



Newcastle University ePrints

Chen X, Sanayei M, Thiele A. [Perceptual learning of contrast discrimination in macaca mulatta](#). *Journal of Vision* 2013, 13(13), 22.

Copyright: The definitive version of this article, published by the Association for Research in Vision and Ophthalmology (2013), is available at: <http://dx.doi.org/10.1167/13.13.22>

Always use the definitive version when citing.

Further information on publisher website: <http://www.journalofvision.org>

Date deposited: 6th June 2014

Version of file: Author final



This work is licensed under a [Creative Commons Attribution-NonCommercial 3.0 Unported License](#)

ePrints – Newcastle University ePrints

<http://eprint.ncl.ac.uk>

Perceptual learning of contrast discrimination in macaca mulatta

X. Chen^{1,2}, M. Sanayei^{1,2}, and A. Thiele¹

¹Institute of Neuroscience, Newcastle University, Newcastle-upon-Tyne, UK

²These authors contributed equally to this work.

Corresponding author: A. Thiele, alex.thiele@ncl.ac.uk

Abstract

Rhesus monkeys underwent training in a contrast discrimination task, in which grating stimuli were presented at parafoveal and peripheral visual field locations. Subjects had to compare a sample stimulus that had a fixed contrast of 30%, to a test stimulus that varied in contrast from trial to trial. Extensive practise yielded improvements in contrast discrimination that were observed across the full range of test stimulus contrasts. These improvements occurred across multiple sessions, as well as across trials within individual sessions. The finer the contrast discriminations required, the longer it took for subjects to improve.

Improvements in psychophysical performance resulted in the steepening of psychometric functions, and/or shifts in the point of subjective equality towards the contrast of the sample stimulus. Enhancement in discrimination was especially pronounced around the contrast level of the sample stimulus, to which the subject was consistently exposed. The changes resulted in increased accuracy overall, lower discrimination thresholds, and faster response times. Partial transfer of learning, from vertically-oriented training stimuli, to horizontally-oriented testing stimuli, was observed, while transfer to stimuli with different spatial frequencies was less pronounced. The results demonstrate the existence of perceptual learning in the contrast domain, whereby learning affects multiple performance-related psychophysical metrics.

Keywords

Perceptual learning, contrast discrimination, macaque

Introduction

Perceptual learning (PL) is a long-lasting improvement in the ability to make fine perceptual discriminations, achieved through practise, usually over many training sessions. Studies conducted in the visual modality have reported enhancements in the discrimination of stimulus features, such as the orientation of gratings (Zivari Adab & Vogels, 2011), the degree of separation or alignment between stimuli in a bisection task (Parkosadze, Otto, Malania, Kezeli, & Herzog, 2008), the direction of moving stimuli (Law & Gold, 2008), and the segregation of elements based on texture (Yotsumoto, Watanabe, & Sasaki, 2008); for a review, refer to Sagi (2011).

Visual stimulus contrast is sometimes viewed as a special case- the discrimination of objects with low luminance contrast is a daily component of the visual diet (Balboa & Grzywacz, 2003; Brady & Field, 2000; Frazor & Geisler, 2006), and studies on the development of contrast discrimination faculties of normal humans tend to focus on changes throughout infancy, childhood and adolescence (Stephens & Banks, 1987), with the general assumption that this ability reaches its peak by adulthood, followed by a decline in late adulthood (Owsley, 2011). This view was supported by results from early studies in healthy humans in which learning of contrast-dependent tasks was minimal, or at least, highly specific to the contrast levels used during training (Adini, Sagi, & Tsodyks, 2002; Adini, Wilkonsky, Haspel, Tsodyks, & Sagi, 2004; Dorais & Sagi, 1997). However, subsequent findings from Yu, Klein, and Levi (2004) suggested that improvements in contrast discrimination could be achieved ‘given sufficient practice’ (cited as in Yu, Klein and Levi 2004). This triggered a series of follow-up experiments, involving a variety of roving pedestal contrasts and examining the influence of flanker stimuli on contrast perceptual learning; improvements in contrast discrimination have now been documented in humans

with normal vision (Adini et al., 2004; Kuai, Zhang, Klein, Levi, & Yu, 2005; Xiao et al., 2008; Yu et al., 2004; Zhang et al., 2008; Zhang et al., 2010).

The aim of the current study was to examine the behavioural effects of training on contrast discrimination abilities in macaques. Practise took place using non-rotating grating stimuli that were positioned at two different visual eccentricities, allowing a comparison of learning effects at peripheral and parafoveal locations. The subjects' psychometric performance was monitored throughout the training process to allow continuous assessment of behavioural improvement.

Methods

All procedures were carried out in accordance with the European Communities Council Directive RL 2010/63/EC, the US National Institutes of Health Guidelines for the Care and Use of Animals for Experimental Procedures, the UK Animals Scientific Procedures Act, and the standards outlined in the ARVO Statement for the Use of Animals in Ophthalmic and Vision Research. Two male macaque monkeys (5-14 years of age) were used in this study.

Stimuli

Stimulus presentation was controlled using Cortex software (Laboratory of Neuropsychology, National Institute of Mental Health, <http://dally.nimh.nih.gov/index.html>) on a computer with an Intel® Core™ i3-540 processor. Stimuli were displayed at a viewing distance of 0.54 m, on a 25" Sony Trinitron CRT monitor with display dimensions of 40 cm (W) by 32 cm (H) and a resolution of 1280 by 1024 pixels, yielding a resolution of 31.5 pixels/degree of visual angle (dva). The monitor refresh rate was 85 Hz for monkey 1, and 75 Hz for monkey 2. The output of the red and green guns was combined using a Pelli-Zhang

video attenuator, yielding a luminance resolution of 12 bits/pixel, allowing the presentation of contrasts that were well below contrast discrimination thresholds (Pelli, 1991). A gamma correction was used to linearize the monitor output.

Contrast discrimination task paradigm

Monkeys were engaged in a contrast discrimination task, in which the presentation of a sample stimulus was followed by that of a test stimulus. They had to decide whether the contrast of the test stimulus was higher or lower than that of the sample stimulus (see Figure 1 for an illustration of the task).

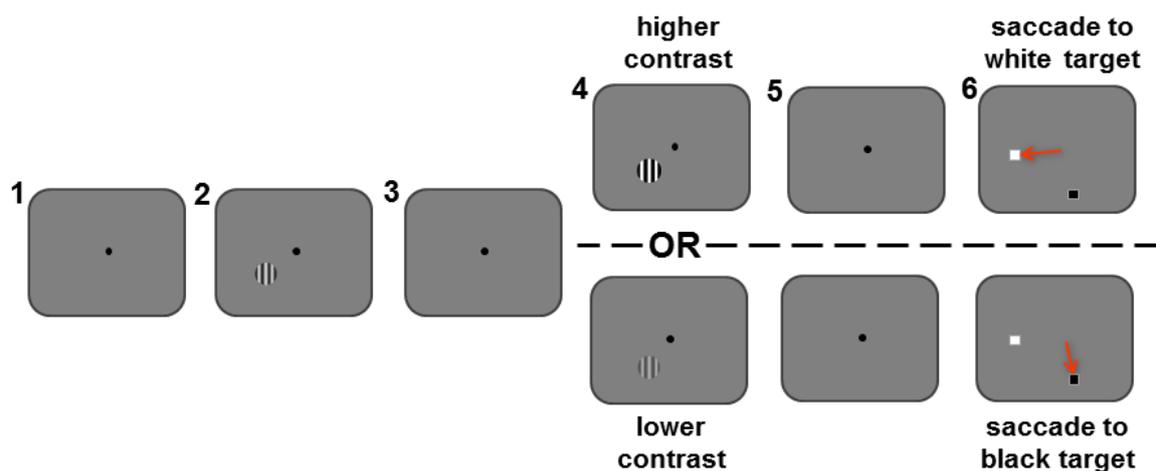


Figure 1. Illustration of the contrast discrimination task. 1) The monkeys were required to fixate upon a central spot, to initiate the trial. 2) While maintaining fixation, a sample stimulus of 30% contrast (either a Gabor patch or a sinusoidal grating) was presented for 512 ms. 3) Presentation of the sample stimulus was followed by an interval lasting 512 ms (except during training at the peripheral location for monkey 1, where the interval lasted for a random duration of 512 to 1024 ms). 4) Next, the test stimulus (another Gabor patch or sinusoidal grating which could be of higher or lower contrast than the sample), was presented for 512 ms, 5) followed by a second interval of 400 ms. 6) Two target stimuli appeared to the left and

right of the location at which the sample and test had previously been presented; the fixation spot changed colour from black to grey, signalling that the animals were allowed to make a saccade to their chosen target. If the test was of a higher contrast (e.g. 32%) than the sample (always 30%), the monkeys had to saccade to the white target; otherwise, if the test stimulus was of a lower contrast (e.g. 28%), they had to saccade to the black target. The red arrows in the figure indicate the direction of saccadic motion for illustrative purposes only; they did not appear onscreen.

