals of the horizontally projecting axons are distributed in discrete clusters. These clusters are registered with the orientation columns – the longest distance connections link columns of similar orientation specificity (Fig. 1, Stettler *et al.* 2002). The lateral connections represent the preponderance of the input that neurons receive, with over 76% of excitatory inputs to neurons arising from outside their resident hypercolumn (originating from neurons  $> 400 \mu\text{m}$  away) (Stepanyants *et al.* 2009).

All these features of the horizontal connections have a striking relationship with the perceptual characteristics of contour integration. This is seen in the phenomenon of contour saliency. If a contour made of a series of collinear line segments is embedded in a complex background of randomly oriented and positioned line segments, it will easily be distinguished from the background, and will 'pop out'. Smooth contours made of similarly oriented consecutive line segments will have this pop out character. As one adds line segments to the contour, it becomes progressively more salient. If the orientations of these elements show more variation, or if the spacing between them is too large, the contour will not pop out (Field *et al.* 1993). This was originally observed by the Gestalt psychologists early in the 20<sup>th</sup> century, who posited several rules of perceptual grouping, which included proximity

and 'good continuation' (or smoothness, Wertheimer, 1938). The properties of neurons in the superficial layers of V1 mirror the detectability of contours and the geometry of contours in natural scenes (Sigman *et al.* 2001): their responses increase with the number of contour segments, and decrease with increasing separation between the segments (Li *et al.* 2006). The geometry of interactions underlying contour saliency suggests the existence of an 'association field', whereby collinear or cocircular line segments are perceptually linked. The circuitry underlying the association field is likely to involve the long range horizontal connections, because of their linkage of columns of similar orientation specificity (Gilbert & Wiesel, 1989; Stettler *et al.* 2002). Moreover, although the facilitation of responses can propagate between neurons with RFs that lie along contours, with facilitation in neuronal responses increasing for contours extending over large parts of the visual field, the propagation is blocked if the separation between contour elements increases beyond a critical distance (Li & Gilbert, 2002). This distance, roughly 2 deg at an eccentricity of 4 deg, is equivalent to the visuotopic extent of the horizontal connections at that eccentricity.

