

Neuropsychologia 2011, 49, 3898-3907

Attentional modulation in visual cortex is modified during perceptual learning

Marco Bartolucci and Andrew T Smith

Department of Psychology
Royal Holloway University of London
Egham, Surrey TW20 0EX
UK

Abbreviated title: Attentional modulation and perceptual learning

Corresponding author:
Dr Andy Smith
Address as above
Email: a.t.smith@rhul.ac.uk
Tel: +44 1784 443717
Fax: +44 1784 434347

ABSTRACT

Practising a visual task commonly results in improved performance. Often the improvement does not transfer well to a new retinal location, suggesting that it is mediated by changes occurring in early visual cortex, and indeed neuroimaging and neurophysiological studies both demonstrate that perceptual learning is associated with altered activity in visual cortex. Theoretical treatments tend to invoke neuroplasticity that refines early sensory processing. An alternative possibility is that performance is improved because of an altered attentional strategy and that the changes in early visual areas reflect locally altered top-down attentional modulation. To test this idea, we have used functional MRI to examine changes in attentional modulation in visual cortex while participants learn an orientation discrimination task. By examining activity in visual cortex during the preparatory period when the participant has been cued to attend to an upcoming stimulus, we isolated the top-down modulatory signal received by the visual cortex. We show that this signal changes as learning progresses, possibly reflecting gradual automation of the task. By manipulating task difficulty, we show that the change mirrors performance, occurring most quickly for easier stimuli. The effects were seen only at the retinal locus of the stimulus, ruling out a generalized change in alertness. The results suggest that spatial attention changes during perceptual learning and that this may account for some of the concomitant changes seen in visual cortex.

Keywords: visual perception; visual learning; attentional modulation; fMRI

1. Introduction

Perceptual learning is defined as practice-induced improvement in the performance of perceptual tasks. Behaviourally, repeated experience with visual stimuli can result in faster detection and improved discrimination of similar stimuli, arguably leading to a more efficient response to the visual information that is prevalent in an individual's environment. Psychophysical studies have shown that effects of learning occur for many low-level perceptual tasks, including motion discrimination (Ball & Sekuler, 1982), orientation discrimination (Vogels and Orban, 1985; Shiu and Pashler, 1992; Schoups et al., 1995), discrimination of complex gratings (Fiorentini 1980; 1981), vernier acuity (Fahle et al. 1995), line bisection tasks (Crist, 1997), structure from motion (Vidyasagar & Stuart, 1993), stereopsis (Ramachandran & Braddick, 1973; Ramachandran 1976) and visual search (Ahissar and Hochstein 1996). Performance may continue to increase over many days of testing but even a small amount of practice can significantly improve performance (Hussain et al, 2009).

A striking characteristic of these improvements in performance is that they do not generalize well. The observed improvements are typically specific to the retinotopic location used for training and are lost or diminished when the stimuli are moved even a few degrees across the retina. Orientation discrimination learning is confined to the stimulus orientation used for training and does not transfer to other orientations (Ramachandran and Braddick, 1973; Fiorentini and Berardi, 1981; Ahissar and Hochstein, 1997), while direction discrimination is confined to the direction used for training (Ball & Sekuler, 1982). Learning on one hyperacuity task does not transfer to another (Fahle, 1997). In some cases, perceptual learning may even be lost simply if

the stimuli are not presented to the eye that was used during training (Karni and Sagi, 1991). The specificity of perceptual learning has been taken to indicate (e.g. Karni & Sagi, 1991) that the neural changes underlying at least some types of perceptual learning may take place at an early stage of processing, such as the primary visual cortex. In the case of specificity for location, a recent alternative view (Xiao et al, 2008; Zhang et al, 2010) is that perceptual learning may occur more centrally but needs to be associated by training with a specific location, accounting for the lack of transfer.

There is some physiological evidence that improved discrimination following learning may reflect increased sensitivity or sharpening of neural tuning to the trained attribute. For instance, the ability to detect global motion in a noisy random-dot kinematogram increases with practice (in terms of the threshold number of signal dots needed for correct identification of direction) and this improvement correlates with increased responsiveness of neurons in area MT (Zohary et al., 1994). Sharpened orientation tuning curves have been reported in V1 (Schoups et al., 2001) and V4 (Yang and Maunsell, 2004) after training on an orientation discrimination task. This plasticity is spatially specific, in line with behavioural results, being absent in cells with receptive fields at the locations of task-irrelevant stimuli. Other physiological changes associated with learning have also been reported in early visual areas, including changes in the surround properties of neurons (Crist & Gilbert, 2001) and changes in the proportions of neurons that are responsive to the trained feature (Ghose et al., 2002). The relationship between perceptual and physiological changes is far from obvious. It is not even clear that learning can be expected to result in increased neural activity; one possibility (Ghose, 2004) is that learning reflects improved ability

to suppress responses to irrelevant stimuli. Several reviews of the specificity of perceptual learning and the underlying neural changes have been published (Karni, 1996; Gilbert et al., 2001; Ghose, 2004; Fahle, 2004).

Human imaging studies have also found changes in activation in early visual areas, including the primary visual cortex, during perceptual learning. Some authors report reductions in activity, for example reductions have been seen after training in contrast discrimination (Schiltz et al., 1999) and in discriminating complex gratings (Mukai et al., 2007). However, other studies have reported increases in activity following perceptual learning; increases have been claimed for texture discrimination (Schwartz et al., 2002), contrast detection (Furmanski et al., 2004), curvature discrimination (Maertens & Pollmann, 2005) and letter detection (Lewis et al., 2009). Sigman et al., (2005) reported increases in some brain regions and decreases in others following training in a shape identification task, while Yotsumoto et al. (2008) found that over a protracted time period activity in V1 first increased with learning and then returned to its original level. As in the case of single-unit physiology, the imaging literature is replete with documented changes but their relation to the associated perceptual changes is not always clear.

It is unclear whether learning-related changes in the visual cortex result from plasticity in response to bottom-up sensory input, or instead reflect feedback influences from later visual processing stages. It has been suggested by some that perceptual learning cannot occur without persistent and intensive attention to the feature to be learned (e.g. Ahissar and Hochstein, 1993). In contrast, there is evidence that perceptual learning can occur without perceptual awareness (e.g. Watanabe et al

2001). Nonetheless it is agreed that attention can be important for learning at least in some circumstances. This raises the possibility that perceptual learning of the kind that is mediated by early visual areas such as V1 may require, or be enhanced by, the well-documented phenomenon of attentional modulation in the visual cortex (Fahle, 2009). It has been shown that attentional modulation plays a major role in visual responsiveness, both at the level of individual neurons (e.g. Reynolds and Chelazzi, 2004; Maunsell and Treue, 2006) and averaged across populations of cells, as measured by blood oxygenation level-dependent (BOLD) neuroimaging (Kastner and Ungerleider, 2001; Corbetta and Shulman, 2002; Pessoa et al., 2003; Sapir et al., 2005; Giesbrecht et al., 2006; Sylvester et al., 2007, 2008). Attentional modulation has also been found in the absence of visual stimulation, during an anticipatory period prior to onset of a cue target, again both in single unit recording (Luck et al., 1997) and human brain imaging (Luks and Simpson, 2004; Sapir et al., 2005; McMains and Kastner, 2007; Sylvester et al., 2007) and also for cueing a particular feature of the target (Stokes et al., 2009). Some studies suggest, based on a lack of trial-to-trial correlation between the two attentional effects, that they reflect separate processes (Nakamura and Colby, 2000; Recanzone and Wurtz, 2000). However, Sylvester et al. (2009) have argued that anticipatory and stimulus-evoked BOLD responses reflect a common attentional control signal.

Previous imaging studies of perceptual learning have focussed on the effects of learning on the magnitude of responses to the learned stimuli. In such studies, it is difficult to establish whether the change reflects a change in bottom-up processing or a change in top-down influences such as attention. Ito et al. (1998) showed that attentional effects on perception can be influenced by learning, while Gilbert et al.

(2000, 2001) have argued that attentional modulation in early visual areas shows changes with learning. In this study we investigate, for the first time in the context of neuroimaging, the relationship between attentional modulation and perceptual learning. Attentional effects are isolated by studying anticipatory changes in activity that occur in the absence of visual stimulation, after a stimulus is cued but before it appears.