Stages of training on the main contrast discrimination task

The performance of the two subjects (monkeys 1 and 2) in the main contrast discrimination task was assessed over 52 and 53 sessions respectively. This was carried out in three stages (Stages 1 to 3), with stimuli positioned peripherally during the first and third stages, and parafoveally during the second stage, as described below. Properties of the stimuli used throughout each stage of training are listed in Table 1.

Stage 1: Training with Gabor stimuli at a peripheral location

Subjects performed the task with a Gabor stimulus, for several weeks (monkey 1: 30 sessions, spanning a period of 8 weeks; monkey 2: 26 sessions, spanning 6 weeks), until their performance reached a plateau. The sample stimulus had a contrast of 30%, while the test stimulus was presented at one of 14 possible contrasts [10, 15, 20, 25, 27, 28, 29, 31, 32, 33, 35, 40, 50, and 60%].

Property	Monkey 1			Monkey 2		
	Stage 1	Stage 2	Stage 3	Stage 1	Stage 2	Stage 3
No. of sessions	30	17	5	26	22	5
Location	peripheral	parafoveal	peripheral	peripheral	parafoveal	peripheral
Coordinates of centre (dva)	(-5, -16)	(-3.5, -3)	(-5, -16)	(-5, -16)	(-0.7, -1.3)	(-5, -16)
Size (dva)	16	3	16	14	0.75	14
SF (cpd)	2	2	2	2	4	2
Orientation	vertical for all sessions but the last	vertical	vertical	vertical for all sessions but the last	vertical	vertical
Stimulus type	Gabor	sinusoidal grating	sinusoidal grating	Gabor	sinusoidal grating	sinusoidal grating

Table 1. Stimulus parameters used at each stage of contrast discrimination training.

At the end of training with a peripherally located Gabor stimulus, we carried out an additional session during which the Gabor stimuli were horizontally, rather than vertically, oriented. This was to determine whether perceptual improvements would transfer to stimuli of an orthogonal orientation.

Stage 2: Training with sinusoidal grating stimuli at a parafoveal location

Following training at the peripheral location, monkeys were trained to discriminate contrasts at a parafoveal location. The stimulus diameter was reduced from 16 to 3 dva in monkey 1 and from 14 to 0.75 dva in monkey 2. The sample stimulus had a contrast of 30%, while the test stimulus was presented at one of fourteen possible contrasts [5, 10, 15, 20, 22, 25, 28, 32, 35, 40, 45, 50, 60, and 90%].

In addition, a sinusoidal grating stimulus was used, instead of a Gabor. This was because the perceived size of a Gabor changes with its peak contrast, such that a low-contrast

Gabor seems smaller than a high-contrast one (Foley & Legge, 1981; Fredericksen, Bex, & Verstraten, 1997; Polat, 1999). Data were collected over 4-6 weeks (monkey 1: 17 sessions; monkey 2: 22 sessions).

Stage 3: Training with sinusoidal grating stimuli at a peripheral location

To examine the effects of apparent size on task performance, we carried out a control experiment at peripheral visual field locations, in which we used sinusoidal grating stimuli, instead of Gabor patches. This control was carried out for 5 sessions (1 week) for each of the subjects. As with the training carried out in Stage 1, the sample stimulus had a contrast of 30%, while the test stimulus was presented at one of fourteen possible contrasts [10, 15, 20, 25, 27, 28, 29, 31, 32, 33, 35, 40, 50, and 60%].

Measures of perceptual learning

To investigate the effects of perceptual learning, several metrics of performance were monitored over the course of training: the proportion of correct responses made by the subjects; the slope and the point of subjective equality (PSE) of the psychometric function; the psychometric threshold, and the rate of learning for different contrasts.

The proportion of trials in which subjects made correct responses was calculated for each test contrast condition, yielding fourteen values of the contrast-dependent proportion of correct trials ($P_{condition}$) per session. The average performance for each session ($P_{session}$) was simply the mean across these fourteen values of $P_{condition}$ and provided a broad overview of the subjects' daily performance across test contrast conditions.

From $P_{condition}$, we could calculate $P_{reporhigher}$, which was the proportion of trials in which subjects reported the test contrast as being higher than the sample contrast. A Weibull

function was fitted to values of $P_{report\ higher}$ using a maximum likelihood estimates method (Matlab, Mathworks), thus generating a psychometric curve for each session. The Weibull function was defined as

$$F_{\alpha,\beta}(x) = \delta - \gamma e^{-\left(\frac{x}{\alpha}\right)^\beta} \quad \dots (1)$$

where $F_{\alpha,\beta}(x)$ is the fitted value of $P_{report\ higher}$; x is the contrast of the test stimulus; γ is the range, δ is the maximum value, and α is the contrast at which $F_{\alpha,\beta}(x)$ reaches 63.2% of its maximum, which is occasionally used as a threshold measure when $F_{\alpha,\beta}(x)$ ranges from 0 to 1. In cases where $F_{\alpha,\beta}(x)$ does not range from 0 to 1 because γ and δ are free parameters, it should not be considered to be a threshold, but simply corresponds to $F_{\alpha,\beta}(x)$ when $x = \alpha$. Finally, β is the slope of the psychometric curve at $x = \alpha$.

While the above equation yielded a slope for the contrast at $x = \alpha$, this value did not necessarily provide an accurate representation of perceptual sensitivity at the most interesting and task-relevant part of the psychometric curve, i.e. close to contrasts of 30%. We therefore also determined the slope of the psychometric function at the point where the contrast was 30% (hereafter referred to simply as the ‘slope’). This was calculated by finding the tangent to the fitted curve at the point $x = 30\%$, according to the formula

$$slope = \frac{dF}{dx} \left[\delta - \gamma e^{-\left(\frac{30}{\alpha}\right)^\beta} \right] = 30^{\beta-1} \beta \gamma e^{-\left(\frac{30}{\alpha}\right)^\beta} \left(\frac{1}{\alpha}\right)^\beta \quad \dots (2)$$

Finally, we determined the PSE of the psychometric function, which indicated the contrast at which the subject reported the test stimulus as being indistinguishable from the sample. The PSE was calculated by finding the contrast at which the value $F_{\alpha,\beta}(x)$ of the fitted function was equal to 0.5. For a perfect observer, the value of the PSE would lie at

exactly 30%; in our subjects, any deviation in the PSE from the value of 30% indicated a bias in their criterion level.

To monitor changes in performance that occurred for each individual condition, values of $P_{report\ higher}$ were plotted against session number. An exponential curve was fit to the data for each test contrast condition, according to the formula

$$y = 0.5 - a + a[e^{-x}]^b \quad \dots (3)$$

where y is the fitted proportion of trials during which the subject reported the contrast of the test as being higher than that of the sample, x is the session number, and a and b are freely varying parameters with the bounds $-\infty \leq a \leq \infty$ and $0 \leq b \leq 1$.

Contrast-dependent variations in discriminative abilities

According to the threshold versus contrast (TvC) function in humans, for base contrasts above detection threshold, the size of the just-noticeable difference (JND) in luminance contrast between a stimulus and its increment depends on the absolute values of the contrasts being compared (Legge & Foley, 1980; Tsodyks, Adini, & Sagi, 2004; Wilson, 1980), in a manner similar to that predicted by the Weber-Fechner law (Fechner, 1860; Green & Swets, 1966; Weber, 1850). Accordingly, conditions with a lower-contrast test stimulus should yield smaller JNDs than conditions with a higher-contrast test stimulus.

To address this possibility, we separated the conditions into two ‘test contrast categories,’ where the test contrast was (a) higher or (b) lower than the sample contrast (termed groups C_H and C_L , respectively). These values were plotted against the absolute difference between the sample and test contrasts, and a Weibull curve was fitted to the data in each category, according to the formula

$$G_{\alpha,\beta,\lambda}(|\Delta C|) = 0.5 + (0.5 - \lambda)(1 - e^{-\left(\frac{|\Delta C|}{\alpha}\right)^\beta}) \quad \dots (4)$$

where $G_{\alpha,\beta,\lambda}(|\Delta C|)$ is the fitted value of $P_{session}$ with the bounds $0.5 \leq G_{\alpha,\beta,\lambda}(|\Delta C|) \leq \max(P_{session})$; $|\Delta C|$ is the absolute difference between the sample and test contrasts; α is the threshold (yielding two thresholds, T_L and T_H , for conditions where the contrast of the test stimulus was lower and those where it was higher, respectively); β is the slope with the bounds $0 \leq \beta \leq 5$; and λ is the proportion of erroneous responses for the condition which gave the highest value of $|\Delta C|$ during a given session (set separately for each of the groups C_H and C_L).