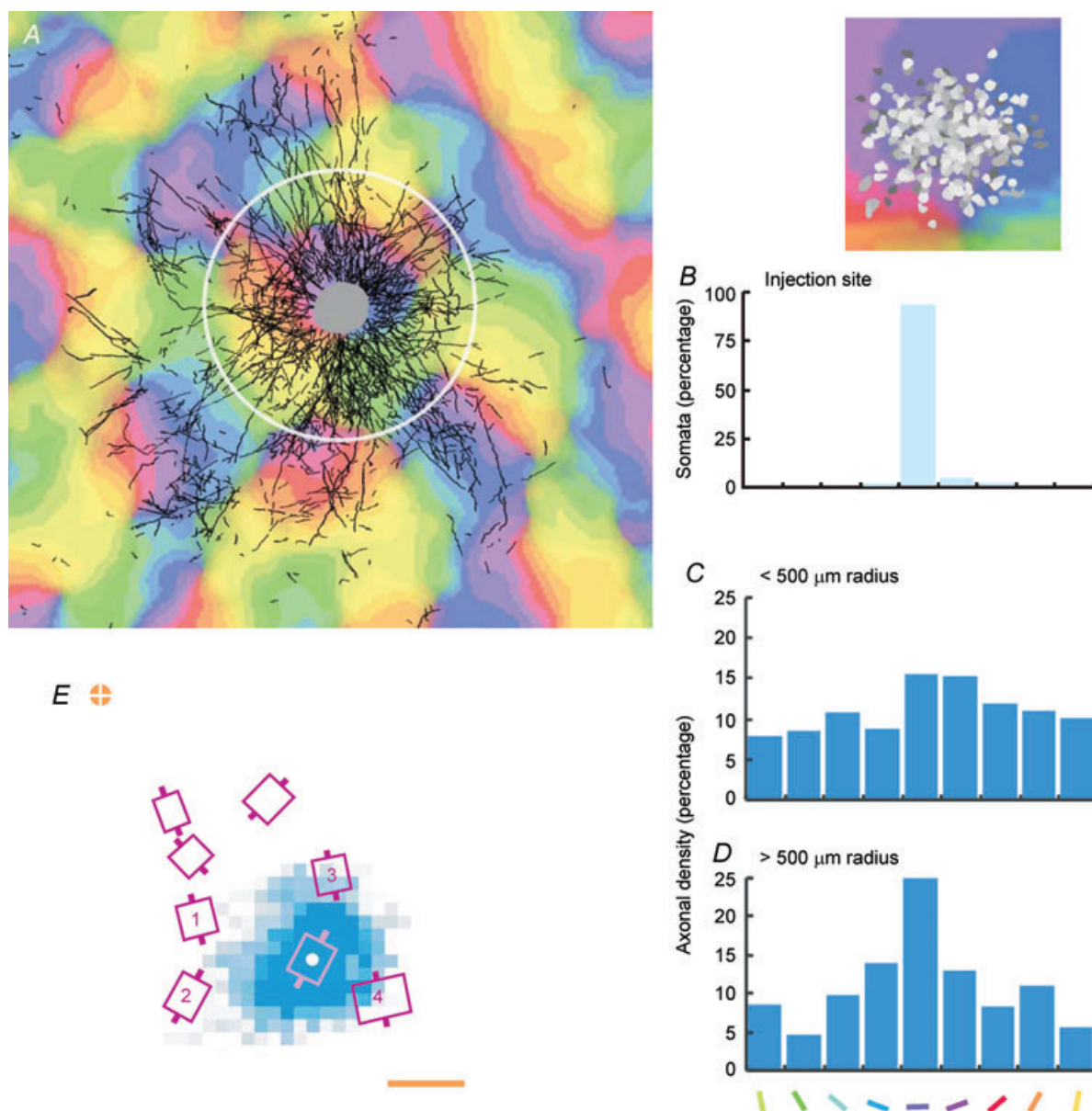
Contour saliency is subject to perceptual learning. In fact, the ability to detect the embedded contours such as those shown in Fig. 2 is not present at birth, but in humans has been shown to improve over the first 10 years of life (Kovacs, 2000). Even in adults, practice on this detection task can lead to an improvement in the ability to detect contours, with thresholds dropping so that observers can detect contours composed of fewer line segments, or contours with greater separation between the constituent line segments (Li & Gilbert, 2002; Li *et al.* 2008). Along with this improvement, we see an increase in contour related facilitation of neuronal responses in V1 (Fig. 2). Using ROC analysis to relate contour detectability and neuronal responses to contour length, we see a shift upward in the curves from the initial to the latter parts of training. As training progresses the neurometric curves converge with the psychometric curves, meaning that the observers' performance on the task can be accounted by the activity of fewer neurons.

The neuronal properties related to contour detection are not constitutively expressed, but are subject to task-dependent top-down influences. This is seen in experiments where we train animals on a sequence of tasks: initially in fixation, where neurons show no facilitation in their responses even as contour length is increased, then in a brightness discrimination task at the contour location, where again the neurons fail to respond to the contour, and finally in the contour detection task, when the facilitation finally appears (Fig. 3, Li *et al.* 2008). The fact that no facilitation is observed when animals attend to the contour location, but are not performing the contour detection,

task implies that the top-down influence required for the facilitation is not spatial attention but the task of contour detection itself. Here, finally, we see the interaction between contextual influences, perceptual learning, and

top-down influences converging to produce the neuronal substrate for contour integration.

We propose that the circuit mechanisms underlying these observations are based on an interaction between