If pre-stimulus activity alters during learning, changes in attentional modulation during learning are implicated. The change might be either a decrease or an increase in attentional modulation and it might be correlated or uncorrelated with changes in the magnitude of the response evoked by the stimulus itself. Thus, the aim was to evaluate three possible outcomes. The first is that there is no change in pre-stimulus activity, despite the expected and well-documented change in stimulus-evoked activity. If perceptual learning and the associated changes in neural activity result from changes in bottom-up processing that do not involve or require changes in top-down attentional modulation, then there is no reason to expect that pre-stimulus attention-related activity will change during learning. The second and third possible outcomes are that pre-stimulus activity does change during learning, in a way that is uncorrelated or correlated, respectively, with changes in the stimulus-evoked response. If the effects are uncorrelated, for example if one is an increase and the other a decrease, this suggests two separate and independent processes, such as a change of attention affecting pre-stimulus activity and neural plasticity affecting the stimulus-evoked response. Such plasticity could reflect either bottom-up or top-down changes: it is possible that top-down modulation could cause long-lasting changes in response properties (such as gain changes or sharpening of the tuning of neuronal

representation) as learning progresses. This might result in altered bottom-up processing, which might be evident independent of attentional state, having become hard-wired in visual cortex.

If the two effects of learning prove to be similar (outcome 3), and if we assume that pre-stimulus activity reflects attention, this outcome might suggest that the changes in the stimulus-evoked response seen during learning reflect changes in attentional modulation alone, rather than changes in bottom-up processing of the stimulus. This would suggest that improved performance purely reflects deployment of attention in a more efficient way, in which case improved performance after learning would not occur independently of current attentional state. Rather, maintaining the new, learned attentional state would remain crucial to maintaining the new, learned level of performance.

To address the role of attention in the changes seen in visual cortex during learning, we use an orientation discrimination task. Learning-related changes in the BOLD responses are measured both during an anticipatory period and also following stimulus presentation. By looking at pre-stimulus activity changes over time, the three possible outcome described above are dissociated.

2. Methods

2.1 Participants, stimuli and procedure

fMRI data were acquired using a 3T Siemens TRIO scanner equipped with a standard (whole-head) Siemens 8-channel array head coil and a custom-built 8-channel array coil (Stark Contrast, Erlangen, Germany) optimised for the occipital cortex (referred to as a posterior array or PA coil).

Visual stimuli, constructed using C++ and OpenGL were projected onto a screen at the end of the scanner bore by an LCD projector. Participants viewed the screen, whilst lying supine in the bore of the scanner, via a mirror positioned ~15 cm from their eyes. The screen refresh rate was 60 Hz and the resolution was 1024*768 pixels. The visible portion of the screen was approximately circular (diameter 30°).

Eight participants (one male; age 19-32) participated in the study. They were tested in two separate scan sessions on different days. The first session was conducted using the standard headcoil, for even brain coverage. It included a high-resolution anatomical scan of the whole brain to which all the functional images were aligned (MDEFT; Deichmann et al., 2004; 176 axial slices, in-plane resolution 256 x 256, 1 mm isotropic voxels, TR = 7.92 ms, TE = 2.45 ms, flip angle = 16, bandwidth = 195 Hz/pixel]. This scan was chosen because, although slow to acquire, it gives very high contrast between grey and white matter. In addition, retinotopic areas V1-V3 were demarcated using standard retinotopic mapping procedures (Engel et al., 1994; Sereno et al., 1995). Two stimulus runs were performed, with binocular viewing via a standard mirror. In each run, a counterphasing checkerboard “wedge” stimulus (a 24° sector) rotated clockwise at a rate of 64 s/cycle (eight cycles per run). The counterphase frequency was 8 Hz and the rotating wedge covered an area 24° visual angle in diameter. Check size was scaled by eccentricity in approximate accordance

with the cortical magnification factor. Images were acquired and pre-processed with a standard echoplanar (EPI) sequence (28 slices, TR 2000ms, TE 30 ms, 3 mm slices, 3x3 mm in-plane resolution).

The second session was conducted using the PA coil, for optimum sensitivity in occipital cortex. It consisted of a fast 3D anatomical scan (MP-RAGE, Siemens), used in the re-alignment process. This was followed by eight functional runs with the main task [EPI, 35 slices, TR 2.5s, TE 30 ms, 3 mm slices, 3x3 mm in-plane resolution, 115-125 volumes (according to the event timings), total duration 5min (average)]. Each of these eight runs contained eighteen orientation discrimination trials performed while the subject was fixating a square in the centre of the screen. In addition to the eight functional runs, several short EPI scans were acquired with the PA coil and an integral body coil, to assist with co-registration.

The task was orientation discrimination. Trials at four levels of difficulty were randomly inter-mixed across the whole experiment. This ensured that participants could perform the task sufficiently well on some trials from the start, while also allowing scope for improving performance over time in harder trials. Each trial consisted of a cue followed by a pair of grating stimuli. The cue was displayed for 500 ms. It informed the participant of the difficulty of the trial by means of a small arrow at fixation pointing in one of four different directions (where 0 degrees is vertical and directions progress clockwise: 300deg - very easy; 330deg - easy; 30deg - difficult; 60deg - very difficult). The stimulus was presented for 1000 ms and was composed of two counterphasing Gabors (0.25 c/deg, 3 Hz, SD 1deg, truncated at 3 deg radius, peak contrast 100%). These were located on the horizontal meridian, one

on the left and one on the right side of the fixation square, centered at an eccentricity of 5 deg. They had slightly different orientations and the task was to identify whether the orientation of the left Gabor was rotated clockwise or counterclockwise compared with the right one, by pressing one of two buttons. The reference Gabor (right) could appear in any of seven different, equally spaced orientations (30-60 degrees where 0 is vertical, steps of 5 degrees). The comparison Gabor (left) differed from the reference Gabor by $\pm 2, 4, 6$ or 8 degrees, in accordance with the difficulty cue. No feedback was provided. The difficulty level of the task was varied randomly from trial to trial according to a rectangular probability distribution that was different for each run. Over the eight runs, each difficulty level was presented 36 times.

Figure 1 about here

Between the difficulty cue and the stimulus the screen was blank, apart from the fixation square, for a random time (rectangular probability distribution between 6 and 9 sec for 75% of the trials and between 3 and 6 sec for the remaining 25% of the trials; average 6.75s). This arrangement gives a long enough mean interval to allow separate detection of responses to the cue and stimulus, while discouraging the subject from ignoring the first few seconds and attending only towards the end of the interval. After the stimulus presentation, the fixation square turned blue for two seconds indicating that the subject should respond. The subject was requested to keep fixating the fixation point throughout the whole experiment. The use of two simultaneous locations was intended to discourage eye movements towards the targets during trials: performing the task is easiest and most natural when fixating midway between the two Gabor patches.

Each run contained 18 trials separated by an inter-trial interval in which the screen was uniform apart from the fixation square. The interval varied between 4 and 12 sec with a Poisson probability distribution (see Hagberg et al, 2001). The mean interval was 6 sec, the maximum and minimum were 12 sec and 4 sec and the interval varied in steps of 0.5sec. Eight runs were conducted, each using a different random sequence of trials, with short breaks between runs. The scan duration was approximately 45 minutes including the anatomical scan. Before entering the scanner, the participant was familiarized with the task and then completed one practice run.

2.2 Analysis

All data were pre-processed and analyzed with *BrainVoyager QX* (version 1.10, Brain Innovation, The Netherlands). The first five volumes of each run were excluded from the analysis to allow for saturation effects. EPIs were corrected for head motion and slice timing, and were filtered with a temporal high-pass filter of 0.01 Hz. All functional images were aligned to an EPI volume acquired at the beginning of the scan session. This was co-registered to the MDEFT anatomical volume.

Analysis was conducted within the General Linear Model (GLM). Regressors of interest were constructed from the onset times of the events. Separate regressors were used for the cue and the task and for each of the 4 levels of difficulty (8 regressors of interest in total). As well as the eight event regressors, six head-movement regressors

were included, derived from the realignment of the images. The regressors were tested to ensure that they were not significantly correlated, setting the maximum allowable correlation between any pair of regressors at 0.2.

Each stimulus presentation was modeled as a boxcar of 1 s duration and each pre-stimulus period, commencing with a difficulty cue presentation, was modelled as a boxcar of 0.5 s duration, convolved in each case with a canonical haemodynamic response function. The choice of model for the pre-stimulus period is not straightforward. It might be expected that any attention-related increase in BOLD would commence following the cue and be maintained until the stimulus appears. However, Sylvester et al. (2007) found that in early visual areas, pre-stimulus activity peaks at 6-8 sec after the cue and then decreases, even though behavioural data showed that attention was maintained until stimulus onset. Thus, the timecourse was not very different from the haemodynamic impulse response function (HIRF). In order to estimate the temporal profile of activity in the pre-stimulus period it is necessary to separate the overlapping responses to the various events. To do this, we performed a deconvolution analysis. First, each timeseries was temporally re-sampled to produce a timeseries with a resolution of 0.5s (the unit of time used for defining stimulus events) by sinc interpolation. Each re-sampled timeseries was then low-pass temporally filtered to remove high frequency artefacts introduced by the re-sampling. The re-sampled timeseries were averaged across all the voxels in a given region of interest (defined below). Finally, the temporal profile of the pre-stimulus activity was estimated by deconvolution, The analysis confirmed that the BOLD response is transient and in fact differed little from the standard HIRF (see Results), and so it was decided to use a standard model.