Inclusion of the parameter λ in equation 4 was based on the assumption that task performance depended on two distinct skills: 1) An understanding of the task contingencies (i.e. to comprehend that the basic requirement of the task was to make a comparison between the stimuli- a skill which can occur through associative learning and which may depend on levels of attention). 2) The ability to perform the task at a fine level (i.e. to make accurate discriminations in contrast). During early training sessions, learning would be expected to occur primarily at an associational level. Once subjects had learnt the underlying principles of the task, then refinements in perception were likely to occur at a more specific level (Ahissar & Hochstein, 2004).

In order to distinguish between these two types of task learning, we assumed that engagement of the latter skill was essentially absent for the easiest task condition, due to the large difference in contrast between the stimuli. Changes in performance for this particular condition over the course of training would thus be attributable to improvements of contingency/associational relationships between the task stimuli and the reward, while poor performance for these conditions during later stages of training would likely be due to

attentional lapses or saccade direction errors. Thus, inclusion of this model parameter enabled the examination of fine contrast discrimination learning, independent of conceptual task learning and of daily or trial-wise fluctuations in attention (Law & Gold, 2008).

Note that the inclusion of two fitting procedures (in equations 1 and 4) allowed us to monitor distinct measures of perceptual learning: equation 1 was fitted across data from all the test contrast conditions, yielding measurements of the slope and PSE (and thus the amount of bias in the decision criterion), while equation 4 was fitted to two sets of data, yielding upper and lower threshold values.

Reaction times

The monkeys' reaction time (RT) was defined as the time taken by the subjects to make a saccade to the target, from the moment that the fixation spot changed colour. A Pearson's correlation analysis was performed separately for RTs on correct and incorrect trials, to determine whether RTs were correlated with session number.

Corrections for multiple comparisons

For all tests of significance that involved multiple comparisons, a False Discovery Rate (FDR) correction for α -levels was applied where appropriate, to reduce the likelihood of making either too many false positives or too many incorrect rejections (Benjamini & Hochberg, 1995). This procedure yielded a ' q -value,' which acted as an FDR analogue to the p -value.

Results

Perceptual learning with stimuli at peripheral and parafoveal locations

Performance during trials with variable interval durations

For monkey 1, when stimuli were presented at a peripheral location, the duration of the blank interval between the presentation of sample and test stimuli was a randomly chosen value from 512 to 1024 ms. To examine whether interval duration had any effect on the monkey's performance, trials were categorised based on interval length (two groups: first versus last quarter of interval length). No significant main effect of trial duration was observed (three-way ANOVA, $F(3,819) = 2.03$, $p = .108$) and there was no interaction between trial duration and the other factors (trial duration \times test contrast: $F(39,819) = 0.93$, $p = .588$; trial duration \times session: $F(84,819) = 0.85$, $p = .822$). Thus, Stage 1 data from this subject were combined with the rest of the data for subsequent analyses.

Perceptual learning for individual test contrast conditions

To investigate whether learning rates differed between test contrast conditions, performance was plotted separately for each condition. The measure of performance used, $P_{report\ higher}$, was the proportion of trials in which the subject reported that the test contrast was higher than that of the sample. A visual inspection revealed that for the easier conditions, performance increased relatively quickly and reached a plateau within a few sessions, whereas for harder conditions, performance levels rose more gradually over a longer period of time (Figures 2A & 2B: peripheral location; 2C & 2D: parafoveal location).

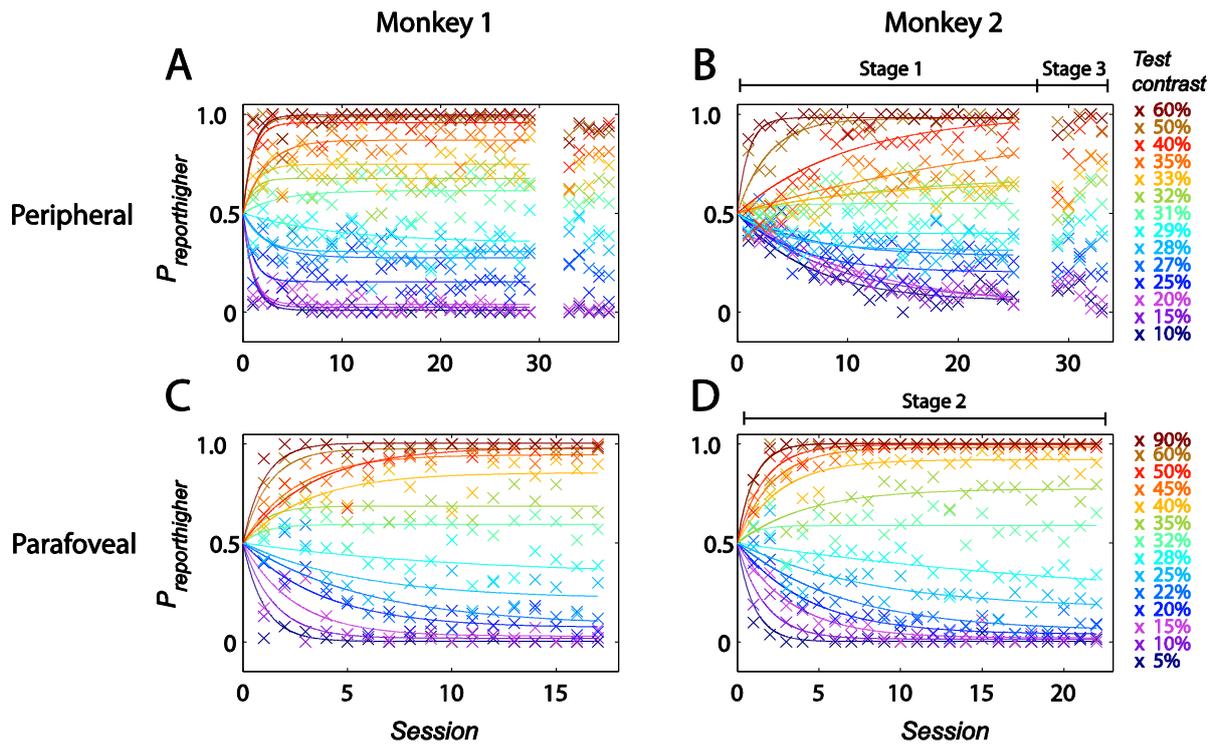


Figure 2. Proportion of trials during which the contrast of the test stimulus was reported to be higher than that of the sample, plotted against session, for each test contrast condition (coded by colour). Left column: monkey 1; right column: monkey 2. Upper row: peripheral location (Stage 1, followed by five data points from Stage 3); lower row: parafoveal location (Stage 2). 'X' markers correspond to measured data, while lines depict the best-fit exponential curves.

A comparison of the adjusted R^2 error values generated by model predictions from an exponential fit versus those from a linear fit showed that an exponential function yielded a better fit to the data in the majority of cases [$R^2_{\text{exponential}} > R^2_{\text{linear}}$ in 39 out of 56 comparisons; $39/56 = 70\%$], thus an exponential function was used. The value of coefficient a from the best-fit exponential function provided a measure of the rate of learning for each test contrast condition, allowing a comparison to be made between learning rate and task difficulty.

Values of a were plotted against the absolute differences between test and sample stimulus contrasts (Figure 3), for two sets of conditions- those where the contrast of the test

stimulus was lower than that of the sample (C_L), and those where the contrast of the test stimulus was higher than that of the sample (C_H). For easy conditions (i.e. when the difference between sample and test contrasts was large), values of a tended to be high, indicating that gains in performance occurred rapidly. For difficult conditions (i.e. when the contrast difference was small), values of a were relatively low. Thus, the finer the contrast discrimination required, the longer subjects took to improve.

