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Signal but not noise changes with perceptual learning

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Perceptual discrimination improves with practice. This 'perceptual learning' is often specific to the stimuli presented during training[1–5], indicating that practice may alter the response characteristics of cortical sensory neurons[6,7]. Although much is known about how learning modifies cortical circuits[8], it remains unclear how these changes relate to behaviour. Different theories assume that practice improves discrimination by enhancing the signal[1,9,10], diminishing internal noise[11,12] or both[13]. Here, to distinguish among these alternatives, we fashioned sets of faces and textures whose signal strength could be varied, and we trained observers to identify these patterns embedded in noise. Performance increased by up to 400% across several sessions over several days. Comparisons of human performance to that of an ideal discriminator showed that learning increased the efficiency with which observers encoded task-relevant information. Observer response consistency, measured by a double-pass technique in which identical stimuli are shown twice in each experimental session[14,15], did not change during training, showing that learning had no effect on internal noise. These results indicate that perceptual learning may enhance signal strength, and provide important constraints for theories of learning.

In our experiments, observers identified which of 10 possible visual signals was presented on each trial. To make identification difficult, two-dimensional gaussian noise was added to the signals on the visual display. An ideal strategy for this task[16] is to cross-correlate the stimulus (the signal-plus-noise) with 10 different templates which match the spatial and temporal characteristics of the 10 possible signals, and then select the template that yields the largest response. The performance of such an ideal observer is limited only by the similarity of the items and by the amount of noise added to the signal.

Of course, additional factors constrain human performance. For example, the optics of the eye degrade the stimulus, and neural mechanisms may further attenuate the stimulus and/or introduce noise. In addition, human observers may encode stimuli with filters that are not matched precisely to the spatial and/or temporal characteristics of the signal, or use suboptimal decision rules to select a response. These additional constraints on human performance have been modelled successfully as a two-component system containing a constant, internal noise added to the external stimulus, followed by a noiseless, contrast-invariant calculation[17–19]. The calculation can be thought of as the application of a linear filter, or template, that reduces the input to a single number used to make a decision about the stimulus. To the extent that the template does not match the signal, the efficiency of the calculation is reduced relative to ideal efficiency[17]. In this model, human thresholds follow the form

$$E = k(N_e + N_i) \qquad (1)$$

where E is threshold contrast energy (the squared root mean square (r.m.s.) contrast multiplied by stimulus area), N_e is the spectral density of the external noise, and k and N_i are free parameters[18]. N_i is an index of the total internal noise which affects performance, whereas k is inversely proportional to calculation efficiency (see Methods for a definition of calculation efficiency). Equation (1) suggests that human observers differ from ideal observers in two ways. First, unlike ideal observers, human observers have internal noise. Second, unlike ideal observers, human observers use sub-
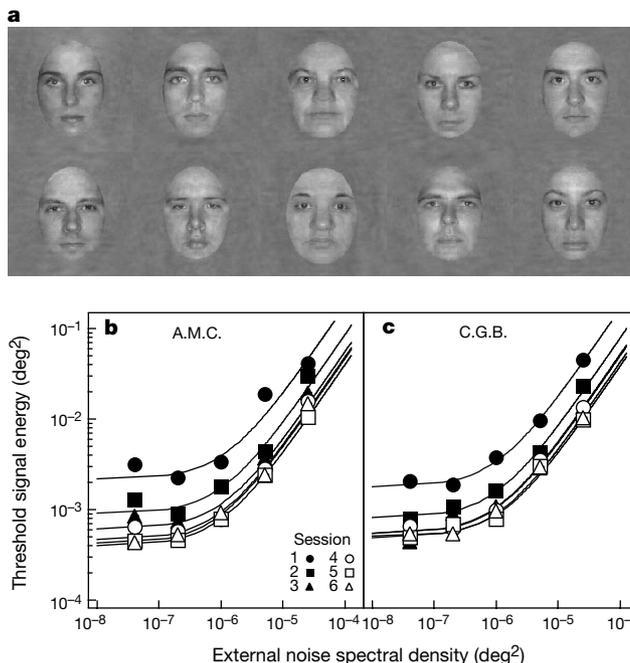
Figure 1 Faces and their noise masking functions. **a**, Stimuli used in the face identification experiment (see Methods). **b**, **c**, Contrast energy thresholds plotted as a function of external noise spectral density (power per unit bandwidth) for two observers in the face identification task. Each data point corresponds to a single threshold. Error bars correspond to ±1 s.e. of the threshold estimate. Often, the error bars are smaller than the symbols. The solid lines are the weighted least-squares fits to equation (1).

