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The essential role of stimulus temporal patterning in enabling perceptual learning

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Little is known about how temporal stimulus factors influence perceptual learning. Here we demonstrate an essential role of stimulus temporal patterning in enabling perceptual learning by showing that 'unlearnable' contrast and motion-direction discrimination (resulting from random interleaving of stimuli) can be readily learned when stimuli are practiced in a fixed temporal pattern. This temporal patterning does not facilitate learning by reducing stimulus uncertainty; further, learning enabled by temporal patterning can later generalize to randomly presented stimuli.

Perceptual learning refers to improvement, through practice, in the ability to discriminate fine differences in visual and other sensory features such as contrast[1,2], orientation[3,4] and Vernier and other positional acuities[5,6] (see refs. 7 and 8 for recent reviews). Many studies have investigated the effects of spatial factors—such as stimulus contrast, spatial frequency and orientation—on perceptual learning. However, the role of stimulus temporal factors in perceptual learning has been largely overlooked.
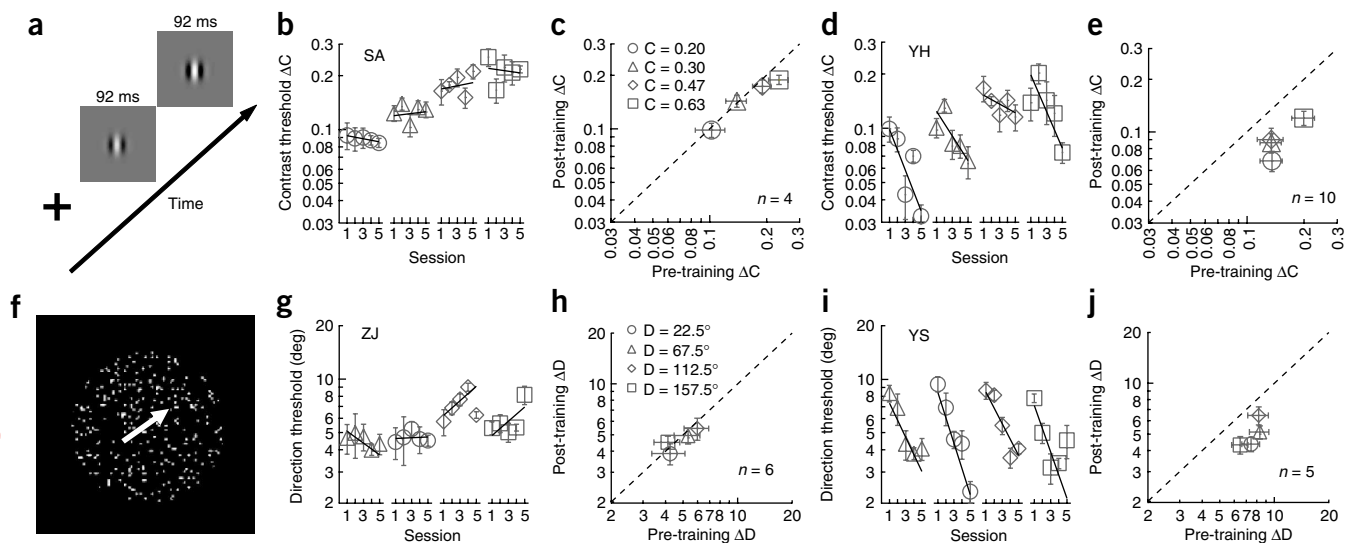