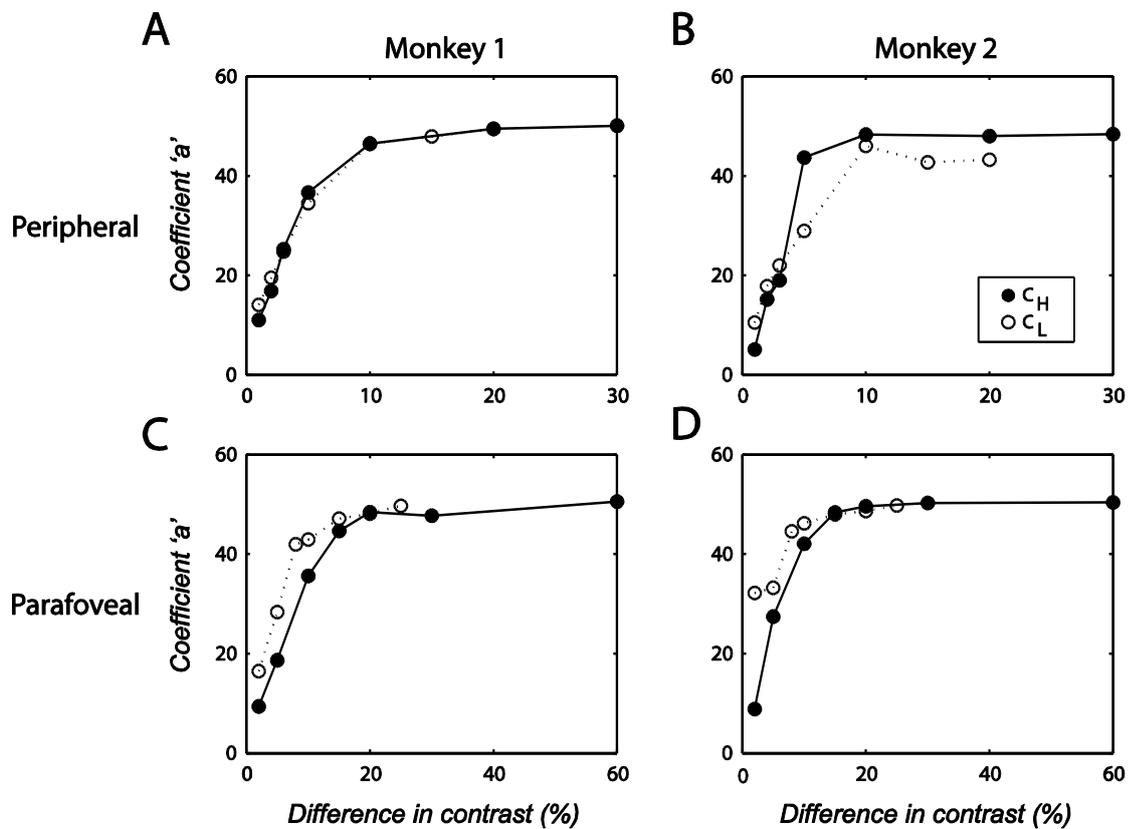


Figure 3. Plots of coefficient a (generated from the fitting of an exponential curve to graphs of $P_{report\ higher}$ against session number, as shown in Figure 2), against the absolute difference in contrast between test and sample stimuli, for C_L and C_H conditions. Upper row: peripheral location (Stage 1); lower row: parafoveal location (Stage 2). Left column: monkey 1; right column: monkey 2. Unfilled markers: C_L conditions (the test stimulus was of a lower contrast than the sample); filled markers: C_H conditions (the test stimulus was of a higher contrast than the sample).

Perceptual learning across all fourteen test contrast conditions

Performance was assessed across all fourteen test contrast conditions, using three measures for each session: 1) the mean proportion of correct responses, 2) the slope of the psychometric curve at 30% contrast, and 3) the PSE of the psychometric curve (Figures 4A, 4B & 4C: peripheral location; 4D, 4E & 4F: parafoveal location).

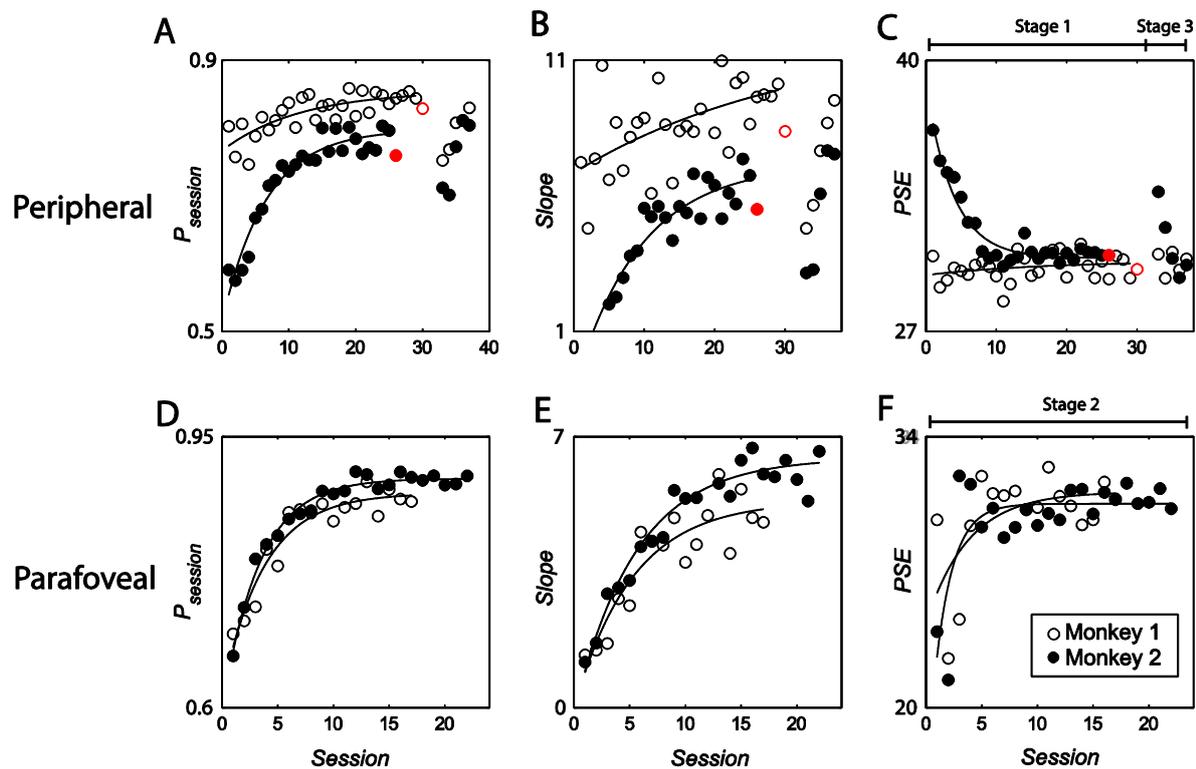


Figure 4. Performance in the contrast discrimination task over the course of training. Left column: proportion of correct responses ($P_{session}$); middle column: slope of the psychometric function (corresponding to the derivative at 30% contrast); right column: PSE. Upper row: peripheral location (Stage 1, followed by five data points from Stage 3); lower row: parafoveal location (Stage 2). Unfilled dots: monkey 1; filled dots: monkey 2. Black markers: vertically-oriented stimuli; red markers: horizontally-oriented stimuli. Black lines depict the best-fit exponential curves. Test contrasts used in Stages 1 and 3 were identical.

Mean task performance, M , was compared between the first and last 30% of sessions (M_{early} and M_{late}) within each stage. For both subjects and both stimulus locations, the proportion of correct trials (P_{session}) and the slope were significantly higher for later sessions, compared with earlier ones (monkey 1, slope at the peripheral location: $t(8) = -4.68$, $q = .00184$; P_{session} at the peripheral location: $t(8) = -6.34$, $q < .001$; slope at the parafoveal location: $t(6) = -4.67$, $q < .001$; P_{session} at the parafoveal location: $t(6) = -7.78$, $q < .001$; monkey 2, slope at the peripheral location: $t(6) = -13.3$, $q < .001$; P_{session} at the peripheral location: $t(6) = -7.78$, $q < .001$; slope at the parafoveal location: $t(5) = -7.45$, $q < .001$; P_{session} at the parafoveal location: $t(5) = -4.20$, $q = .00163$, $\alpha = .05/12*9 = .0375$, FDR corrected, unpaired two-sample t -test).

In monkey 1, the PSE did not change with training (peripheral location: $t(8) = -0.96$, $q = .377$; parafoveal location: $t(6) = 5.32$, $q = .162$). This was likely due to a ceiling effect, as the PSE had shifted rapidly towards 30% within the first few training sessions, leaving little room for subsequent improvement. This trend was also observed for monkey 2, for training undertaken with parafoveally-located stimuli ($t(5) = -1.44$, $q = .154$). However, when stimuli were located peripherally for monkey 2, the PSE was relatively high ($M_{\text{early}} = 34.1\%$) during early sessions, and it shifted towards 30% over the course of training, reaching a mean value of 30.7% during late sessions ($t(6) = 5.19$, $q < .001$, unpaired two-sample t -test).

Psychometric thresholds for conditions with higher or lower test contrasts

The curve fitting allowed us to examine the effects of two distinct types of learning on performance, in which the parameter λ represents the associational/ attention-based component of learning (also sometimes termed the ‘finger error’ in studies where human subjects indicate their response through keyboard presses), while changes in the slope and threshold represent genuine perceptual learning.