A separate analysis was conducted for each participant. The regressors were entered into a multiple regression analysis to generate parameter estimates for each regressor at every voxel. Correction for effects of serial autocorrelations, which we regard as essential in single-subject analyses (Smith et al, 2007), was applied using the AR(1) method.

The results were visualized using flattened representations of each person's grey matter derived from the MDEFT anatomical scan. The flattened representation was created by segmenting and reconstructing the border between grey and white matter within each hemisphere of the MDEFT scan using with *BrainVoyager*. The resulting surfaces were smoothed, inflated, and cut along the calcarine sulcus. Finally, the surface was flattened and corrected for linear distortions. Retinotopic mapping data were analyzed by fitting a model to the timecourse obtained with the rotating wedge stimulus. This consisted of a rectangular wave of duty cycle 24/360, reflecting the duration of stimulation at any portion of the visual field, convolved with the HRF. The phase of the fitted response was taken as an index of visual-field location, in terms of polar angle. Reversals of the direction of phase change across the cortical surface were taken as boundaries of visual areas. The boundaries of visual areas V1–V3 were drawn by eye, on the basis of these reversals viewed on a flattened version of each participant's reference anatomy.

Statistical maps for each subject were thresholded ($p < 0.001$ uncorrected). Within each visual area (V1, V2, V3) defined by retinotopic mapping, a region of interest (ROI) was defined based on the activations due to the stimulus presentation in the main

experiment (average of all 8 runs). Basing the ROI on stimulus-related activations rather than pre-stimulus (anticipatory) responses means that the ROIs used for examining the pre-stimulus responses, which was the object of the study, are based on different data from those being evaluated. In the case of the stimulus-related response, use of the same data for the ROI may bias the effect size estimates towards larger effects, but this is unimportant because no comparisons between anticipatory and stimulus response magnitudes were made. Stimulus-related responses, which have been examined in several previous studies, are shown only for comparison. Visual areas were defined separately in each hemisphere, yielding six ROIs in total. ROIs so defined are illustrated for one participant in Fig. 2.

Figure 2 about here

3. Results

3.1 Performance data

The behavioural data are summarized in Fig. 3a. Performance is around 90% at the two easiest difficulty levels and then declines, reaching about 60% at the hardest level (chance is 50%). To reveal any changes that might occur over time as learning progressed, the trials were divided into early (trials from the first four runs) and late (those from the last four runs). Performance increases over time for all difficulty levels, as shown by the difference between the early and late trials. The performance data confirm that a suitable range of difficulties was chosen and that the participants were learning the task and did not decrease their efforts over time.

To quantify the effects of learning more fully, performance was plotted as a function of time, separately for each difficulty level. Performance at a given time was estimated as the average of the outcome of the trial at that time point and the two neighbouring trials of the same type before and after it (5 trials total). This was plotted as a moving average, over time. An example (difficulty level 2) is shown in Fig. 3B. The other difficulty levels show a similar pattern. Although the learning curves show saturation, a linear function was fitted in order to give a simple index of learning that could be compared across conditions, and the slope of this fit was taken as the index of learning at a given difficulty level (e.g. zero slope indicates no learning). A plot of slope against difficulty (Fig. 3c) shows that the rate of learning is greatest in the easiest task condition. Fig. 3c was derived primarily for comparison with the imaging data.

Figure 3 here

Fig. 3 shows clearly that performance improved over the course of the experiment. However, given that the training period was relatively short, we were concerned that the improvement might reflect factors other than orientation discrimination *per se*, such as learning to interpret the difficulty cues or learning the response mapping. The signature of perceptual learning is that it usually does not transfer to new locations or stimuli. This was not tested during the fMRI experiment and so a separate behavioural test was performed. The task was re-created outside the scanner and four new participants (two male and two female, age 21-32) with no experience of the task were tested. Each performed 8 runs identical to those used for fMRI, with the same

stimuli, timings and task. Immediately following this, two additional runs were completed with the same task but with the orientation of the Gabors rotated by 90 deg, to test for transfer of learning to the orthogonal orientation. Figure 4 shows the results, averaged across participants. Performance is plotted as a function of time during training with the original set of orientations (Fig. 4a) and then when tested with orthogonal orientations (fig.4b). The performance data show a clear effect of learning during training with the original set of orientation, as in Fig. 3. During subsequent testing with orthogonal orientations, performance returns to the initial level, indicating that the learning is specific for the set of orientations we used and does not transfer. The results are shown only for one difficulty level in Fig. 4 but the other three levels showed the same effect. The results of this test indicate that the improvement reflects genuine perceptual learning rather than incidental learning or familiarization with the task.

Figure 4 here

3.2 Imaging data

3.2.1 Deconvolution analysis

The profile of the pre-stimulus (attention-related) response, as estimated by deconvolution analysis, is shown in Fig. 5. The profile was similar in all three visual areas and so the mean is shown. This analysis confirms the surprising finding of Sylvester et al. (2007) that attention-related activity in visual cortex is transient, peaking at about 5s from cue onset and then declining in accord with a typical HIRF,

and is not sustained throughout the pre-attention period. One interpretation is that attention was not in fact sustained, but both our behavioural data and the analyses of Sylvester et al. (2007) suggest that there is a genuine discrepancy between attention as measured behaviourally and the modulation it causes in visual cortex. More sustained attention-related activity was reported by Silver et al. (2007) and the reason for the discrepancy is unclear, but our results clearly show transient activity.

Figure 5 here

3.2.2 Response magnitude

Mean BOLD responses were calculated, separately for pre-stimulus (attention-related) activity and for the response to the visual stimulus. In each case, results were averaged across the left and right ROIs, separately for each of three visual areas (V1, V2 and V3). Although several other visual areas were reliably identified with retinotopic mapping, it was not always possible to identify within them a discrete response to the peripheral stimuli used in the main experiment and so analysis was confined to these three regions, in which responses were evident in every case. As with the behavioural data, the trials were divided into early (trials from the first four runs) and late (those from the last four runs). The overall results for the three visual areas, averaged across left and right hemispheres and also across the four difficulty levels, are shown in Figure 6.

Figure 6 here

The results are similar in the three visual areas examined. They show a consistent reduction of the measured BOLD response in late trials (light bars) relative to early trials (dark bars). Importantly, the reduction is evident not only for responses to the grating stimuli (right panel), as found in several previous studies, but also for pre-stimulus (anticipatory) responses. The latter effect cannot reflect altered stimulus processing since no stimulus is present in this period. Instead, we attribute it to altered influences of attention. It is unlikely to reflect a general decline in attention due to fatigue because this would be accompanied by a decline in performance, whereas in fact performance clearly improved over time (Fig. 3). It is therefore more likely to reflect learning-related changes in attention. The possible nature of the change is considered in the Discussion.

To permit examination of any differences between task difficulty levels, the four levels were modelled with separate regressors and Fig 6 simply shows the average result. The same data are shown separated in Fig 7. The response reduction in late runs compared to early runs is apparent in most cases. In the case of pre-stimulus activity, it is greatest for the easiest trials (difficulty level 1) and progressively lessens, being absent for level 4, the hardest. For stimulus-evoked activity, the reduction is similar for all difficulty levels. The pattern of results is similar for the three visual areas in all respects.

Figure 7 here

For each event type (pre-stimulus and stimulus), a separate three-way ANOVA was conducted with factors visual area (V1-V3), learning (early or late) and task difficulty (4 levels). There was no main effect of visual area in either analysis. Task difficulty was significant for pre-stimulus activity ($F(3,384) = 4.6, p < 0.01$) but not for stimulus-related activity. The main effect of learning was significant both for pre-stimulus activity ($F(1,384) = 29.3, p < 0.0001$) and for stimulus-related activity ($F(1,384) = 6.9, p < 0.01$). The interaction (learning x difficulty) was significant for the pre-stimulus activity ($F(3,384) = 6.8, p < 0.0001$) but not for the stimulus-evoked response.