optimal templates, which reduces their relative calculation efficiency. Our experiments determined whether perceptual learning lowers thresholds by decreasing internal noise or by increasing calculation efficiency.

Face identification thresholds were measured for 10 unfamiliar human faces (Fig. 1a) embedded in static, two-dimensional gaussian white noise of various spectral densities. A single, randomly selected face-plus-noise stimulus was presented on each trial. Thresholds increase as a function of external noise and decrease as a function of practice (Fig. 1b, c). The smooth curves in Fig. 1b, c are the best fitting form of equation 1 for each set of thresholds. When plotted in log–log coordinates, as in Fig. 1b, c, changes to k result in uniform vertical shifts of the curve, whereas changes to N_i result in lateral shifts of the curve's inflection point. Figure 1b, c indicates that practice reduced k but had no effect on N_i. Thus, our results indicate that perceptual learning may increase calculation efficiency without affecting internal noise. Calculation efficiency and internal noise estimated from the data in Figs 1 and 2 are shown in Fig. 3, where the circular symbols show the above result more clearly.

Previous studies have suggested that specialized mechanisms process faces[20,21]. Therefore, our results may not be characteristic of perceptual learning in general. To test this idea, we applied the same technique to a stimulus without the spatial structure and social significance of human faces: band-pass filtered gaussian noise textures (Fig. 2a). Texture identification thresholds increased as a function of external noise and decreased as a function of practice (Fig. 2b, c). Calculation efficiency and internal noise estimated from the data in Fig. 2 are shown by the square symbols in Fig. 3. As with faces, practice increased calculation efficiency (reduced k) but had no effect on internal noise (N_i did not vary). Thus, this pattern of results is not specific to faces, and may be generally representative of how people learn to identify visual patterns.

The increase in calculation efficiency with practice is consistent with the idea that learning modifies observers' templates to extract more of the potential signal. However, another interpretation is possible. The internal noise N_i in equation (1) does not depend on the strength of the external noise or the signal, but physiological[22] and psychophysical[15] evidence indicates that the variability of visual mechanisms may increase with stimulus contrast. These results imply that there are two sources of internal noise: a constant component N_c and a multiplicative component which is proportional to the input[15]. A decrease in multiplicative noise has the same effect as an increase in calculation efficiency (that is, a uniform downward shift in the functions shown in Figs 1b, c and 2b, c)[15,18]. This can be seen more clearly when equation (1) is rewritten so that internal noise, N_i, is the sum of constant (N_c) and multiplicative ($m\{N_e + N_c + E\}$) components:

$$E = k(N_e + N_c + m(N_e + N_c + E))$$
$$= (k(1 + m)/(1 - km))(N_e + N_c) \qquad (2)$$
$$= k'(N_e + N_c)$$