Changes in the value of λ with training can be seen in Figure 2, by examining changes in $P_{reporhigher}$ for the conditions with the highest (dark brown markers) and lowest (dark purple markers) test contrasts, respectively. When stimuli were presented at the peripheral location for either monkey, the value of λ was large during early training sessions, and the number of erroneous responses decreased over the course of training, eventually reaching values of around zero (Spearman's correlation, monkey 1, C_L condition: $r(27) = -.582$, $q < .001$; C_H condition: $r(27) = .476$, $q = .0091$; monkey 2, C_L condition: $r(23) = -.755$, $q < .001$; C_H condition: $r(23) = .439$, $q = .0283$). At the parafoveal location, the value of λ tended to already be very small at the start of the training sessions, thus it only changed significantly for 1/4 comparisons (monkey 1, C_L condition: $r(17) = -.615$, $q = .0087$; C_H condition: $r(17) = .307$, $q = .230$; monkey 2, C_L condition: $r(5) = -.600$, $q = .350$; C_H condition: $r(5) = .700$, $q = .233$, FDR correction, $\alpha = .05/8*5 = .0313$).

Psychometric thresholds (T_L and T_H for the C_L and C_H test contrast conditions, respectively) are shown in Figure 5. A Spearman's rank correlation analysis was carried out between threshold and session number, to identify changes in threshold over time. Significant decreases in upper and lower thresholds were observed in all comparisons but one (Spearman's rank correlation, monkey 1, peripheral location, lower threshold: $r(27) = -.418$, $q = .0248$, higher threshold: $r(27) = -.420$, $q = .0243$; parafoveal location, lower threshold: $r(15) = -.600$, $q = .0124$, higher threshold: $r(15) = -.811$, $q < .001$; monkey 2, peripheral location, higher threshold: $r(23) = -.758$, $q < .001$; parafoveal location, lower threshold: $r(20) = -.874$, $q < .001$, higher threshold: $r(20) = -.582$, $q = .00522$, FDR correction for multiple comparisons: $\alpha = .05 \times 7/8 = .0438$). The only exception was for monkey 2 during training at the peripheral location- in this case, no significant change in the lower threshold was observed (Spearman's rank correlation, $r(23) = -.175$, $q = .400$).

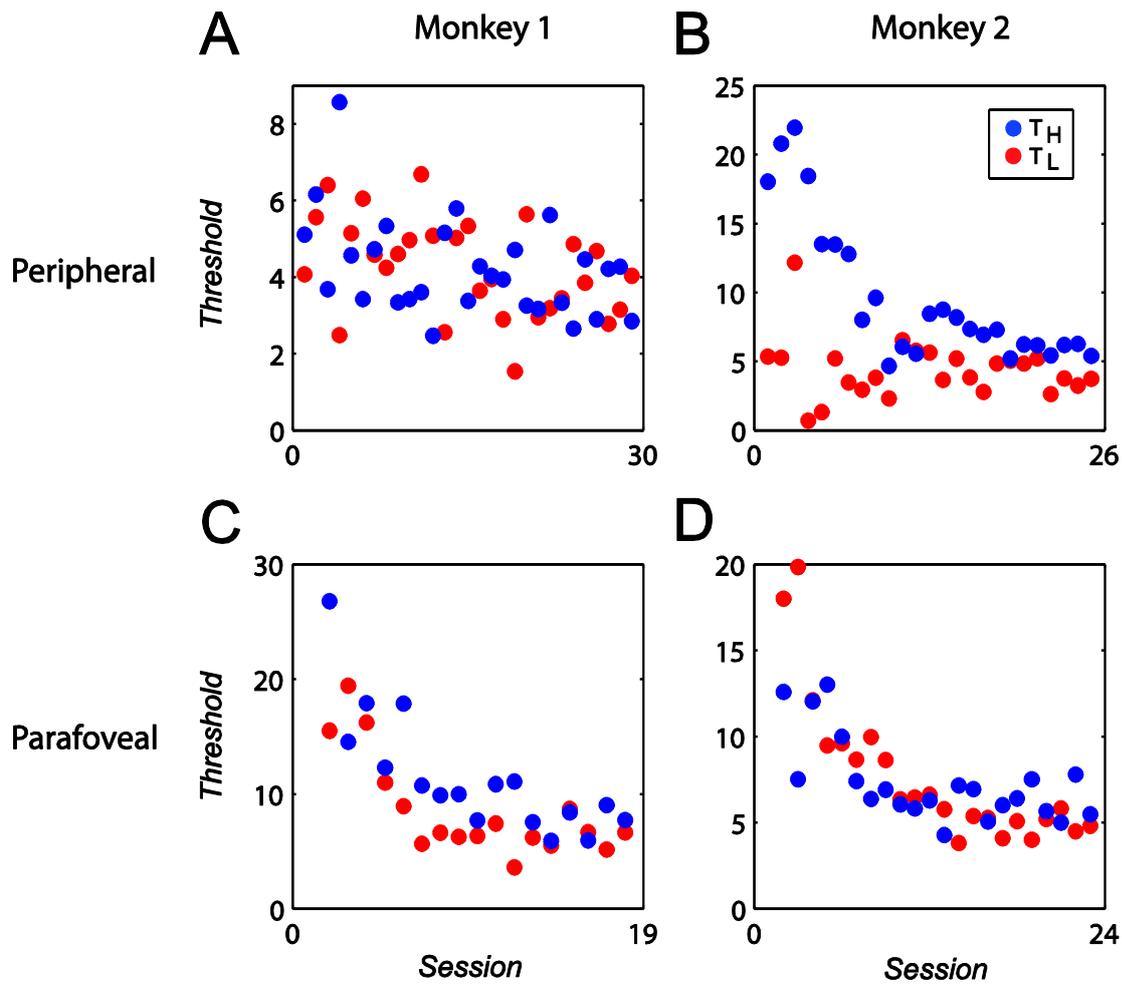


Figure 5: Psychometric thresholds T_L and T_H as a function of training session. Left column: monkey 1; right column: monkey 2. Upper row: peripheral location; lower row: parafoveal location. Red markers: C_L conditions (the test contrast was lower than that of the sample); blue markers: C_H conditions (the test contrast was higher than that of the sample). Significant decreases in T_H and T_L were observed in both monkeys at both locations, in 7/8 comparisons.

Next, to investigate whether condition-dependent threshold differences might be affected by the stage of training, a four-way repeated measures ANOVA was performed with condition type (T_L or T_H) as the within-session variable, and the training phase (first or second half of training sessions); subject (monkey 1 or 2); and area of stimulus presentation (peripheral or parafoveal) as the between-sessions variables. A significant main effect of

condition type was observed ($F(1,185) = 18.6, p < .001$), and a post hoc analysis revealed that threshold values were significantly higher for low than for high test contrast conditions (T_L : $M = 6.2, SE = 0.3, 95\% CI = [5.8, 6.6]$; T_H : $M = 8.1, SE = 0.3, 95\% CI = [7.7, 8.5]$).

Note that the threshold measure used here was not the test contrast at which the subjects' performance reached a particular level of performance (e.g. 81.6% correct); rather, it was simply the value of the α parameter in the fitted function to the psychophysical data. Given the inclusion of the parameter λ in the fitted function, it could be argued that α is not an accurate reflection of the threshold (i.e. a specific level of performance). We therefore repeated the analysis using the test contrast at which the subjects' performance would be at 81.6% correct (Green & Swets, 1966; Thiele, Dobkins, & Albright, 2000); results were qualitatively similar between the two measures of threshold.

Perceptual learning within individual sessions

Learning was observed across multiple sessions; could changes be detected within shorter periods of time, such as that spanned by an individual session? To investigate this, we examined the first and last 30% of trials in a given session (termed 'beginning' and 'end' trials, respectively). The proportion of correct trials, the slope of the psychometric function, and the PSE were calculated separately for these two groups of trials. In both subjects, the proportion of correct trials was significantly higher for the last 30% than for the first 30% of trials, for training undertaken at the parafoveal location (Table 2, paired t -test).

Monkey	Location	$P_{session}$			Slope			PSE		
		t	df	q	t	df	q	t	df	q
1	peripheral	-1.57	28	.129	-0.01	28	.993	1.42	28	.165
	parafoveal	-4.52	16	< .001*	-2.68	16	.0166	-1.33	16	.201
2	peripheral	1.53	24	.14	1.04	24	.308	-2.32	24	.0295
	parafoveal	-4.2	21	< .001*	-2.13	21	.0452	0.395	21	.697

* $q < \alpha$

Table 2. Differences in performance within individual sessions. For both subjects, when performance was compared between the first and last 30% of trials, the proportion of correct responses was significantly higher towards the later part of each session, for stimuli at the parafoveal location (paired t -test, FDR correction for α -levels, proportion correct: $\alpha = .05 \times 2/4 = .025$; slope: $\alpha = .05 \times 1/4 = .0125$; PSE: $\alpha = .05 \times 1/4 = .0125$).