Figure 1 Effects of stimulus roving and temporal patterning on perceptual learning of contrast and motion-direction discrimination. (**a**) Stimuli for contrast discrimination in a two-alternative forced-choice (2-AFC) trial. A fixation cross was followed by two Gabor stimuli (spatial frequency $sf = 6$ cycles per degree, presented for 92 ms each separated by a 600-ms interstimulus interval; s.d. $\sigma = 0.07°$.) The observers' task was to judge which stimulus had higher contrast. Discrimination thresholds were measured with a three-down–one-up forced-choice staircase method. (**b**) Observer SA's unchanged session-by-session contrast thresholds (ΔC) for each reference contrast with contrast roving. Throughout: error bars, s.e.m.; solid lines, linear fits. Training sessions were typically 2 h and included 1,000–1,200 trials. (**c**) Comparison of mean post- and pre-training contrast thresholds obtained with contrast roving showed no significant learning ($F_{1,3} = 3.26$, $P = 0.169$; data points significantly below dashed diagonal line indicate that learning has taken place). (**d**) Observer YH's session-by-session reduction in contrast thresholds during practice with temporally patterned contrasts. (**e**) Comparison of mean post- and pre-training contrast thresholds obtained with temporal patterning showed significant learning ($F_{1,9} = 40.8$, $P = 0.000$). (**f**) Stimuli for motion direction discrimination. A circular window of diameter 8° held 1,000 random dots, all moving in the same direction at a speed of 10° per s. In a 2-AFC trial, two sets of dots (for clarity, fewer dots are shown) were presented for 500 ms each, with a 200-ms interval between presentations. The observers' task was to judge in which interval the random dots moved more clockwise. (**g**) Observer ZJ's session-by-session motion direction thresholds (ΔD) with direction roving. (**h**) Comparison of mean post- and pre-training motion direction thresholds showed no significant improvement after practice with direction roving ($F_{1,5} = 0.007$, $P = 0.936$). (**i**) Observer YS's session-by-session lowering of direction thresholds with temporally patterned directions. (**j**) Comparison of mean post- and pre-training motion direction thresholds showed that significant learning took place under stimulus temporal patterning ($F_{1,4} = 17.7$, $P = 0.014$).
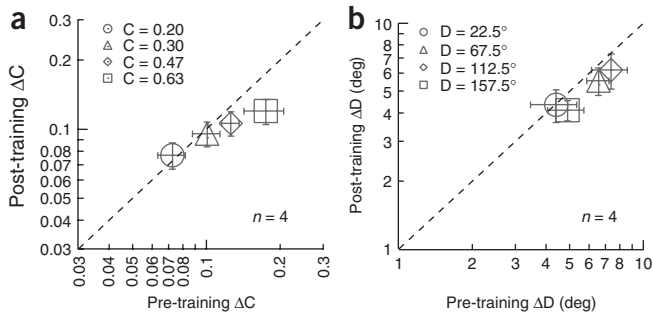
Figure 2 The effects of pre-cueing on contrast and motion direction learning with stimulus roving. (**a,b**) Comparisons of the mean post- and pre-training thresholds for (**a**) contrast discrimination and (**b**) motion direction discrimination showed no significant learning (see text for *F*-test results).
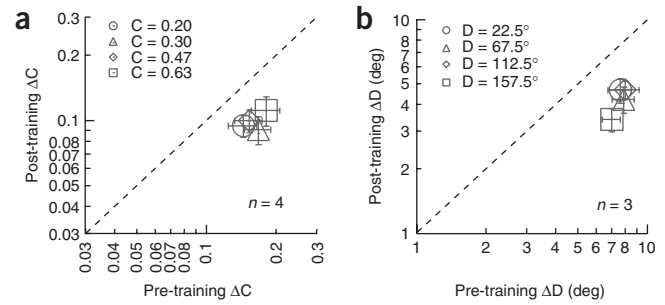

Figure 3 Perceptual learning generalizes to unpracticed temporal conditions. (**a,b**) After learning with stimulus temporal patterning, discrimination thresholds with stimulus roving were significantly lower than the pre-training levels for (**a**) contrast discrimination and (**b**) motion direction discrimination (see text for *F*-test results).

Recently[1] we found that contrast discrimination for Gabor stimuli (Gaussian-windowed sinusoidal gratings; **Fig. 1a**) is unlearnable if the several contrasts that are to be learned are randomly interleaved trial by trial (a condition we refer to as 'contrast roving'; see also ref. 2). On average, the ratio of contrast discrimination thresholds after training to the same thresholds before training is 0.93 ± 0.09 (mean ± s.e.m.; data replotted in **Fig. 1b,c**), indicating no significant threshold reduction or perceptual learning after practice. Learning is possible only when contrast discrimination is practiced one contrast at a time in block trials[1]. The 'knock-out' of learning by contrast roving suggests that stimulus information may need to be organized in a certain temporal pattern if perceptual learning is to take place.

In the current study, we presented the same four contrasts as in ref. 1 in two fixed temporal patterns: for seven observers, the contrast increased monotonically (0.2–0.3–0.47–0.63), and for three other observers, the contrast varied non-monotonically (0.2–0.47–0.3–0.63). After five such 'temporal patterning' practice sessions, the observers' contrast discrimination improved significantly (**Fig. 1d,e**). The ratio of the mean post-training to mean pre-training thresholds (**Fig. 1e**) was 0.61 ± 0.06, comparable to the 0.64 ± 0.04 we obtained in our original blocked-trials learning[1]. An analysis of variance (ANOVA) further confirmed that the effects of contrast roving and temporal patterning on contrast learning were significantly different ($F_{1,12} = 13.2$, $P = 0.003$). Thus, practice with contrast interleaving is just as effective as practice with blocked trials in facilitating perceptual learning, as long as the contrasts are temporally patterned.