where k' is a constant equal to $k(1 + m)/(1 - km)$. Note that reductions in k' can be caused either by reducing multiplicative noise (lowering the value of m) or by increasing calculation efficiency (lowering k). Thus, within the context of our model, it
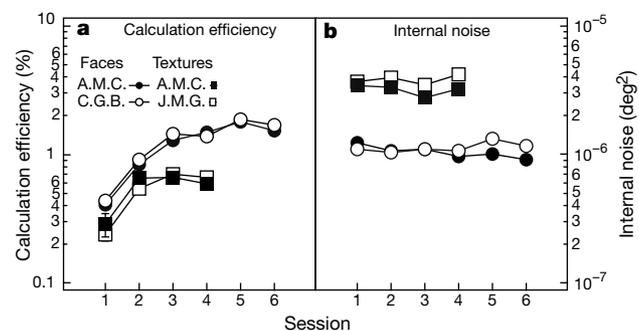
Figure 3 Calculation efficiency and internal noise estimates. **a**, Calculation efficiency; **b**, internal noise spectral density estimates from the data in Figs 1 and 2, plotted as a function of practice. Error bars correspond to ±1 s.e. of the estimate.
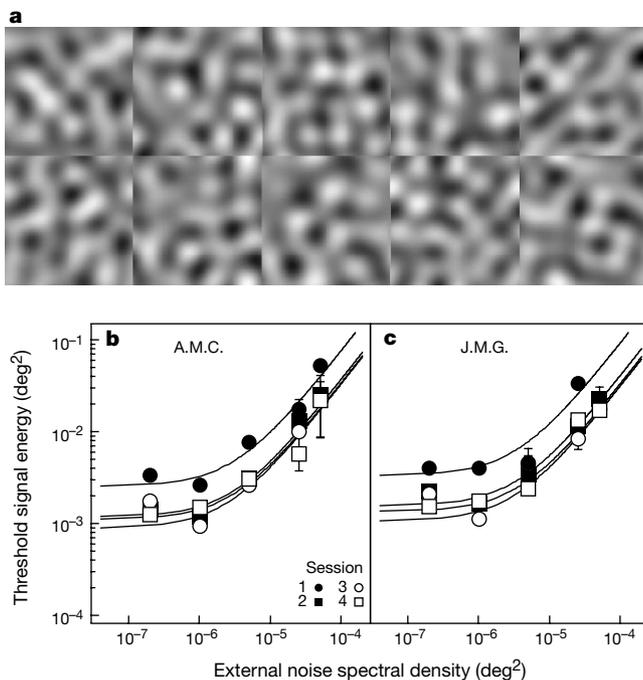
Figure 2 Band-pass texture patterns and their noise masking functions. **a**, Stimuli used in the texture identification experiment (see Methods). **b**, **c**, Contrast energy thresholds plotted as a function of external noise spectral density for two observers in the texture identification task. Observer A.M.C. (**b**) also participated in the face identification experiment (Fig. 1b). Plotting conventions are as in Fig. 1.
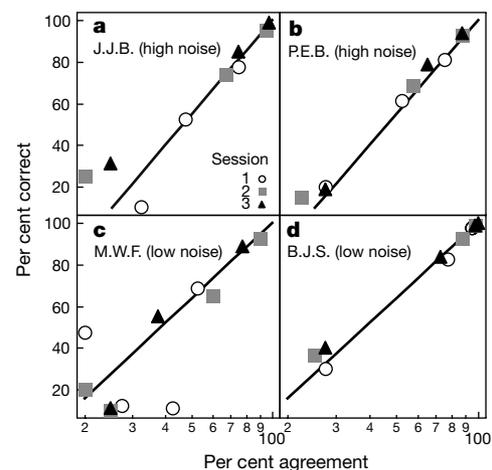
Figure 4 Response consistency in high and low external noise. High (**a**, **b**) and low (**c**, **d**) external noise consistency measures in the face identification task. Each panel plots per cent correct performance as a function of per cent agreement. Each data point corresponds to the combination of per cent correct and per cent agreement at a single stimulus level. All observers showed the same degree of improvement across test sessions as found in the first experiment. Solid lines show the predictions for an observer with an internal/external noise ratio of 1.0 (**a**, **b**) and 2.0 (**c**, **d**).

is impossible to know whether the effects of practice on identification thresholds are due to reductions in multiplicative noise or to increases in calculation efficiency.