The improvements in performance seen within sessions, for training at the parafoveal location, might have been due to a trade-off between speed and accuracy- the animals might have made faster responses at the beginning of each session out of impatience to receive their reward, and then slowed down as they grew satiated. To test this possibility, we compared subjects' reaction times (RTs) between the first and last 30% of trials in each session ($RT_{beginning30}$ and RT_{end30} , respectively), for each of the training locations. When stimuli were placed in the parafoveal location, RTs did not differ significantly between the beginning and end of each session, for either subject (monkey 1: $t(16) = -0.0112$, $p = .991$; monkey 2: $t(21) = 1.21$, $p = .242$, paired t -test). Thus, the within-session improvements in performance that were observed when stimuli were in the parafoveal location were not due to a speed-accuracy trade-off.

When stimuli were placed in the peripheral location, RTs were significantly longer at the end of each session, compared to at the beginning, for monkey 1, whereas they were significantly shorter at the end of each session, for monkey 2 (monkey 1: $t(28) = 2.03$, $p =$

.0414; monkey 2: $t(24) = -6.60$, $p < .001$, paired t -test). Thus, the lack of improvement observed at peripheral locations over the course of individual sessions could not be attributed to a speed-accuracy trade-off either.

Control task with horizontally-oriented Gabor stimuli at a peripheral location

To determine whether contrast discrimination levels remained the same if the stimulus orientation was altered, horizontal Gabor stimuli were presented during a single control session (indicated by red markers in each of the upper subplots in Figure 4).

By and large, the change from vertical to horizontal Gabors did not have much effect on the monkeys' performance during the control session (X_h), indicating that learning was not specific to stimulus orientation (see Table 3).

Performance	Monkey 1			Monkey 2		
	Late Stage 1 sessions, range $X_{\min} - X_{\max}$	Horizontal Gabor session, X_h	Last vertical grating session, X_g	Late Stage 1 sessions, range $X_{\min} - X_{\max}$	Horizontal Gabor session, X_h	Last vertical grating session, X_g
P_{session}	0.823-0.854	0.829	0.83	0.762-0.803	0.759	0.804
Slope	7.6-11.0	8.4	9.5	5.2-7.4	5.5	7.5
PSE	29.5-31.2	30.0	30.5	30.3-31.0	30.6	30.2
RT_{correct}	146-166	149	166	149-164	167	155
RT_{error}	153-179	156	196	154-172	174	156

Table 3. Comparison of subjects' performance during control sessions, against that seen at the end of Stage 1. $X_{\min} - X_{\max}$: Ranges of performance seen during late Stage 1 sessions, in which vertically-oriented Gabor stimuli were presented. X_h : Performance recorded during the single session in which horizontally-oriented Gabor stimuli were presented. X_g : Performance recorded during the last of the Stage 3 sessions, in which vertically-oriented grating stimuli were presented. Stimuli were located at the peripheral location during all of these sessions.

Control task with sinusoidal grating stimuli at a peripheral location

Stage 3 consisted of five consecutive sessions in which subjects practised a contrast discrimination task with vertically-oriented sinusoidal gratings at the peripheral location, allowing us to estimate the extent to which subjects had relied on cues from the perceived size of the stimulus, to carry out the task. We expected the subjects' performance during the first few sessions of Stage 3 to be relatively poor as stimulus locations had just been switched from the parafoveal location back to the peripheral location. Thus, our analysis focused on data that was obtained from the last of these five sessions.

For the most part, subjects' performance during this session (X_g) fell within the ranges of values seen during the late phase of Stage 1 (Table 3).

Thus, the monkeys' ability to discriminate contrast levels was largely comparable between sessions with Gabor and sinusoidal grating stimuli, indicating that our subjects had relied primarily on contrast differences, rather than on perceived differences in stimulus size, to complete the task.

Control task with stimuli of different spatial frequencies at a parafoveal location

After extensive training on the contrast discrimination task, an additional control experiment was carried out with monkey 2 over two testing sessions, in which sinusoidal grating stimuli of two different spatial frequencies were positioned at the parafoveal location. The SF of the stimuli varied randomly from trial to trial. This allowed us to assess the degree to which learning on the contrast discrimination task transferred from the trained SF (4 cpd) to an untrained SF (2 cpd). Stimulus parameters and contrast levels remained otherwise identical to those used during training at the parafoveal location.

When the SF differed from that used during previous training sessions, performance was worse- the proportion of correct trials was lower, and the PSE lay further away from the sample contrast (first session, SF 4: $P_{session} = 0.86$, slope = 5.2, PSE = 25.3; SF 2: $P_{session} = 0.75$, slope = 2.5, PSE = 37.1; second session: SF 4: $P_{session} = 0.89$, slope = 6.2, PSE = 28.1; SF 2: $P_{session} = 0.81$, slope = 3.0, PSE = 32.4).

Thus, task performance was consistently better when the spatial frequency was the same as that used throughout prior training (at 4 cycles per degree), than when it was altered (to 2 cpd).

Control task with only the test, not the sample stimulus, at a parafoveal location

Finally, a single testing session was carried out with monkey 2, to determine how well the monkey performed in the absence of an external reference stimulus. The test stimulus was presented at a parafoveal location as before, while the sample was omitted. The monkey was not explicitly instructed on how to perform the task in the absence of the sample stimulus. However, assignation of correct and incorrect targets remained the same, and the monkey was thus provided with continuous feedback regarding his choices.

Performance in terms of the mean proportion of correct trials and the slope of the psychometric function was poorer in the absence of the sample stimulus, when compared to that attained on preceding days in the presence of the sample (performance in the absence of a sample: $P_{session} = 0.78$, slope = 2.5).

Importantly, however, the PSE of the psychometric function was 30.9%, i.e. still very close to the sample contrast. This indicated that the subject was able to perform the task based on an internalised contrast reference of 30%.

Reaction times

For each session, mean RTs were calculated separately for correct and incorrect trials, across all 14 test contrast conditions. RTs decreased significantly with training in monkey 1, at both the peripheral and the parafoveal locations, for correct as well as for incorrect trials (Pearson's correlation coefficient, peripheral location, correct trials: $r(27) = -.968$, $q < .001$, incorrect trials: $r(27) = -.905$, $q < .001$; parafoveal location, correct trials: $r(15) = -.846$, $q < .001$, incorrect trials: $r(15) = -.796$, $q < .001$). For monkey 2, significant reductions in RT occurred during training at the peripheral location for correct and incorrect trials (Pearson's correlation coefficient, correct trials: $r(23) = -.715$, $q < .001$, incorrect trials: $r(23) = -.648$, $q < .001$), as well as at the parafoveal location for incorrect trials ($r(15) = -.409$, $q = .0241$), while a trend (non-significant) towards a decrease in RT was seen at the parafoveal location for correct trials ($r(15) = -.479$, $q = .059$).

Discussion

We make frequent evaluations of subtle contrast differences in our visual environment, and often under challenging illumination conditions, whether photopic, scotopic or mesopic. Our contrast discrimination abilities are rigorously honed from an early age, and we continue to carry out these fine perceptual judgments throughout our lifetimes. Thus, the issue of whether substantial improvement in contrast discrimination is possible during later periods in life, such as during adulthood- and the circumstances that allow this- has sometimes come under discussion (Adini et al., 2002; Dorais & Sagi, 1997; Phan & Ni, 2011; Polat, Ma-Naim, Belkin, & Sagi, 2004; Yu et al., 2004).

Our adult macaque subjects underwent extensive training on a contrast discrimination task, in which stimuli were positioned at a variety of peripheral and parafoveal locations. We

observed substantial improvements in our subjects' psychophysical performance, which included higher success rates in their responses, steepening of their psychometric functions, and shifts in the point of subjective equality towards the contrast of the sample stimulus. Significant progress was often observed across training sessions that spanned several weeks; it also took place within the time frame of individual sessions which lasted just a few hours.

Thus, our study demonstrates that perceptual learning can occur during adulthood for contrast discrimination tasks, thereby complementing studies which have documented similar effects of learning in humans with normal vision (Adini et al., 2004; Kuai et al., 2005; Phan & Ni, 2011; Xiao et al., 2008; Yu et al., 2004; Zhang et al., 2008; Zhang et al., 2010). Previous studies presented subjects with Gabor patches during the task, raising the concern that subjects may have used the perceived size of stimuli as a secondary cue. We addressed this issue by presenting our monkeys with grating stimuli during a series of control sessions, and thus verified that their perceptual improvements were attributable to differences in stimulus contrast rather than to differences in perceived stimulus size.