The role of stimulus temporal patterning in perceptual learning was also evident in a completely different task: motion-direction discrimination (**Fig. 1f**). As in the contrast learning task, observers who practiced with 'direction roving'—with motion stimuli in four reference directions that varied randomly from trial to trial—showed post- to pre-training threshold ratios either close to 1 (indicating that no learning had taken place) or even higher (indicating that observers' performance was actually worse after practice) (**Fig. 1g,h**); on average, post- to pre-practice threshold ratios were 1.17 ± 0.23. However, observers who practiced an equivalent amount of trials with stimuli possessing a fixed temporal pattern (same four directions as in the roving condition, changing clockwise as follows: 22.5°–67.5°–112.5°–157.5) showed improved discrimination: the overall post- to pre-training threshold ratio was 0.64 ± 0.11 (**Fig. 1i,j**), comparable to the 0.61 ± 0.06 ratio in contrast learning with temporal patterning (**Fig. 1e**). Again, roving and temporal patterning had significantly

different effects on learning motion direction ($F_{1,9} = 6.1$, $P = 0.036$). Taken together, the results of our contrast and motion-direction learning experiments indicate that stimulus temporal patterning has an essential role in enabling at least low-level perceptual learning.

Does temporal patterning facilitate perceptual learning by reducing stimulus uncertainty[1,2,9]? With stimulus roving, observers may be uncertain about the contrast or motion direction in the first interval of a 2-AFC trial, resulting in judgments within the uncertain range of the contrast or motion direction. This stimulus uncertainty may knock out learning[2,9]. To test this possibility, we had observers practice contrast and motion-direction discrimination with roving, but we presented a pre-cue to minimize stimulus uncertainty. The pre-cue, appearing 1 s before the first interval of each roving trial, was an identical Gabor or moving random-dot stimulus with the same reference contrast (Gabor) or motion direction (moving dot) and the same duration as the stimulus itself.

The results demonstrated that, with stimulus roving, pre-cueing was insufficient to significantly improve contrast or motion-direction discrimination (**Fig. 2**). The ratio of mean post-training to pre-training thresholds was 0.88 ± 0.1 for both tasks ($F_{1,3} = 5.47$, $P = 0.101$ for contrast discrimination; $F_{1,3} = 3.57$, $P = 0.155$ for motion-direction discrimination). For both contrast and motion-direction discrimination, the effects of pre-cued roving were not significantly different from those of uncued roving ($F_{1,6} = 0.404$, $P = 0.549$ for contrast discrimination; $F_{1,8} = 0.487$, $P = 0.505$ for motion-direction discrimination) but were significantly different from the effects of temporal patterning ($F_{1,12} = 9.54$, $P = 0.009$ for contrast discrimination; $F_{1,7} = 7.01$, $P = 0.003$ for motion-direction discrimination). These results ruled out reduction in contrast uncertainty as a plausible explanation for the facilitation of perceptual learning by stimulus temporal patterning.

Does the improved discrimination in the post-practice period remain specific to the practiced temporal pattern? This kind of specificity would be uneconomical because observers would have to re-learn the same stimuli whenever the stimulus temporal pattern changes. To examine this issue, we measured both the contrast and the motion-direction discrimination with stimulus roving, but we used observers who had demonstrated successful learning in the temporal patterning condition. These observers' post-training discrimination thresholds were significantly lower than their pre-training thresholds (**Fig. 3**; $F_{1,3} = 29.1$, $P = 0.012$ for contrast discrimination; $F_{1,2} = 30.8$, $P = 0.031$ for motion-direction discrimination). The ratios of the mean post- and pre-training thresholds were 0.61 ± 0.06

and 0.55 ± 0.05 for contrast and motion-direction discrimination, respectively, suggesting that learning obtained with temporal patterning generalized to the stimulus roving condition. A similar learning generalization was also found with unpracticed fixed temporal patterns in contrast discrimination (data not shown). Our data therefore provide no evidence for post-learning temporal specificity and instead suggest that human visual learning is highly efficient.

We hypothesize that the fixed temporal patterns may temporally chunk discrete stimuli together, thus facilitating the encoding of stimulus information (as memory traces) into visual long-term memory (LTM), but that interference by stimulus roving interrupts such encoding. For learning to occur, the top-down developing LTM traces must interact with the bottom-up sensory input and guide stimulus discrimination. This continuous interaction between the bottom-up stimulus inputs and top-down LTM traces enhances and refines the stored memory traces, which eventually improves discrimination. Further work will be needed to explain how temporally chunked LTM can apply to roving and other unpracticed temporal patterns after learning has taken place (**Fig. 3**).

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