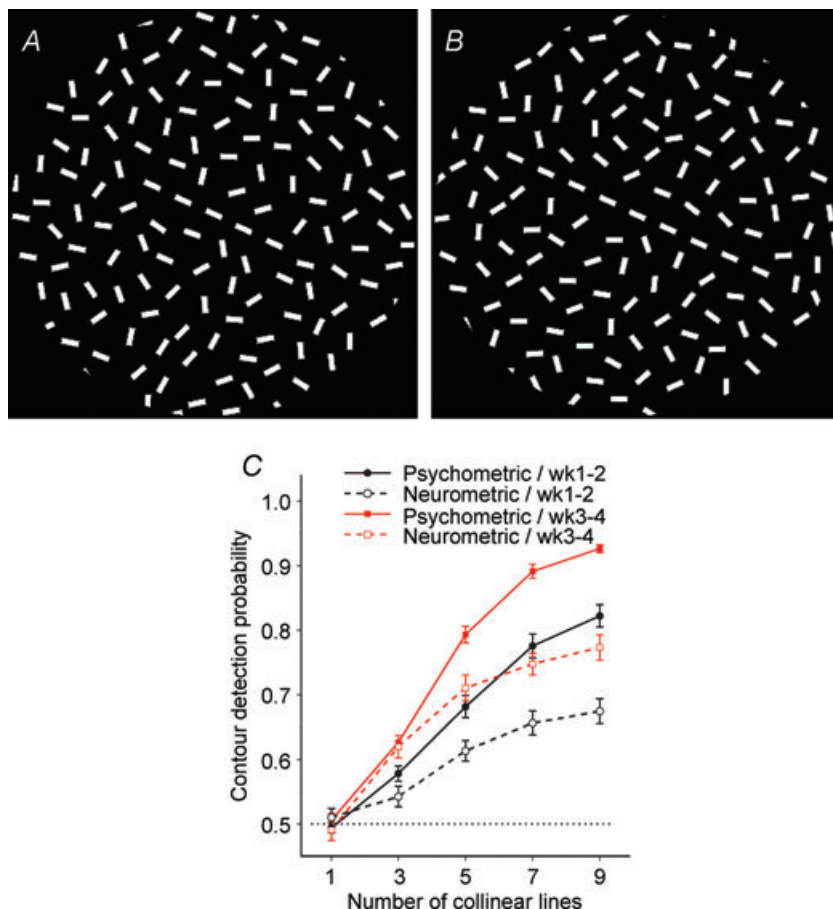
**Figure 1. Long range horizontal connections in V1**

Cortical pyramidal cells have axons that extend for long distances parallel to the cortical surface. In this figure these connections are visualized by injecting a genetically engineered adenovirus containing the eGFP gene. Neurons transduced with this virus synthesize the eGFP protein, rendering their full dendritic and axonal arbors fluorescent. Combined with optical imaging and electrophysiological recordings, this technique allows us to establish the relationship between the horizontal connections and the cortical functional architecture. *A*, surface view of visual cortex with a reconstruction of axonal arbors of  $\sim 6000$  neurons transduced with eGFP adenovirus, superimposed on optically imaged map of orientation columns. *B*, the injection site (top right) labelled neurons within a narrow range of orientation columns *C*, within a  $500\ \mu\text{m}$  radius of the injection site axons contacted orientation columns non-selectively. *D*, beyond the  $500\ \mu\text{m}$  radius the axons specifically innervated orientation columns with the same orientation preference as the injection site. *E*, the visuotopic extent, at the eccentricity of the injection (4 deg, fovea shown at orange circle), is shown in the shaded blue squares. The labelled axons covered an area  $\sim 4$  deg in diameter, or extending 2 deg from the injection site. Scale bar = 1 deg. Adapted from Stettler *et al.* 2002.

intrinsic long range horizontal connections within V1 and feedback connections to V1 originating from higher order cortical areas. The relationship between the horizontal connections and the visuotopic and columnar architecture of cortex makes them an appropriate substrate for the association field. But since the integrative properties of V1 neurons underlying contour integration are dependent on perceptual task, the contextual interactions mediating contour integration, and hence the effectiveness of the horizontal connections, are likely to be subject to top-down interactions, and are therefore gated by feedback connections. Though the association field is consonant with the horizontal connections, a process of input selection and amplification, mediated by cortical feedback, can enhance portions of the association field.

### Perceptual learning and shape discrimination

We have further evidence for the long term functional changes induced by perceptual learning, and the short term dynamics in the expression of these changes. Here we train subjects to do two different discrimination tasks with the identical visual stimulus. The tasks are a 3-line bisection task and a Vernier discrimination task. In the three-line bisection task, subjects determine whether, in a set of three parallel lines, the central line is located closer to the flanking line on one side or the other. The threshold in the task is the amount of offset of this line from the central position required to reliably determine to which flanking line it is closer. After doing this task thousands of times over a period of weeks, the threshold can decrease to a fraction of its original value (Fig. 4A). This improvement is specific to the orientation and position of the lines presented