In addition, we considered the possibility that other types of nonlinearities within the nervous system (such as those seen in the transducer function) might have aided our subjects' task performance. In two-alternative-forced-choice (2AFC) tasks involving contrast discriminations by human subjects, the relationship between pedestal contrast and threshold is widely known to take on a 'dipper' shape, which may be characterised by two features: an accelerating nonlinearity at low contrasts (around detection threshold, i.e. below our lowest test contrast of 5%); and a compressing nonlinearity for higher contrasts (Campbell & Kulikowski, 1966; Foley & Legge, 1981; Legge & Foley, 1980). As our task involved solely suprathreshold stimulus contrasts (5% to 90%), the former nonlinearity was unlikely to have affected our subjects' discrimination performance. As for the compressive nonlinearity, this

might potentially have contributed to an asymmetry between the discrimination of increments and decrements (i.e. higher and lower test contrasts than sample contrasts); however, this factor would not have provided the animals with additional cues for carrying out the task.

When we examined performance levels for individual test contrast levels, we found (unsurprisingly) that the more difficult the discriminations required, the longer it generally took for subjects to improve. In order to distinguish between changes that accompanied the learning of coarse contrast discriminations as opposed to fine ones, we adopted a curve-fitting procedure that included a term, λ , which described the error incurred during easy task conditions (Law & Gold, 2008). The value of λ was allowed to vary between sessions, and thereby accommodated potential differences in the rates of acquisition of broad and narrow perceptual skills. We found that the learning of associational/attention-based aspects of the task occurred predominantly during the early stages of training, whereas the acquisition of fine contrast discrimination abilities was more gradual and prolonged. For the hardest conditions, involving contrasts differences of just 1% to 2%, extensive training yielded maximum levels of accuracy in the range of 0.6 to 0.7 in both of our monkeys. The separation of learning into these distinct components provided clear evidence that improvements were not mere indications of basic task learning, but were also driven by enhancements in perceptual sensitivity.

How do these two ‘fast’ and ‘slow’ modes of learning- identifiable through psychophysical measurements- come about? A candidate theory, termed the ‘reverse hierarchy of perceptual learning,’ provides a model of how distinct learning pathways might be implemented in the brain (Ahissar & Hochstein, 2004; Ahissar, Nahum, Nelken, & Hochstein, 2009; Hochstein & Ahissar, 2002). It proposes that when naïve, untrained performers first engage in a task, initial reorganisation occurs at higher cortical regions, and

that this state of plasticity contributes to the acquisition of broad perceptual skills, which are transferable across a variety of related tasks. With continued practice, changes propagate downwards, towards lower-level neuronal populations in the visual hierarchy. Gradually, areas that are responsible for making relatively fine perceptual distinctions become ‘wired up’ more efficiently. An alternative line of reasoning argues that changes in lower-level cortical regions are relatively minimal, and that adjustments occur predominantly via improvements in the ‘reading out’ of information that is conducted by higher-level areas (Garrigan & Kellman, 2008; Mollon & Danilova, 1996; Petrov, Doshier, & Lu, 2005).

In relation to our findings, several key questions emerge: Firstly, how is perceptual learning of contrast discrimination mediated in different visual areas? In our task, for example, when subjects were trained to make comparisons between stimuli of around 30% contrast, were their behavioural improvements attributable to changes in neuronal properties at the level of V1 and V2 (Bao, Yang, Rios, He, & Engel, 2010; Carmel & Carrasco, 2008; Ghose, Yang, & Maunsell, 2002; Li, Piëch, & Gilbert, 2004; Schoups, Vogels, Qian, & Orban, 2001; Yotsumoto et al., 2009), the frontal cortex (Kahnt, Grueschow, Speck, & Haynes, 2011), attention-network-related parts of the parietal lobe (Mukai et al., 2007), or some intermediate region in the visual and cognitive processing hierarchy such as V4 (Mukai et al., 2007; Raiguel, 2006; Rainer, Lee, & Logothetis, 2004; Williford, 2006; Yang & Maunsell, 2004; Zivari Adab & Vogels, 2011)? Neuronal correlates of perceptual learning have been reported for areas V1 (Schoups et al., 2001) and V4 (Raiguel, 2006; Yang & Maunsell, 2004; Zivari Adab & Vogels, 2011) in orientation discrimination tasks, but it remains to be seen whether this also holds true for contrast discrimination tasks in primates.

Secondly, if changes take place at the neuronal level in a specialized cortical area, what are the mechanisms that allow this learning to transfer to tasks involving different

stimulus features? How does learning transfer across e.g. different stimulus orientations? After a period of training with sample stimuli of 30% contrast, would transfer of learning occur if sample stimuli of 20% or 40% contrast were used instead?

Lack of transfer is often used as an argument that the site at which learning occurs must be one that shows high selectivity for the feature of interest. Specificity has been shown to occur in the domains of orientation (Ahissar & Hochstein, 1993; Dorais & Sagi, 1997; Ghose et al., 2002; Levi & Polat, 1996; Parkosadze et al., 2008; Raiguel, 2006; Schoups et al., 2001; Shapley, 2003), spatial frequency (Sowden, Rose, & Davies, 2002), contrast (Crist, Li, & Gilbert, 2001), and size (Ahissar & Hochstein, 1993), as well as for visual field location (Schoups et al., 2001; Sowden et al., 2002; Xiao et al., 2008). However, Zhang et al. (2010) has shown that partial transfer of learning on a contrast discrimination task is in fact possible between stimulus orientations, and complete transfer can occur when training on a contrast discrimination task is accompanied by exposure to orthogonal stimuli during training on an orientation discrimination task. In line with Zhang et al. (2010) and Sowden et al.'s results (2002), we found that improvements in contrast discrimination transferred to different stimulus orientations. Thus, neurons with high orientation selectivity are unlikely to be the main originators of improved perceptual abilities. On the other hand, we found that transfer to a different spatial frequency was limited (see also Sowden et al., 2002), which suggests that spatial-frequency-selective filters are strongly involved in contrast discrimination learning. Closer study of the neuronal mechanisms that underlie the process of contrast discrimination learning is thus needed to shed light on these issues.

Acknowledgements

This research was supported by the Medical Research Council, UK, G0700976. The authors would like to thank the Comparative Biology Centre staff at Newcastle University for their excellent technical support.

References

- Adini, Y., Sagi, D., & Tsodyks, M. (2002). Context-enabled learning in the human visual system. *Nature*, *415*(6873), 790-793.
- Adini, Y., Wilkonsky, A., Haspel, R., Tsodyks, M., & Sagi, D. (2004). Perceptual learning in contrast discrimination: The effect of contrast uncertainty. *Journal of Vision*, *4*(12). doi: 10.1167/4.12.2
- Ahissar, M., & Hochstein, S. (1993). Attentional control of early perceptual learning. *Proceedings of the National Academy of Sciences of the United States of America*, *90*(12), 5718-5722.
- Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Sciences* *8*(10), 457-464
- Ahissar, M., Nahum, M., Nelken, I., & Hochstein, S. (2009). Reverse hierarchies and sensory learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1515), 285-299. doi: 10.1098/rstb.2008.0253
- Balboa, R. M., & Grzywacz, N. M. (2003). Power spectra and distribution of contrasts of natural images from different habitats. *Vision Research*, *43*(24), 2527-2537. doi: [http://dx.doi.org/10.1016/S0042-6989\(03\)00471-1](http://dx.doi.org/10.1016/S0042-6989(03)00471-1)
- Bao, M., Yang, L., Rios, C., He, B., & Engel, S. A. (2010). Perceptual Learning Increases the Strength of the Earliest Signals in Visual Cortex. *Journal of Neuroscience*, *30*(45), 15080-15084. doi: 10.1523/jneurosci.5703-09.2010
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, *57*(1), 289-300. doi: 10.2307/2346101
- Brady, N., & Field, D. J. (2000). Local contrast in natural images: normalisation and coding efficiency. *Perception*, *29*(9), 1041-1055.
- Campbell, F. W., & Kulikowski, J. J. (1966). Orientational selectivity of the human visual system. *The Journal of Physiology*, *187*(2), 437-445.
- Carmel, D., & Carrasco, M. (2008). Perceptual Learning and Dynamic Changes in Primary Visual Cortex *Neuron*, *57*(6), 799-801.
- Crist, R., Li, W., & Gilbert, C. (2001). Learning to see: experience and attention in primary visual cortex. *Nature Neuroscience* *4*(5), 519-526.
- Dorais, A., & Sagi, D. (1997). Contrast Masking Effects Change with Practice. *Vision Research*, *37*, 1725-1733.
- Fechner, G. T. (1860) *Elemente der Psychophysik* (Vol. 2). Leipzig: Breitkopf & Härtel.
- Foley, J. M., & Legge, G. E. (1981). Contrast detection and near-threshold discrimination in human vision. *Vision Research*, *21*(7), 1041-1053. doi: [http://dx.doi.org/10.1016/0042-6989\(81\)90009-2](http://dx.doi.org/10.1016/0042-6989(81)90009-2)
- Frazor, R. A., & Geisler, W. S. (2006). Local luminance and contrast in natural images. *Vision Research*, *46*(10), 1585-1598. doi: <http://dx.doi.org/10.1016/j.visres.2005.06.038>
- Fredericksen, R. E., Bex, P. J., & Verstraten, F. A. J. (1997). How big is a Gabor patch, and why should we care? *The Journal of the Optical Society of America*, *14*(1), 1-12.
- Garrigan, P., & Kellman, P. J. (2008). Perceptual learning depends on perceptual constancy. *Proceedings of the National Academy of Sciences*, *105*(6), 2248-2253. doi: 10.1073/pnas.0711878105
- Ghose, G., Yang, T., & Maunsell, J. (2002). Physiological Correlates of Perceptual Learning in Monkey V1 and V2 *Journal of Neurophysiology*, *87*(4), 1867-1888.
- Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. Oxford, England: John Wiley.
- Hochstein, S., & Ahissar, M. (2002). View from the Top: Hierarchies and Reverse Hierarchies in the Visual System *Neuron*, *36*(5), 791-804.
- Kahnt, T., Grueschow, M., Speck, O., & Haynes, J.-D. (2011). Perceptual Learning and Decision-Making in Human Medial Frontal Cortex. *Neuron*, *70*(3), 549-559. doi: 10.1016/j.neuron.2011.02.054