In the analyses presented above, the effects of learning were summarized by simply dividing the runs into two groups, early and late. In each run, a single regressor was used to model all events of a particular type in that run. To examine trial-by-trial changes, an additional analysis was performed in which each event was modelled with a separate regressor. This leads to very noisy estimates of the BOLD response but it permits the trend to be tracked and compared to the learning curve. The analysis is presented for the effect of learning on pre-stimulus activity, since this is the novel finding. Figure 8(a) shows the BOLD response during the pre-stimulus period for every trial conducted at a medium difficulty level (level 2), as a scatter plot. It can be seen that the change over time evident in Figs 6 and 7 is gradual. Presumably the true function is a decay function that asymptotes, but over this limited time span it can be approximated as a linear function with negative slope. The slope is plotted for the four difficulty levels in Figure 8(b). The slope is most negative (i.e. BOLD response declines fastest) for the easiest trials and is near-zero for the hardest trials. Thus, the change in BOLD response mirrors the performance data (Fig. 3c), which show that

performance improves most rapidly in easy trials. From this it can be deduced that pre-stimulus activity (Fig. 6, top) is reduced in proportion to the learning that has occurred. In contrast, stimulus-related activity seems to reduce as a function of exposure to the stimuli, irrespective of performance change (Fig 6, bottom).

Figure 8 here

We performed a final analysis to test the relationship between attentional load in pre-stimulus activity and performance on the task. To do this, we measured the pre-stimulus BOLD response in V1 separately for trials in which the subject gave a correct response and trials in which an incorrect response was given. Figure 9 shows the result, averaged across participants for all trials and also separately for each difficulty level. Correct responses yielded a significantly greater BOLD response overall ($F=15.110$, $p<0.001$) and for each difficulty level considered alone except the easiest one. From this it can be deduced that attentional deployment predicts the performance on the task. We performed similar analyses based on the first half of the trials alone and on the second half alone. The results (not shown) show a non-significant trend towards larger BOLD responses on correct trials in both halves. Moreover pre-stimulus activity for correct trials shows a trend of decrease between the first and second halves. From this it can be deduced that attentional deployment reduces with time but is still necessary in order to perform the task even at the end.

Figure 9 here

4. Discussion

4.1 Perceptual learning and attention

Many studies have demonstrated changes in the magnitude of stimulus-evoked activity in visual cortex as learning progresses but the origin and cause of these changes remains unclear. Most fundamentally, it is not clear whether learning-related changes in the visual cortex result from plasticity in response to bottom-up sensory input, or instead reflect feedback influences from later processing stages. This study examined the role of attention in the change that occurs in visual cortex during perceptual learning. When the magnitude of activity evoked by a stimulus during learning is measured, as in several previous studies, it is difficult to know whether the observed change reflects a change in local processing or a change in an extrinsic modulatory signal, such as that related to attention. To separate these two possibilities, we measured pre-stimulus BOLD activity, occurring after a trial was cued but before the stimulus appeared, as an index of attentional modulation. During the pre-stimulus interval, no processing of the stimulus occurs and activity is strictly preparatory; the key preparation required is to attend to the expected location and parameters of the upcoming stimulus. The task learned during the experiment was an orientation discrimination task, in which learning is thought likely to reflect localized changes in visual cortex (e.g. Ramachandran and Braddick, 1973; Fiorentini and Berardi, 1981; Vogels and Orban, 1985; Shiu and Pashler, 1992; Schoups et al., 1995; Ahissar and Hochstein, 1997). Learning was confined to a single one-hour session, whereas many behavioural studies have examined learning over multiple sessions on different days, but it has been shown that some perceptual learning occurs even with a

small amount of practice (e.g. Hussein et al, 2009) and some other MRI studies have used similarly short learning periods (e.g. Mukai et al., 2007).

We show that attention-related pre-stimulus activity in early visual areas decreases during perceptual learning. This change was accompanied by a reduction of stimulus-evoked activity similar to that previously demonstrated during learning of similar tasks. Our results are consistent with the suggestion that attention is closely involved in perceptual learning (Ahissar and Hochstein, 1993). If it is accepted that pre-stimulus activity reflects attentional modulation then it is clear from our results that attentional modulation changes as learning progresses. The change could, in principle, reflect either a change in attention itself or a change in the relationship between attention and the modulation it causes in visual cortex.

A trivial explanation of the results would be simply that participants tire during the course of the scan and that their attention wanes, leading to a reduction in attention-related activity in visual cortex. To examine this possibility, we analysed behavioural performance. If participants become fatigued, performance will deteriorate and learning will be reduced. Therefore it is important to establish that learning, as indexed by improved performance, was actually occurring over the full duration of the experiment and that there was no fatigue-related deterioration. The behavioural data obtained during scanning show clear evidence (Fig. 3) of a gradual improvement in performance over the entire session. This strongly suggests that attention was sustained throughout the experiment.

Having discounted a fatigue explanation, it is reasonable to interpret the change in activity during the pre-stimulus period as a learning-related change. However a possible interpretation of the results might be that the learning that occurs relates to some other factor than the orientation task, such as learning the response mapping or learning an efficient strategy. A conventional test of genuine perceptual learning is that transfer to another stimulus (in this case orientation) is poor. We show clearly that this is the case (Fig. 4), rendering such alternative interpretations unlikely. The criteria for identifying low-level perceptual learning have recently become more uncertain, with evidence emerging that learning can sometimes transfer to another stimulus (Jeter et al, 2010; Zhang et al, 2010) or to another retinal location (Pavlovskaya and Hochstein, 2011). However, if performance enhancement does not in fact transfer, it is widely accepted that this indicates perceptual learning.

Pre-stimulus activity of the kind we have measured is generally regarded as being related to spatial attention (Luks and Simpson, 2004; Sapir et al, 2005; McMains and Kastner, 2007; Sylvester et al., 2007) or alternatively feature-based attention (Giesbrecht et al., 2003; Shibata et al., 2008). Modulation by feature-based attention occurs not at a particular retinotopic location but in the whole visual area, and the fact that in our study significant activation was found only in the specific location where the stimulus was appearing suggests that subjects were attending to a particular location of the visual field rather than a particular stimulus attribute. The spatial distribution of the response also discounts the interpretation that pre-stimulus activity reflects a generalized alerting effect. It can be seen in Fig. 2 that pre-stimulus activity (Fig. 2c) has a similar spatial distribution to the stimulus-evoked response (Fig. 2b), showing that it is restricted to the locations where stimuli are expected. Like feature-

based attention, a generalized arousal effect would be evident in all parts of visual cortex. Thus, we reach the conclusion that during perceptual learning, a change occurs in the modulation of visual cortex by spatial attention. The similarity in form between the observed gradual BOLD activity change (Fig 8a) and the gradual change in performance (Fig 3b) is consistent with such an interpretation.

In our experiment, we intermixed four levels of task difficulty. For pre-stimulus activity, the change in attentional modulation occurred more quickly for easier than harder trials (Figs 7 and 8). This suggests that attentional modulation changes with learning in a way that is specific to difficulty. Rather than a single change occurring that is applied to the visual cortex whatever the difficulty of the trial, it is as if change is applied in inverse proportion to the difficulty of the trial and in proportion to the rate of learning. The result is reminiscent of the finding (Hochstein & Ahissar, 1997) that the spatial generalization of perceptual learning varies with task difficulty.

4.2 Mechanisms of attentional change

The most parsimonious explanation of our results is that as learning proceeds, the task becomes more automatic, the attentional demand reduces and attentional modulation of the visual cortex becomes less intense as a result. It is well established that learning often involves automation of tasks. The observation that facilitation of activity in sensory cortex lessens during learning makes intuitive sense in this context.

On this account, changes in pre-stimulus activity purely reflect changes in top-down modulatory signals and there is no need to invoke plastic, learning-induced changes in

sensory cortex. This raises the question of whether the same may be true of the change in the response to the visual stimulus itself. Several studies (Schiltz et al, 1999; Mukai et al, 2007) have reported that as perceptual learning progresses, the magnitude of the sensory response to the stimulus declines, and we replicate this finding. Could it be that the change is entirely related to reduced top-down facilitation, reflecting task automation? The fact that the changes are spatially localized is not a barrier to such an interpretation, since modulation by spatial attention is also localized. Previous fMRI experiments (e.g. Kastner et al, 1999) have shown that attention-related pre-stimulus activity in early visual areas is largely confined to the retinotopic location of the representation of the attended stimulus. This indicates that the topography of top-down modulation by attention is the same during the preparatory period and stimulus presentation. Indeed, Sylvester et al. (2009) have argued that the amplitude of pre-stimulus activity is correlated trial-by-trial with the amplitude of the stimulus-evoked response, indicating that a single source of modulation underlies both phenomena. Thus, learning-related changes in stimulus-evoked responses may also reflect changes in attentional modulation. A possible caveat is that although the time-course of change of pre-stimulus activity reflects the difficulty level of the task (Fig 7a), this is not obviously the case for stimulus-evoked activity (Fig. 7b). This might indicate a separation in the causes of the two changes.