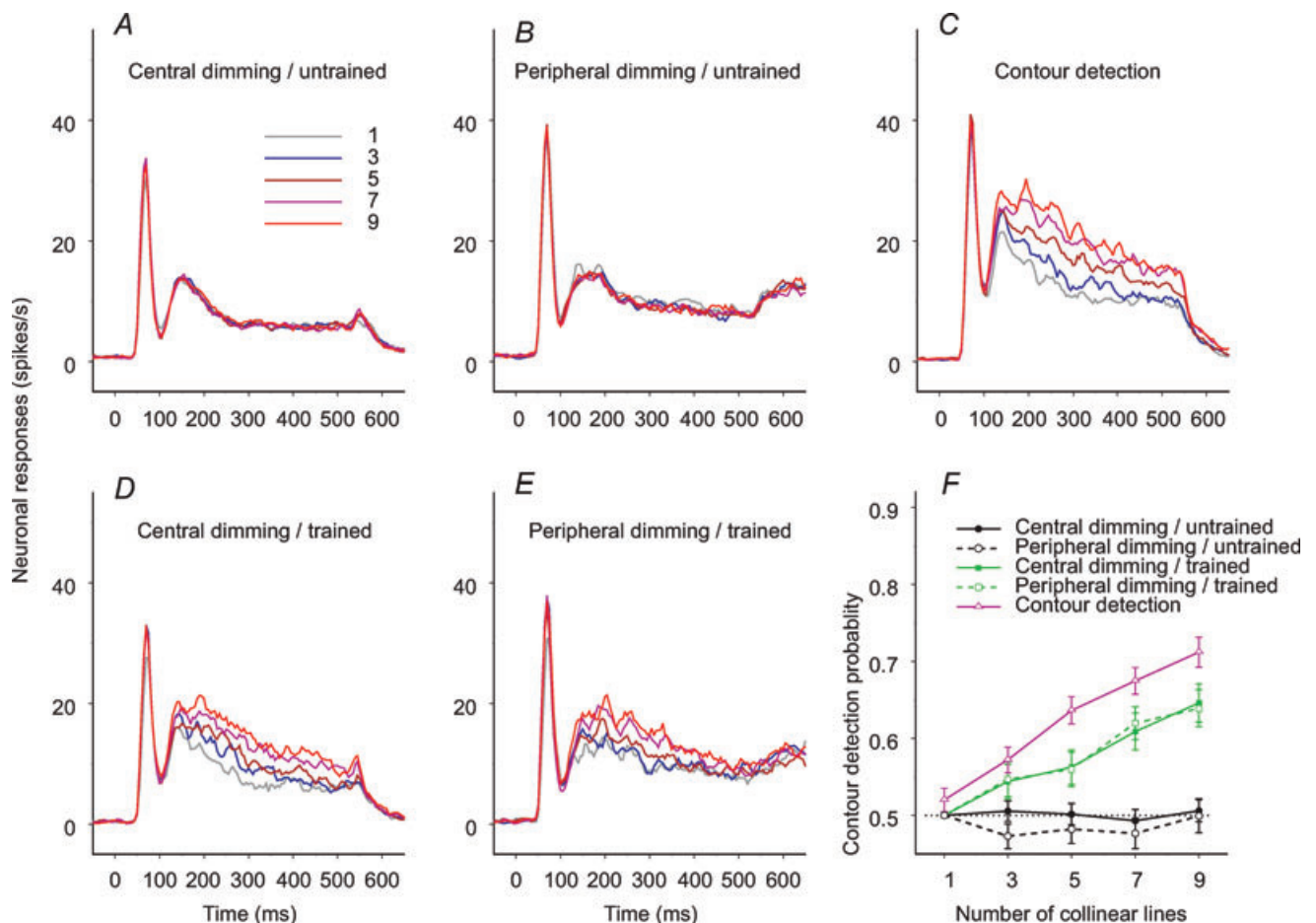
**Figure 2. Perceptual learning in contour detection**

A and B, the saliency of contours formed by collinear line segments embedded in a background of randomly oriented lines increases with the number of lines. C, with practice, subjects improve their detection of contours made of fewer line segments. The neurometric curves (averaged across all recorded neurons) and the psychometric curves (averaged over the corresponding recording sessions) are shown for two different training phases: the first two weeks of training up to the midpoint of training and the following two weeks. Performance in contour detection increases during the period of training, and the amount of facilitation in neuronal responses shows a parallel change. From Li *et al.* 2008.