To address this issue, we adopted a double-pass response consistency procedure which has been used to estimate internal noise for auditory[14] and visual[15,23] detection and discrimination tasks. The technique requires observers to perform a task with two passes through identical sets of stimuli (signal-plus-noise combinations). Because both the signals and noises in both passes are identical, response inconsistencies between passes must be due to observer variability. For a given level of performance (per cent correct), the degree of consistency (per cent agreement) between responses in the two repetitions of the experiment depends only on the internal/external noise ratio[15]. Specifically, as the internal/external noise ratio increases, response consistency decreases. Thus, measures of response consistency are an index of internal noise. Furthermore, the estimate of internal noise does not depend on whether the noise is constant or multiplicative—it simply reflects the total amount of noise present in the system. We used this technique to determine whether internal noise changes with practice in our task.

Four new observers performed the face identification task with two passes through the same signal and noise combinations within each of three sessions. The consistency measures are shown in Fig. 4. If learning reduced internal noise, consistency would increase with practice, and the data in each panel of Fig. 4 should shift systematically to the right. However, for both high and low external noise conditions, the data for all three sessions fall along a single line. Contrary to the predictions of several theories[11–13], internal noise was not altered by learning.

Our results provide strong constraints for models of learning, and support connectionist network models[1,10] and classical learning theories[9] suggesting that learning increases the strength of discriminate signals. Precisely how signal enhancement manifests itself at the neuronal level remains a mystery. Learning produces changes in individual cells[24,25], populations of cells within a single cortical area[26–28] and functional connections across cortical areas[29]. An important challenge for the future is to determine whether some or all of these physiological changes are associated with changes in behaviour. Our results suggest that the neural correlates of behaviour should exhibit improved discrimination among stimuli and constant variability during perceptual learning. □

Methods

Definition of calculation efficiency

It can be shown that identification threshold for an ideal observer is given by $E = k_{ideal} * N_e$, where E and N_e are as defined above and k_{ideal} is a constant that varies with the pattern set and is directly related to the intrinsic difficulty of the task[16]. A human observer's calculation efficiency is defined as k_{ideal}/k.

Stimuli

We used 10 faces (Fig. 1a) and 10 textures (Fig. 2a) as stimuli. The height/width ratio was constant across all faces (198 pixels/140 pixels), subtending $4.0 \times 2.9°$ of visual angle from the viewing distance of 100 cm. The faces were centred within a 256×256 pixel ($5.25 \times 5.25°$) uniform background of average luminance (29 cd m^{-2}). Additional details about the generation of the face stimuli are described elsewhere[30]. The textures were gaussian noise fields (256×256 pixels; $5.25 \times 5.25°$) filtered by a 2–4 c per image rectangular frequency filter.

Procedure

On each trial, a signal (for example, a face) was chosen and added to a two-dimensional static gaussian white noise field (256×256 pixels) of the appropriate contrast variance. The signal-plus-noise combination was shown for 500 ms and was followed by an unlimited time for response by clicking on a selection window containing smaller (100×100 pixels), noise-free, high-contrast versions of all 10 signals. Observers received accuracy feedback after each trial. Thresholds for a d' of 1.47 (50% correct) were determined by varying the contrast energy of the signals across trials according to the method of constant stimuli.

Design of first experiment

See Figs 1–3. Thresholds were determined in each of five levels of levels of external noise:

0.04, 0.20, 1.02, 5.11 and 25.55×10^{-6} deg^2. A unique noise field was generated on every trial, and the level of external noise and the identity of the signal were chosen randomly. A complete session consisted of 155 trials across each of five stimulus contrast energy levels at each noise level, for a total of 775 trials per session. Each session was completed without breaks and lasted about 1 h. Only one session was completed each day. Observers in the face identification task completed six sessions within ten days. Observers in the texture identification task completed four sessions within seven days.

Design of double-pass consistency experiment

See Fig. 4. Two observers performed the face identification task with only the highest level of external noise used in the first experiment (25.55×10^{-6} deg^2), and two with only the lowest level of external noise (0.04×10^{-6} deg^2). Each of three test sessions consisted of two identical blocks of 200 trials across five stimulus contrast energy levels, for a total of 400 trials per session. Signals were chosen randomly and new noise fields were generated on each trial within the first block of a session. Observers were not aware that the first and second blocks of each session were identical.

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