Another possible interpretation of our results is that two types of learning occur in parallel with no causal link between them. It could be that on the one hand, participants learn to perform the orientation task better and on the other, in parallel, they learn to deploy spatial attention more efficiently, resulting in reduced pre-

stimulus activity in visual cortex. We think this unlikely because although two independent effects could easily change activity in the same direction, the probability they do so with the same time-course, by chance, is low.

4.3 Learning-related increases and decreases in activity

We suggest that reductions in sensory activity that occur during perceptual learning may be attention-related effects reflecting task automation. Under this point of view, automation means the process of making performance of the task possible without active cognitive control. Attentional deployment is initially required in order to perform the task and perhaps also to facilitate the learning process. Once automation is complete, attentional deployment is no longer required. In our results, automation (on this account) is not total and the attentional requirement is reduced but not abolished.

However, it is not plausible that all the learning-related sensory changes reported in the literature have this origin because several studies have reported increases, rather than decreases, in activity during learning. Indeed, such studies are more numerous than those reporting decreases. What determines whether activity increases or decreases is quite obscure. A possibility is that where it increases, this reflects increased neural activity, in turn reflecting deeper processing, and that where it decreases it reflects reduced attentional modulation through automation. It might be that both factors are at play in all reported experiments and the result in a given case reflects the balance of the two factors, which may be tipped one way or the other according to circumstances. Tasks that are documented to produce an increase in

activity might require the development of additional sensory processing but be relatively unsuitable for automation, whereas tasks that merely require increased precision for learning, such as orientation discrimination, might be more readily accomplished with existing processing systems and be more amenable to automation. Of the studies that have reported reductions in activity, Schiltz et al (1999) employed a simple orientation discrimination task with gratings, as we did in the present study, while Mukai et al. (2007) used a task involving discriminating contrast changes in one of two components of a grating. These studies fit into an “automation-friendly” category. Of those studies that report increases in activity, Schwartz et al. (2002) and Yotsomoto et al (2008) both used texture discrimination tasks, Maertens & Pollmann (2005) used curvature discrimination, Sigman et al (2005) used a shape identification task and Lewis et al. (2009) used a task involving detection of an inverted letter. It is unclear what these tasks have in common that orientation discrimination lacks, but they all involve relatively complex stimuli and might all fit in a category that makes automation more difficult and slower. However it may be inappropriate to seek to divide tasks into two categories, such as simple and complex; a more fruitful approach may be to consider that different tasks engender different balances, or rates of change, of plasticity (response increase) and attentional change (decrease). The only study we know that does not fit well into this schema is that of Furmanski et al (2004), who used an orientation discrimination task and obtained increases in activity. However, the interpretation of this study is complicated by the fact that training involved detection of low-contrast gratings whereas the increased activity occurred during orientation discrimination with high-contrast gratings, so clearly improvement could not occur by automation but only by altered processing. Thus, all reported studies fit our suggested dichotomy. It will be interesting to test the dichotomy by direct

comparison of the sign of learning-related changes across tasks, and then to explore changes in pre-stimulus activity in circumstances where stimulus-evoked activity increases with learning.

5. Conclusion

So far perceptual learning has been regarded as modulating how the brain processes sensory stimuli. Although some authors have pointed out that attention plays a role in perceptual learning, how the attentional signal that modifies processing in the visual cortex is affected by learning has not previously been studied. This study shows that not only is attention involved in the learning process, but also the attentional modulation of visual cortex is directly affected by learning.

Acknowledgement

The research leading to these results received funding from the European Community's Seventh Framework Programme FP7/2007-2013 under grant agreement number 214728-2.

REFERENCES

- Ahissar, M. & Hochstein, S. (1993) Attentional control of early perceptual learning. *Proceedings of the National Academy of Science U S A*, **90**, 5718-5722.
- Ahissar, M. & Hochstein, S. (1996) Learning pop-out detection: specificities to stimulus characteristics. *Vision Research*, **36**, 3487-3500.
- Ahissar, M. & Hochstein, S. (1997) Task difficulty and the specificity of perceptual learning. *Nature*, **387**, 401-406.
- Ball, K. & Sekuler, R. (1982) A specific and enduring improvement in visual motion discrimination. *Science*, **218**, 697-698.
- Corbetta, M. & Shulman, G.L. (2002) Control of goal-directed and stimulus-driven attention in the brain. *Nature Review Neuroscience*, **3**, 201-215.
- Crist, R.E., Kapadia, M.K., Westheimer, G. & Gilbert, C.D. (1997) Perceptual learning of spatial localization: specificity for orientation, position, and context. *Journal of Neurophysiology*, **78**, 2889-2894.
- Crist, R.E., Li, W. & Gilbert, C.D. (2001) Learning to see: experience and attention in primary visual cortex. *Nature Neuroscience*, **4**, 519-525.
- Deichmann, R., Schwarzbauer, C. & Turner, R. (2004) Optimisation of the 3D MDEFT sequence for anatomical brain imaging: technical implications at 1.5 and 3 T. *NeuroImage*, **21**, 757-767.
- Engel, S.A., Rumelhart, D.E., Wandell, B.A., Lee, A.T., Glover, G.H., Chichilnisky, E.J. & Shadlen, M.N. (1994) fMRI of human visual cortex. *Nature*, **369**, 525.
- Fahle, M. (2004) Perceptual learning: a case for early selection. *Journal of Vision*, **4**, 879-890.
- Fahle, M., Edelman, S. & Poggio, T. (1995) Fast perceptual learning in hyperacuity. *Vision Research*, **35**, 3003-3013.
- Fahle, M. (2009) Perceptual learning and sensorimotor flexibility: cortical plasticity under attentional control? *Philosophical Transactions of the Royal Society of London Series B*, **363**, 313-319.
- Fiorentini, A. & Berardi, N. (1980) Perceptual learning specific for orientation and spatial frequency. *Nature*, **287**, 43-44.
- Fiorentini, A. & Berardi, N. (1981) Learning in grating waveform discrimination: specificity for orientation and spatial frequency. *Vision Research*, **21**, 1149-1158.

- Furmanski, C.S., Schluppeck, D. & Engel, S.A. (2004) Learning strengthens the response of primary visual cortex to simple patterns. *Current Biology*, **14**, 573-578.
- Ghose, G.M. (2004) Learning in mammalian sensory cortex. *Current Opinion in Neurobiology*, **14**, 513-518.
- Ghose, G.M., Yang, T. & Maunsell, J.H. (2002) Physiological correlates of perceptual learning in monkey V1 and V2. *Journal of Neurophysiology*, **87**, 1867-1888.
- Giesbrecht, B., Weissman, D.H., Woldorff, M.G. & Mangun, G.R. (2006) Pre-target activity in visual cortex predicts behavioral performance on spatial and feature attention tasks. *Brain Research*, **1080**, 63-72.
- Gilbert, C.D., Sigman, M. & Crist, R.E. (2001) The neural basis of perceptual learning. *Neuron*, **31**, 681-697.
- Hagberg, G.E., Zito, G., Patria, F. & Sanes, J.N. (2001) Improved detection of event-related functional MRI signals using probability functions. *NeuroImage*, **14**, 1193-1205.
- Hussain, Z., Sekuler, A.B. & Bennett, P.J. (2009) How much practice is needed to produce perceptual learning? *Vision Research*, **49**, 2624-2634.
- Ito, M., Westheimer, G. & Gilbert, C.D. (1998) Attention and perceptual learning modulate contextual influences on visual perception. *Neuron*, **20**, 1191-1197.
- Jeter, P.E., Doshier, B.A., Liu, S.H. & Lu, Z.L. (2010) Specificity of perceptual learning increases with increased training. *Vision Research*, **50**, 1928-1940.
- Karni, A. (1996) The acquisition of perceptual and motor skills: a memory system in the adult human cortex. *Brain Research Cognitive Brain Research*, **5**, 39-48.
- Karni, A. & Sagi, D. (1991) Where practice makes perfect in texture discrimination: evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Science U S A*, **88**, 4966-4970.
- Kastner, S., Pinsk, M.A., De Weerd, P., Desimone, R. & Ungerleider, L.G. (1999) Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, **22**, 751-761.
- Kastner, S. & Ungerleider, L.G. (2001) The neural basis of biased competition in human visual cortex. *Neuropsychologia*, **39**, 1263-1276.
- Lewis, C.M., Baldassarre, A., Committeri, G., Romani, G.L. & Corbetta, M. (2009) Learning sculpts the spontaneous activity of the resting human brain. *Proceedings of the National Academy of Science U S A*, **106**, 17558-17563.