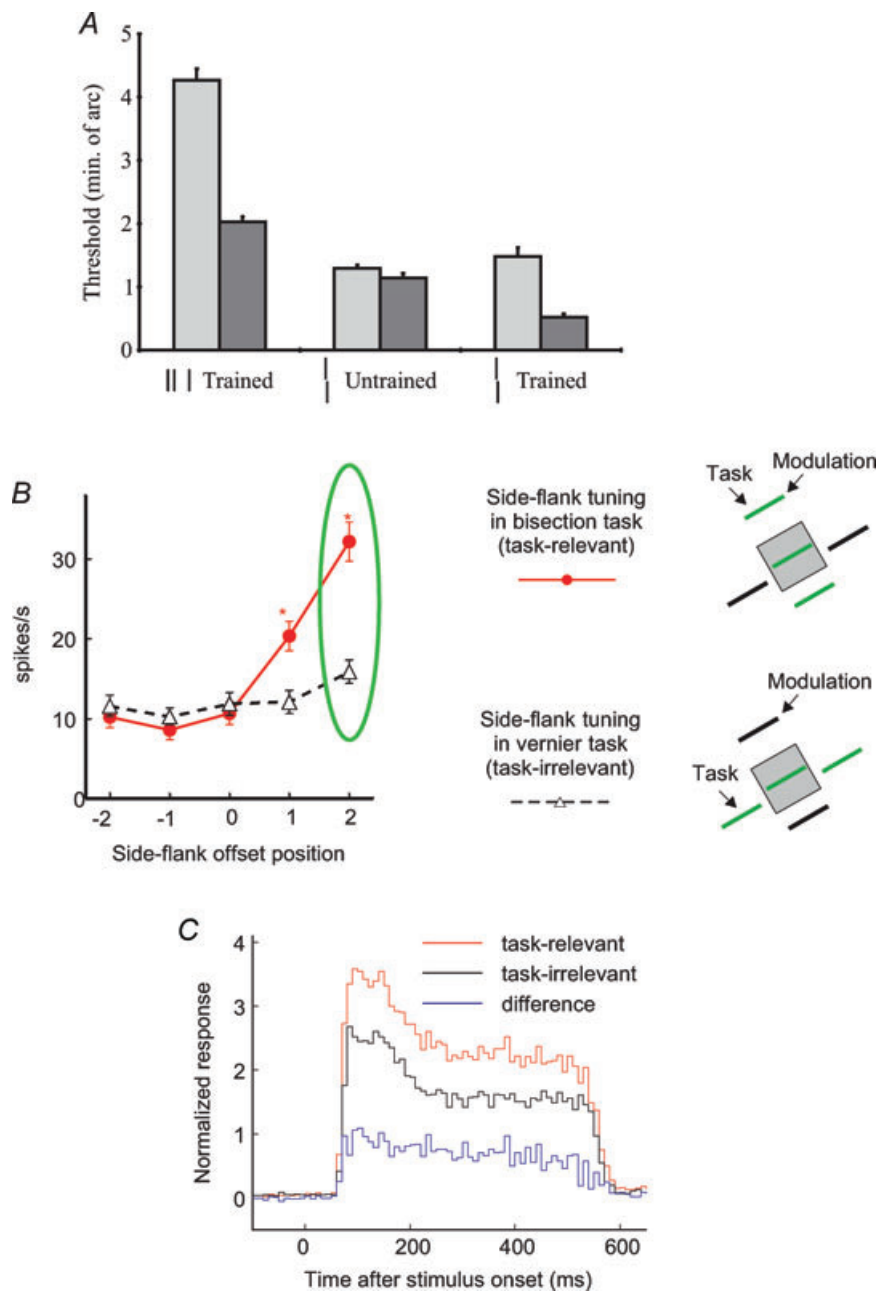
during the training period. Improvement on the three-line bisection task does not transfer, or lead to improvement, in a Vernier discrimination task, even when both tasks involve the same target line with the same position and orientation (Crist *et al.* 1997). Training on the Vernier task itself does lead to a decrease in the threshold of that task. Therefore, perceptual learning is highly specific to context (parallel *versus* collinear lines), and the cortical mechanism must account for that specificity. One suggested mechanism for perceptual learning is cortical recruitment, an increase in the amount of cortical territory dedicated to the trained part of the sensory surface (Recanzone *et al.* 1993). But if this were the case in the experiments described here, one would expect transfer between tasks involving the same cortical locus. Furthermore, an increase in the representation of the trained part of the visual field would