- Kuai, S.-G., Zhang, J.-Y., Klein, S. A., Levi, D. M., & Yu, C. (2005). The essential role of stimulus temporal patterning in enabling perceptual learning. [10.1038/n1546]. *Nature Neuroscience*, 8(11), 1497-1499.
- Law, C.-T., & Gold, J. (2008). Neural correlates of perceptual learning in a sensorimotor, but not a sensory, cortical area. *Nature Neuroscience*, 11(4), 505-513 doi: doi:10.1038/n12070
- Legge, G. E., & Foley, J. M. (1980). Contrast masking in human vision. *Journal of the Optical Society of America*, 70(12), 1458-1471.
- Levi, D., & Polat, U. (1996). Neural plasticity in adults with amblyopia. *Proceedings of the National Academy of Sciences*, 93(13), 6830-6834.
- Li, W., Piëch, V., & Gilbert, C. (2004). Perceptual learning and top-down influences in primary visual cortex. *Nature Neuroscience* 7(6), 651-657. doi: doi:10.1038/n1255
- Mollon, J. D., & Danilova, M. V. (1996). Three remarks on perceptual learning. *Spatial Vision*, 10, 51-58.
- Mukai, I., Kim, D., Fukunaga, M., Japee, S., Marrett, S., & Ungerleider, L. (2007). Activations in Visual and Attention-Related Areas Predict and Correlate with the Degree of Perceptual Learning. *Journal of Neuroscience*, 27(42), 11401-11411. doi: 10.1523/jneurosci.3002-07.2007
- Owsley, C. (2011). Aging and vision. *Vision Research*, 51(13), 1610-1622. doi: <http://dx.doi.org/10.1016/j.visres.2010.10.020>
- Parkosadze, K., Otto, T. U., Malania, M., Kezeli, A., & Herzog, M. H. (2008). Perceptual learning of bisection stimuli under roving: Slow and largely specific. *Journal of Vision*, 8(1), 1-8.
- Pelli, D., Zhang L. (1991). Accurate control of contrast on microcomputer displays. *Vision Research*, 31(7-8), 1337-1350.
- Petrov, A. A., Doshier, B. A., & Lu, Z.-L. (2005). The Dynamics of Perceptual Learning: An Incremental Reweighting Model. *Psychological Review*, 112(4), 715-743. doi: 10.1037/0033-295x.112.4.715
- Phan, M., & Ni, R. (2011). Training Older Adults to Improve Their Contrast Sensitivity: A Possible or Impossible Task? *Journal of Vision*, 11(11), 4. doi: 10.1167/11.11.1027
- Polat, U. (1999). Functional architecture of long-range perceptual interactions. *Spatial Vision*, 12(2), 143-162. doi: 10.1163/156856899x00094
- Polat, U., Ma-Naim, T., Belkin, M., & Sagi, D. (2004). Improving vision in adult amblyopia by perceptual learning. *Proceedings of the National Academy of Sciences of the United States of America*, 101(17), 6692-6697. doi: 10.1073/pnas.0401200101
- Raiguel, S., Rufin Vogels, Santosh G. Mysore, Guy A. Orban. (2006). Learning to See the Difference Specifically Alters the Most Informative V4 Neurons. *Journal of Neuroscience*, 26(24), 6589-6602.
- Rainer, G., Lee, H., & Logothetis, N. K. (2004). The Effect of Learning on the Function of Monkey Extrastriate Visual Cortex. *PLoS Biology* 2(2), E44.
- Sagi, D. (2011). Perceptual learning in Vision Research. *Vision Research*, 51(13), 1552-1566. doi: <http://dx.doi.org/10.1016/j.visres.2010.10.019>
- Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, 412(6846), 549-553 doi: doi:10.1038/35087601
- Shapley, R., Michael Hawken, and Dario L. Ringach. (2003). Dynamics of Orientation Selectivity Review in the Primary Visual Cortex and the Importance of Cortical Inhibition. *Neuron*, 38(5), 689-699.
- Sowden, P., Rose, D., & Davies, I. (2002). Perceptual learning of luminance contrast detection: specific for spatial frequency and retinal location but not orientation. *Vision Research* 42(10), 1249-1258.
- Stephens, B. R., & Banks, M. S. (1987). Contrast discrimination in human infants. *Journal of Experimental Psychology: Human Perception and Performance*, 13(4), 558-565. doi: 10.1037/0096-1523.13.4.558
- Thiele, A., Dobkins, K., & Albright, T. (2000). Neural Correlates of Contrast Detection at Threshold. *Neuron*, 26(3), 715-724.
- Tsodyks, M., Adini, Y., & Sagi, D. (2004). Associative learning in early vision. *Neural Networks* 17(5-6), 823-832.

- Weber, E. H. (1850). Der Tastsinn und das Gemeingefühl. In R. Wagner (Ed.), *In Handwörterbuch der Physiologie* (Vol. 3, pp. 481–588). Braunschweig, Germany: Vieweg.
- Williford, T., John H. R. Maunsell (2006). Effects of Spatial Attention on Contrast Response Functions in Macaque Area V4. *Journal of Neurophysiology*, *96*(1), 40-54. doi: doi:10.1152/jn.01207.2005
- Wilson, H. (1980). A transducer function for threshold and suprathreshold human vision. *Biological Cybernetics*, *38*(3), 171-178. doi: 10.1007/bf00337406
- Xiao, L.-Q., Zhang, J.-Y., Wang, R., Klein, S., Levi, D., & Yu, C. (2008). Complete Transfer of Perceptual Learning across Retinal Locations Enabled by Double Training. *Current Biology*, *18*, 1-5. doi: DOI 10.1016/j.cub.2008.10.030
- Yang, T., & Maunsell, J. H. R. (2004). The Effect of Perceptual Learning on Neuronal Responses in Monkey Visual Area V4. *Journal of Neuroscience*, *24*(7), 1617–1626.
- Yotsumoto, Y., Sasaki, Y., Chan, P., Vasios, C. E., Bonmassar, G., Ito, N., . . . Watanabe, T. (2009). Location-Specific Cortical Activation Changes during Sleep after Training for Perceptual Learning. *Current Biology*, *19*(15), 1278-1282.
- Yotsumoto, Y., Watanabe, T., & Sasaki, Y. (2008). Different Dynamics of Performance and Brain Activation in the Time Course of Perceptual Learning. *Neuron*, *57*(6), 827–833.
- Yu, C., Klein, S., & Levi, D. (2004). Perceptual learning in contrast discrimination and the (minimal) role of context. *Journal of Vision*, *4*(3), 169-182.
- Zhang, J.-Y., Kuai, S.-G., Xiao, L.-Q., Klein, S. A., Levi, D. M., & Yu, C. (2008). Stimulus Coding Rules for Perceptual Learning. *PLoS Biology*, *6*(8), e197. doi: 10.1371/journal.pbio.0060197
- Zhang, J.-Y., Zhang, G.-L., Xiao, L.-Q., Klein, S., Levi, D., & Yu, C. (2010). Rule-Based Learning Explains Visual Perceptual Learning and Its Specificity and Transfer. *Journal of Neuroscience*, *30*(37), 12323-12328. doi: 10.1523/jneurosci.0704-10.2010
- Zivari Adab, H., & Vogels, R. (2011). Practicing Coarse Orientation Discrimination Improves Orientation Signals in Macaque Cortical Area V4. *Current Biology*, *21*(19), 1661-1666.