- Luck, S.J., Chelazzi, L., Hillyard, S.A. & Desimone, R. (1997) Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology*, **77**, 24-42.
- Luks, T.L. & Simpson, G.V. (2004) Preparatory deployment of attention to motion activates higher-order motion-processing brain regions. *NeuroImage*, **22**, 1515-1522.
- Maertens, M. & Pollmann, S. (2005) fMRI reveals a common neural substrate of illusory and real contours in V1 after perceptual learning. *Journal of Cognitive Neuroscience*, **17**, 1553-1564.
- Maunsell, J.H. & Treue, S. (2006) Feature-based attention in visual cortex. *Trends in Neuroscience*, **29**, 317-322.
- McMains, S.A., Fehd, H.M., Emmanouil, T.A. & Kastner, S. (2007) Mechanisms of feature- and space-based attention: response modulation and baseline increases. *Journal of Neurophysiology*, **98**, 2110-2121.
- Mukai, I., Kim, D., Fukunaga, M., Japee, S., Marrett, S. & Ungerleider, L.G. (2007) Activations in visual and attention-related areas predict and correlate with the degree of perceptual learning. *Journal of Neuroscience*, **27**, 11401-11411.
- Nakamura, K. & Colby, C.L. (2000) Visual, saccade-related, and cognitive activation of single neurons in monkey extrastriate area V3A. *Journal of Neurophysiology*, **84**, 677-692.
- Pavlovskaya, M. & Hochstein, S. (2011) Perceptual learning transfer between hemispheres and tasks for easy and hard feature search conditions. *Journal of Vision*, **11**, 8.
- Pessoa, L., Kastner, S. & Ungerleider, L.G. (2003) Neuroimaging studies of attention: from modulation of sensory processing to top-down control. *Journal of Neuroscience*, **23**, 3990-3998.
- Pollmann, S. & Maertens, M. (2005) Shift of activity from attention to motor-related brain areas during visual learning. *Nature Neuroscience*, **8**, 1494-1496.
- Ramachandran, V.S. (1976) Learning-like phenomena in stereopsis. *Nature*, **262**, 382-384.
- Ramachandran, V.S. & Braddick, O. (1973) Orientation-specific learning in stereopsis. *Perception*, **2**, 371-376.
- Recanzone, G.H. & Wurtz, R.H. (2000) Effects of attention on MT and MST neuronal activity during pursuit initiation. *Journal of Neurophysiology*, **83**, 777-790.
- Reynolds, J.H. & Chelazzi, L. (2004) Attentional modulation of visual processing. *Annual Review Neuroscience*, **27**, 611-647.

- Sapir, A., d'Avossa, G., McAvoy, M., Shulman, G.L. & Corbetta, M. (2005) Brain signals for spatial attention predict performance in a motion discrimination task. *Proceedings of the National Academy of Science U S A*, **102**, 17810-17815.
- Schiltz, C., Bodart, J.M., Dubois, S., Dejardin, S., Michel, C., Roucoux, A., Crommelinck, M. & Orban, G.A. (1999) Neuronal mechanisms of perceptual learning: changes in human brain activity with training in orientation discrimination. *NeuroImage*, **9**, 46-62.
- Schoups, A., Vogels, R., Qian, N. & Orban, G. (2001) Practising orientation identification improves orientation coding in V1 neurons. *Nature*, **412**, 549-553.
- Schoups, A.A., Vogels, R. & Orban, G.A. (1995) Human perceptual learning in identifying the oblique orientation: retinotopy, orientation specificity and monocularly. *Journal of Physiology*, **483 (Pt 3)**, 797-810.
- Schwartz, S., Maquet, P. & Frith, C. (2002) Neural correlates of perceptual learning: a functional MRI study of visual texture discrimination. *Proceedings of the National Academy of Science U S A*, **99**, 17137-17142.
- Sereno, M.I., Dale, A.M., Reppas, J.B., Kwong, K.K., Belliveau, J.W., Brady, T.J., Rosen, B.R. & Tootell, R.B. (1995) Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, **268**, 889-893.
- Shiffrin, R.M. & Schneider, W. (1977) Controlled and Automatic Human Information-Processing .2. Perceptual Learning, Automatic Attending, and a General Theory. *Psychological Review*, **84**, 127-190.
- Shiu, L.P. & Pashler, H. (1992) Improvement in line orientation discrimination is retinally local but dependent on cognitive set. *Perception & Psychophysics*, **52**, 582-588.
- Sigman, M., Pan, H., Yang, Y., Stern, E., Silbersweig, D. & Gilbert, C.D. (2005) Top-down reorganization of activity in the visual pathway after learning a shape identification task. *Neuron*, **46**, 823-835.
- Silver, M.A., Ress, D. & Heeger, D.J. (2007) Neural correlates of sustained spatial attention in human early visual cortex. *Journal of Neurophysiology*, **97**, 229-237.
- Smith, A.T., Singh, K.D. & Balsters, J.H. (2007) A comment on the severity of the effects of non-white noise in fMRI time-series. *NeuroImage*, **36**, 282-288.
- Stokes, M., Thompson, R., Nobre, A.C. & Duncan, J. (2009) Shape-specific preparatory activity mediates attention to targets in human visual cortex. *Proceedings of the National Academy of Science U S A*, **106**, 19569-19574.

- Sylvester, C.M., Jack, A.I., Corbetta, M. & Shulman, G.L. (2008) Anticipatory suppression of nonattended locations in visual cortex marks target location and predicts perception. *Journal of Neuroscience*, **28**, 6549-6556.
- Sylvester, C.M., Shulman, G.L., Jack, A.I. & Corbetta, M. (2007) Asymmetry of anticipatory activity in visual cortex predicts the locus of attention and perception. *Journal of Neuroscience*, **27**, 14424-14433.
- Sylvester, C.M., Shulman, G.L., Jack, A.I. & Corbetta, M. (2009) Anticipatory and stimulus-evoked blood oxygenation level-dependent modulations related to spatial attention reflect a common additive signal. *Journal of Neuroscience*, **29**, 10671-10682.
- Vidyasagar, T.R. & Stuart, G.W. (1993) Perceptual learning in seeing form from motion. *Proceedings. Biological Science*, **254**, 241-244.
- Vogels, R. & Orban, G.A. (1985) The effect of practice on the oblique effect in line orientation judgments. *Vision Research*, **25**, 1679-1687.
- Watanabe, T., Nanez, J.E. & Sasaki, Y. (2001) Perceptual learning without perception. *Nature*, **413**, 844-848.
- Xiao, L.Q., Zhang, J.Y., Wang, R., Klein, S.A., Levi, D.M. & Yu, C. (2008) Complete transfer of perceptual learning across retinal locations enabled by double training. *Current Biology*, **18**, 1922-1926.
- Yang, T. & Maunsell, J.H. (2004) The effect of perceptual learning on neuronal responses in monkey visual area V4. *Journal of Neuroscience*, **24**, 1617-1626.
- Yotsumoto, Y., Watanabe, T. & Sasaki, Y. (2008) Different dynamics of performance and brain activation in the time course of perceptual learning. *Neuron*, **57**, 827-833.
- Zhang, T., Xiao, L.Q., Klein, S.A., Levi, D.M. & Yu, C. (2010) Decoupling location specificity from perceptual learning of orientation discrimination. *Vision Research*, **50**, 368-374.
- Zohary, E., Celebrini, S., Britten, K.H. & Newsome, W.T. (1994) Neuronal plasticity that underlies improvement in perceptual performance. *Science*, **263**, 1289-1292.

FIGURE LEGENDS

Figure 1

Time course of one trial. A cue indicating the difficulty level of the task was followed after a variable interval by a pair of Gabor stimuli, immediately followed by a cue to respond. In the example shown, the cue indicates “very difficult” (arrow points 60 deg clockwise from vertical).

Figure 2

(a) Flattened representation of the occipital cortex of one hemisphere showing retinotopic areas (V1-V3). Stimulus-related BOLD activation is superimposed as a colour overlay, averaged across all 8 runs in the main experiment. The activation largely excludes the fovea and far periphery, reflecting the location of the stimulus. The ROIs used for quantitative analysis are shown. **(b)** Pre-stimulus BOLD activation from the same dataset. The activity that is weaker than the stimulus-related activity, as expected, but has a very similar spatial extent.

Figure 3

(a) Percent correct responses as a function of task difficulty, averaged across participants. Results for early and late trials are plotted separately to show the effect of learning. **(b)** Performance as a function of time averaged across participants at one difficulty level. **(c)** Rate of learning (slope of learning curve) as a function of difficulty, averaged across participants.

Figure 4

Perceptual learning, averaged across four participants, in a supplementary experiment conducted outside the scanner. **(a)** Learning during training equivalent to that given during the MRI experiment **(b)** Failure of transfer of learning when discrimination was subsequently tested at the same location but with the orthogonal orientation.

Figure 5

Estimate of the timecourse of prestimulus activity derived from deconvolution analysis. Time zero represents the onset of the cue. The plot is the average across all participants and is also averaged across visual areas V1-V3.