lead to a decrease in the representation of adjacent areas, and hence a decrement in performance in untrained visual field locations. This does not happen. Therefore cortical recruitment is unlikely to be the mechanism underlying the perceptual learning observed in the three-line and Vernier discrimination tasks. As expected, we see no change in cortical magnification for animals trained on a three-line bisection task (Crist *et al.* 2001). An alternative mechanism suggested for neuronal changes underlying perceptual learning, such as seen in studies involving improvement in orientation discrimination, is a sharpening of the orientation tuning of V1 neurons (Schoups *et al.* 2001). This would then lead to a decrease in the number of neurons responding to the trained stimulus, the opposite of cortical recruitment. Beyond the issue of the change in cortical magnification or activation



**Figure 3. Learning and top-down influences in contour detection**

Animals were trained on a succession of tasks, and the facilitation in responses to increased contour length was measured at each stage. The first stage involved a fixation task (A), the second a peripheral dimming task at the contour location (B) and the third stage was the contour detection task itself (C). Only when the contour detection task was learned did the facilitation appear. The facilitation was markedly reduced, however, when the animal returned to performing either the central dimming (D) or peripheral dimming tasks (E). Neurometric curves based on ROC analysis of these data show that the contour related responses are not only subject to learning, but are dynamically influenced by top-down influences of specific perceptual tasks. From Li *et al.* 2008.



**Figure 4. Perceptual learning in a shape discrimination task and the role of top-down influences**

A, training on a 3-line bisection task involves discriminating between two stimulus configurations – one where the central line of 3 parallel lines is closer to the one on the left or the one on the right. The amount of offset from the central position required to reliably discriminate between the two is the threshold in the task. After thousands of trials, this threshold can decrease by as much as a factor of 3. Training on the 3-line bisection task leads to a marked improvement on that task (left pair of bars) but no change in a related Vernier discrimination task, where the target line is the same but the context is a collinear line as opposed to the 2 flanking parallel lines. Then training on the Vernier task directly leads to a substantial improvement on that task. The lack of transfer in learning between the two tasks demonstrates the specificity of perceptual learning to context. From Crist *et al.* 1997. B, when presented with an array of 5 lines, a central target and 4 flanking lines (2 near collinear lines and 2 parallel flanking lines), animals are cued to perform either a 3-line bisection task, where the parallel flankers are task relevant, or a vernier discrimination task, where they are irrelevant to the task. The tuning of neurons to the different offsets of the side flanks changes with the task being performed. In this example, there is much more modulation in the neurons' response when the side bars are task relevant (red curve) than when they are task irrelevant (dashed black curve). C, the difference in the responses between the task-relevant and task-irrelevant conditions is seen from the outside of the neuronal responses. This suggests that the cortical state is set after the animal is given the cue as to which task it will perform but before the stimulus is presented. From Li *et al.* 2004.

associated with perceptual learning, the lack of transfer in learning between tasks requires a cortical mechanism that can account for the contextual specificity of the learning.

To explore the cortical changes underlying the learning in the two visual discrimination tasks, we trained animals to do each task. They were then presented with an array of five lines and cued to perform one of the two tasks, on alternate trials, with the stimulus array. We recorded from neurons in the superficial layers of V1, and measured the modulation in the responses of neurons to different offset of the parallel lines or the collinear lines when the animals performed either the three-line bisection task or the Vernier discrimination task. We made tuning curves for response *versus* offset of the parallel lines when the animals performed either the three-line bisection task, when the parallel flankers were task relevant, or the Vernier discrimination task, when they were irrelevant to the task. Even though the visual stimuli were identical between the two task conditions, the tuning curves were very different (Fig. 4B). As seen in the example, the neuron's response was much more highly modulated by changing offset of the parallel flankers when the animal did the three-line bisection task than when it did the Vernier discrimination task.