Figure 6

Mean BOLD responses for visual areas V1, V2 and V3 collapsed across the four difficulty levels and averaged across participants and hemispheres. Results for the pre-stimulus and post-stimulus time periods are shown separately. Error bars show ± 1 SEM (n=8).

Figure 7

Mean BOLD responses for visual areas V1, V2 and V3 for each of the four difficulty levels (1 is easiest, 4 is hardest), averaged across participants and hemispheres. Each difficulty level is divided into the first half of the trials and the second half, as in Fig. 5. Results for the pre-stimulus and post-stimulus time periods are shown separately. Error bars show ± 1 SEM (n=8).

Figure 8

(a) Sample scatter plot showing trial-by-trial amplitudes (beta values) during the pre-stimulus interval as a function of time, for one difficulty level. The data for all participants are included and each point represents the estimated BOLD response for one trial in one participant, averaged across all the voxels in the V1 ROI. The 8 runs are concatenated. The best-fit straight line is also shown. **(b)** The slope of the best-fit linear function for each difficulty level, averaged across participants, derived from plots like that in (a).

Figure 9

Mean BOLD responses in V1 shown separately for trials in which the subject gave a correct response (hit) and trials in which an incorrect response was given (miss), averaged across participants. The results are shown for each difficulty level and also for the mean of all trials.

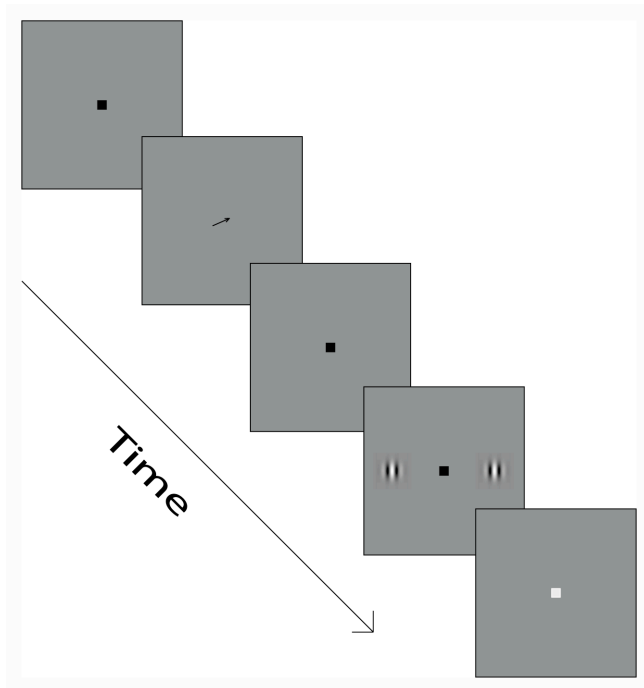


Figure 1

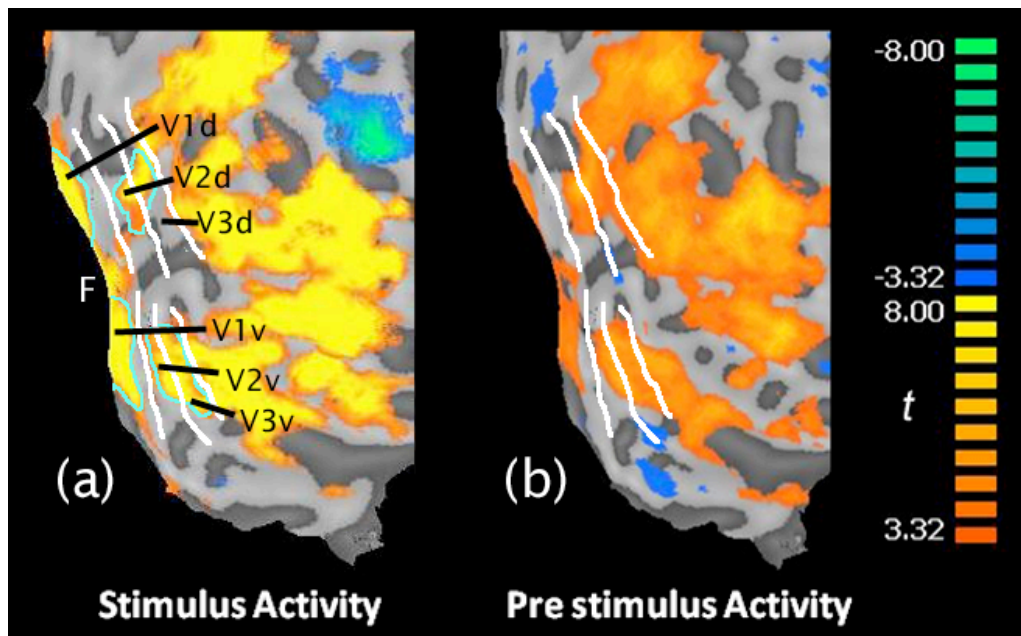


Figure 2

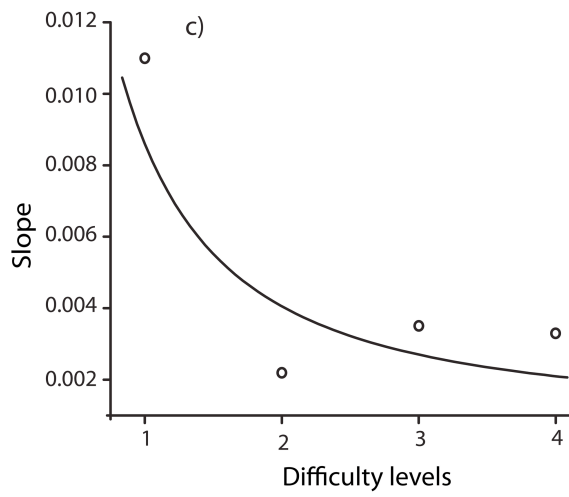
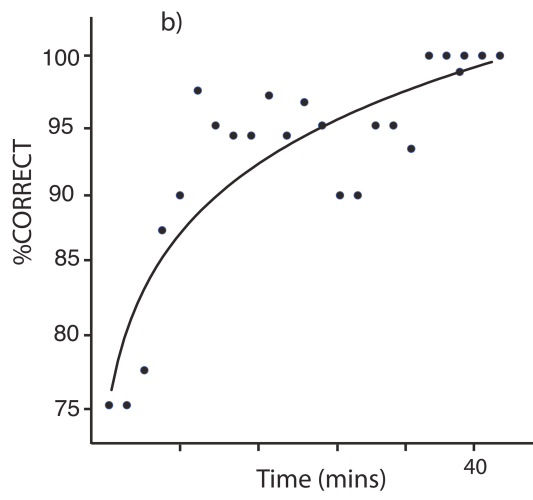
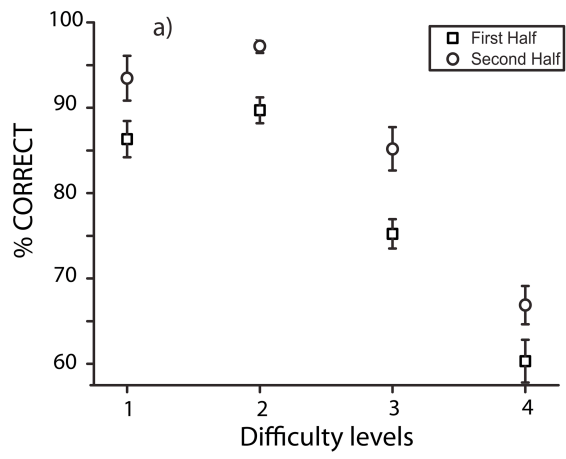


Figure 3

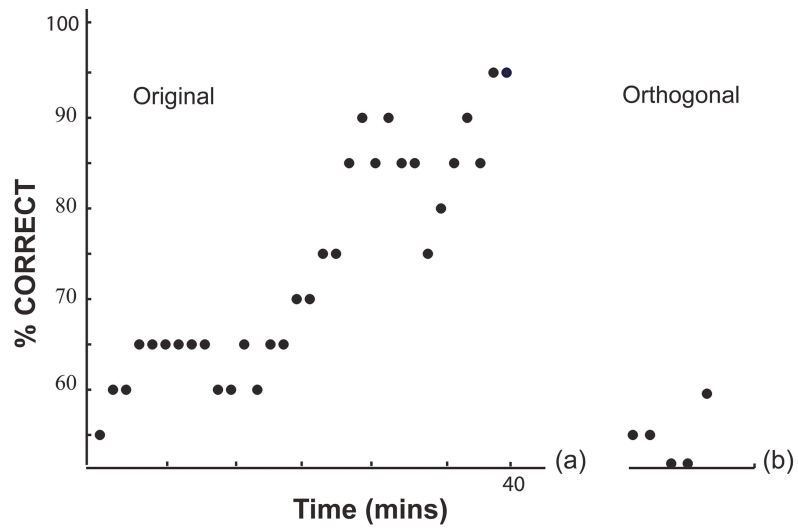


Figure 4

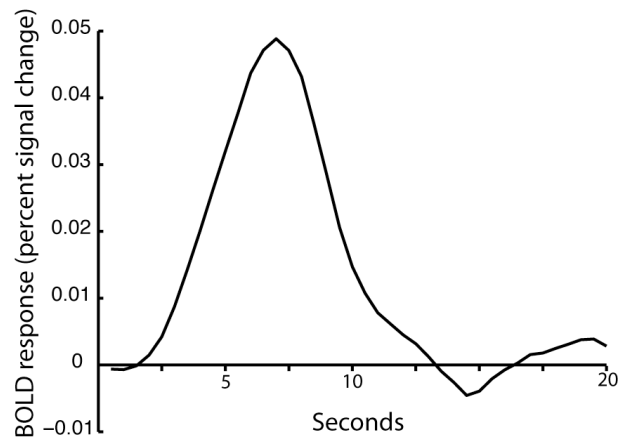


Figure 5

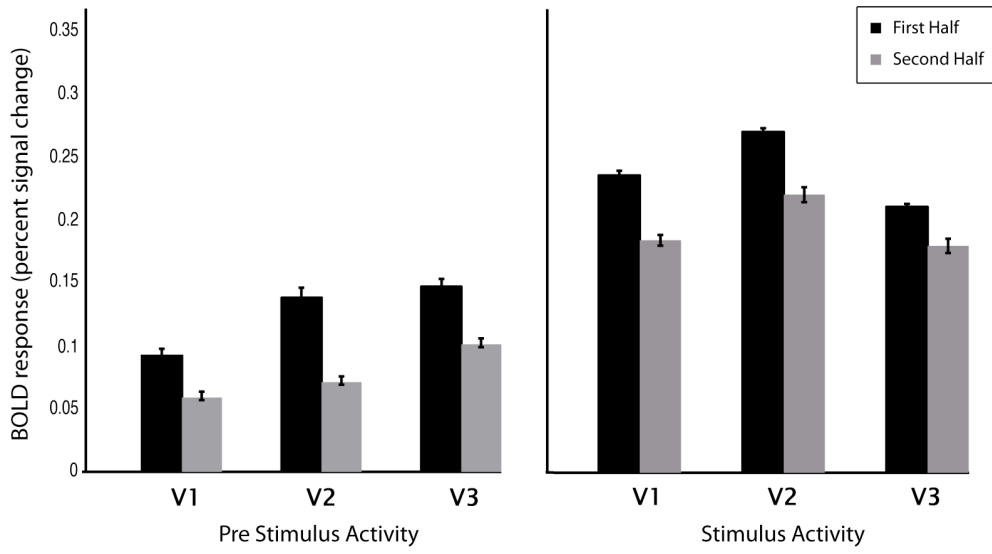


Figure 6

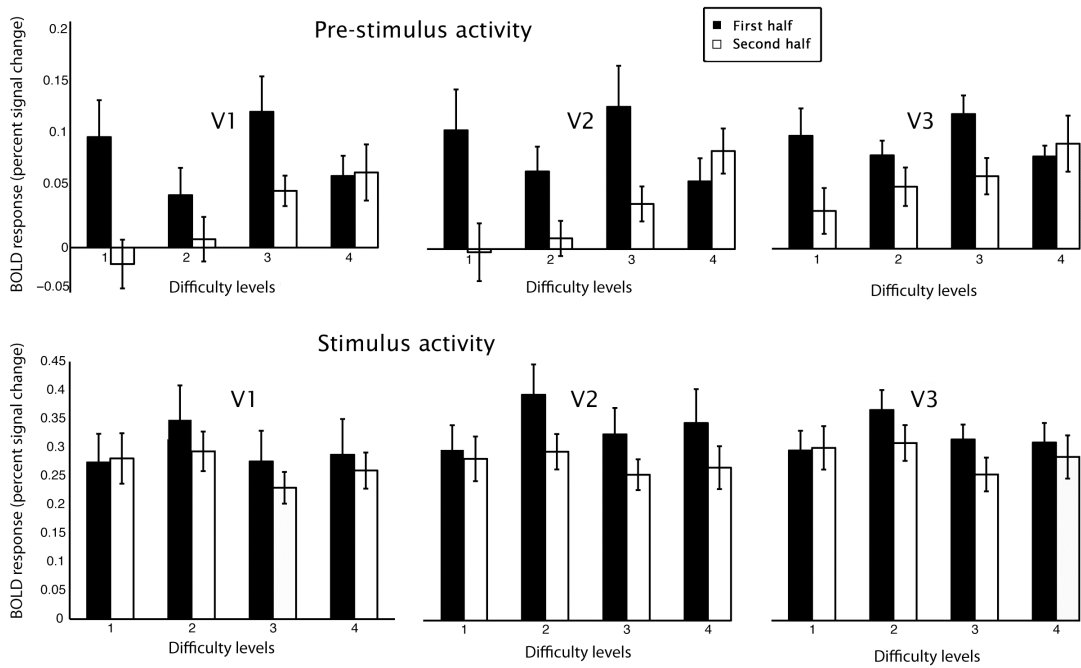


Figure 7

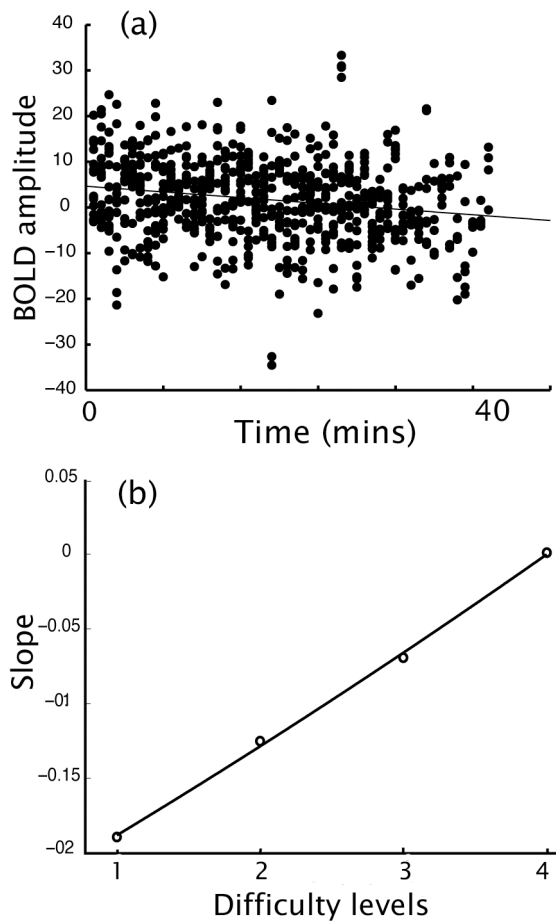


Figure 8

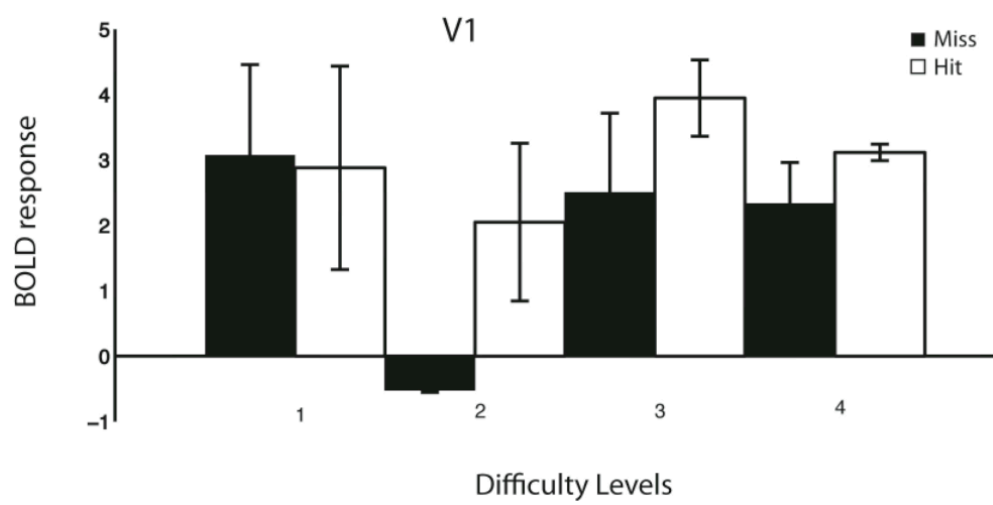


Figure 9