In this experiment the animal was cued to the task to be performed before the stimulus onset. If one compares the time course of responses to the identical stimulus when the animal performs either of the two tasks, the difference in the response arises at the outset of the neurons' responses (Fig. 4C). Therefore it is likely that the top-down information conveying the task instruction sets the cortex to a state that then enables analysis of the stimulus in a fashion that is relevant to the task.

There are several implications of the result. First, the response characteristics of neurons, even in V1, are as dependent on the behavioural context as they are on the visual stimuli themselves. Furthermore, once again the information conveyed by the top-down influence is not simply attention to the location of the stimulus, but the task that the animal is performing. The result shows that a neuron is not a fixed 'labelled line', but that it multiplexes its function, and the functional significance of its response changes from moment to moment, according to the perceptual tasking being executed at the time. From the standpoint of perceptual learning, this top-down influence is therefore invoked both during the encoding of the information that is learned and in its recall. One has to distinguish between the long term effects of the training and the short term dynamics of expressing the training effects. Over the long term the perceptual thresholds change and the neurons' responses become more modulated by and correlated with the stimulus differences. Over the short term, as the animal switches between perceptual tasks, different sets of functional characteristics are expressed. The alternative

outcome could have been that the information involved in performing a particular task would be encoded by a subset of neurons specializing in that task, and that separate neuronal ensembles would mediate different tasks. On the contrary, the neurons in V1 appear to multiplex their function, playing a role in many different perceptual tasks, and changing their tuning characteristics according to the task being performed. We have seen that at least half of the neurons in V1 show this differential tuning according to task. Our observations on the functional changes associated with perceptual learning can account for its contextual specificity. The learning affects only the subset of neuronal inputs that are active under a specific stimulus context, and neurons' responses are unaffected when a different context is presented. Therefore training on one stimulus configuration does not influence neurons' responses to other configurations.

In all of our experiments the strongest top-down effects are exerted on contextual interactions. This is seen when the top-down influence is spatial attention, where the locus of attention affects collinear facilitation by lines outside the RF (Ito *et al.* 1998; Ito & Gilbert, 1999). It is also seen in the way perceptual task influences neural responses. For example, responses to extended contours differ according to whether the animal performs a contour detection task or a brightness discrimination task. Other examples of task dependence of V1 responses include shape discrimination and shape expectation (Crist *et al.* 2001; Li *et al.* 2004, 2006, 2008; McManus *et al.* 2007). We have proposed that many contextual influences can be mediated by the long range horizontal connections within each cortical area, and that the top-down effects involve gating the lateral inputs. In fact, this idea speaks to the functional purpose of the horizontal connections, one in which their functional connectivity is not fixed but can be selectively expressed. If the integrative properties of superficial layer cortical neurons were fixed, one could generate them by feedforward connections alone (thalamocortical or interlaminar, for example) and by having suitably large RFs. But if one needs to generate different integrative functions under different task conditions, then the value of the horizontal connections is to allow them to be selectively and dynamically expressed on a moment to moment basis, according to task demands. Consequently each neuron acts as an adaptive processor, selecting different inputs to perform different functional roles. Perceptual learning involves establishing the interaction between cortical feedback and intrinsic connections, a heterosynaptic interaction requiring addressing of the appropriate subset of horizontal inputs by the feedback connections that are active during the execution of a given task (Gilbert & Sigman, 2007).

The experiments we've described thus far have implicated V1 neurons in perceptual learning because of changes in their tuning characteristics that track

the improvement in performance. These results should not lead one to believe, however, that the learned information is entirely resident in V1, or that the internal representations of learned information are always localized to individual areas. The interaction between top-down information and intrinsic cortical circuits suggests that learned information is based on an interaction between multiple cortical areas, rather than being exclusively represented in a single area. Also, we have seen from fMRI studies in human observers that as visual information is learned, different areas can change their involvement in perceptual discrimination or detection tasks. Based on a visual search task requiring subjects to recognize a shape embedded in an array of distractors, there is an improvement in detection of initially unfamiliar shapes after a period of practice. Although the target shape appears randomly at different positions within the array of distractors, the improvement develops in a point by point fashion, at different visual field locations (Sigman & Gilbert, 2000). This suggests the possible involvement of retinotopically organized areas at early stages in the visual cortical pathway. fMRI confirms this, with a greater activation and a stronger correlation with performance in recognition of trained shapes in V1/V2, whereas untrained shapes show higher activation and correlation with performance in later occipital cortex (LOC, Sigman *et al.* 2005). These results suggest that shapes of equivalent complexity are not represented in the same cortical area, but instead that the area in which they are represented depends on degree of familiarity, and with training can shift their representation from higher to lower order visual cortical areas. The higher activation of trained shapes in the earlier areas does not depend on the presence of the trained shape in the array, but only on the subject looking for the trained shape as the search cue. This suggests again the involvement of top-down influences in the engagement of a visual cortical area in a perceptual task.

### Functional recovery following CNS lesions

More direct evidence for adult cortical plasticity, and for the idea that the horizontal connections constitute the circuit mechanisms for this plasticity comes from the remapping of cortical topography following binocular retinal lesions. Initially after making retinal lesions at homologous positions in the two retinas, the cortical area representing the lesioned part of the retina, or lesion projection zone (LPZ), is silenced. Within minutes after making the lesion, however, the neurons just inside the boundary of the LPZ recover visually driven activity, with their RFs shifting to positions outside the LPZ. Over the following weeks and months, the visual responsiveness progresses inwards towards the centre of the LPZ. Topographically, V1 becomes remapped, with a shrinkage in the representation of the lesioned part of the retina

and an expansion in the representation of the parts of the retina surrounding the lesion (Gilbert *et al.* 1990; Chino *et al.* 1992; Gilbert & Wiesel, 1992; Heinen & Skavenski, 1992; Eysel *et al.* 1999; Calford *et al.* 2000; Baker *et al.* 2005; Giannikopoulos & Eysel, 2006).

This reorganization is cortically based. At a time when the LPZ has completely filled in, there is still a large silent region in the LGN (Darian-Smith & Gilbert, 1995). Furthermore, the thalamocortical afferents do not increase their lateral extent, and therefore cannot provide the visual input to the LPZ. The horizontal connections, on the other hand, are long enough in their lateral spread to provide input from cells lying just outside the LPZ to the centre of the reorganized area. Over a period of time, these connections undergo sprouting and synaptogenesis, adding collaterals to existing axonal clusters (Darian-Smith & Gilbert, 1994). This can account for a change in the effectiveness of these connections, from a modulatory role mediating the RF nonlinearities that play a role in contour integration, to a suprathreshold, driving influence whereby the target neurons shift their RF positions. This is also consistent with the observation that the pattern of orientation columns in the LPZ following functional recovery is the same as that seen before the lesion (Das & Gilbert, 1995). As described above, the horizontal connections run between columns of similar orientation specificity. If sprouting within the preexisting framework of horizontal connections is responsible for the recovery of visual input to the LPZ, then the pattern of orientation columns would also be retained.

### Conclusions

The visual cortex retains the capacity for experience-dependent plasticity into adulthood. This plasticity serves to encode the information acquired during perceptual learning, and can be used for the purpose of functional recovery following CNS lesions. Learning can involve global changes in the representation of shapes, shifting to different areas along the visual pathway. The areas involved can extend as far back as primary visual cortex. The way in which the functional properties are dynamically expressed in a task-dependent fashion implies that each cortical area acts as an adaptive processor, performing different calculations according to the immediate perceptual demands. The manifestation of the functional changes associated with perceptual learning suggests a circuit mechanism that involves an interaction between feedback connections and local cortical circuits. We propose that this interaction is manifest in the way that feedback connections address subsets of intrinsic cortical connections, and the functional properties of a neuron depend on which subset is gated at any given time. The mechanism of perceptual learning may involve the setting up of this addressing, such that



both the encoding and recall of learned information involves the appropriate selection of the inputs that convey information about the stimuli being discriminated. In this view, through a process of input selection, a neuron can take on the functional properties appropriate for the task being performed. The picture that emerges is that the cortical mechanism of object recognition involves dynamic changes in the features represented by cortical neurons. Objects are represented by the state of interactions between multiple cortical areas, with counter-current streams of information flow setting the state of the entire cortical network.

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