

# Stimulus Coding Rules for Perceptual Learning

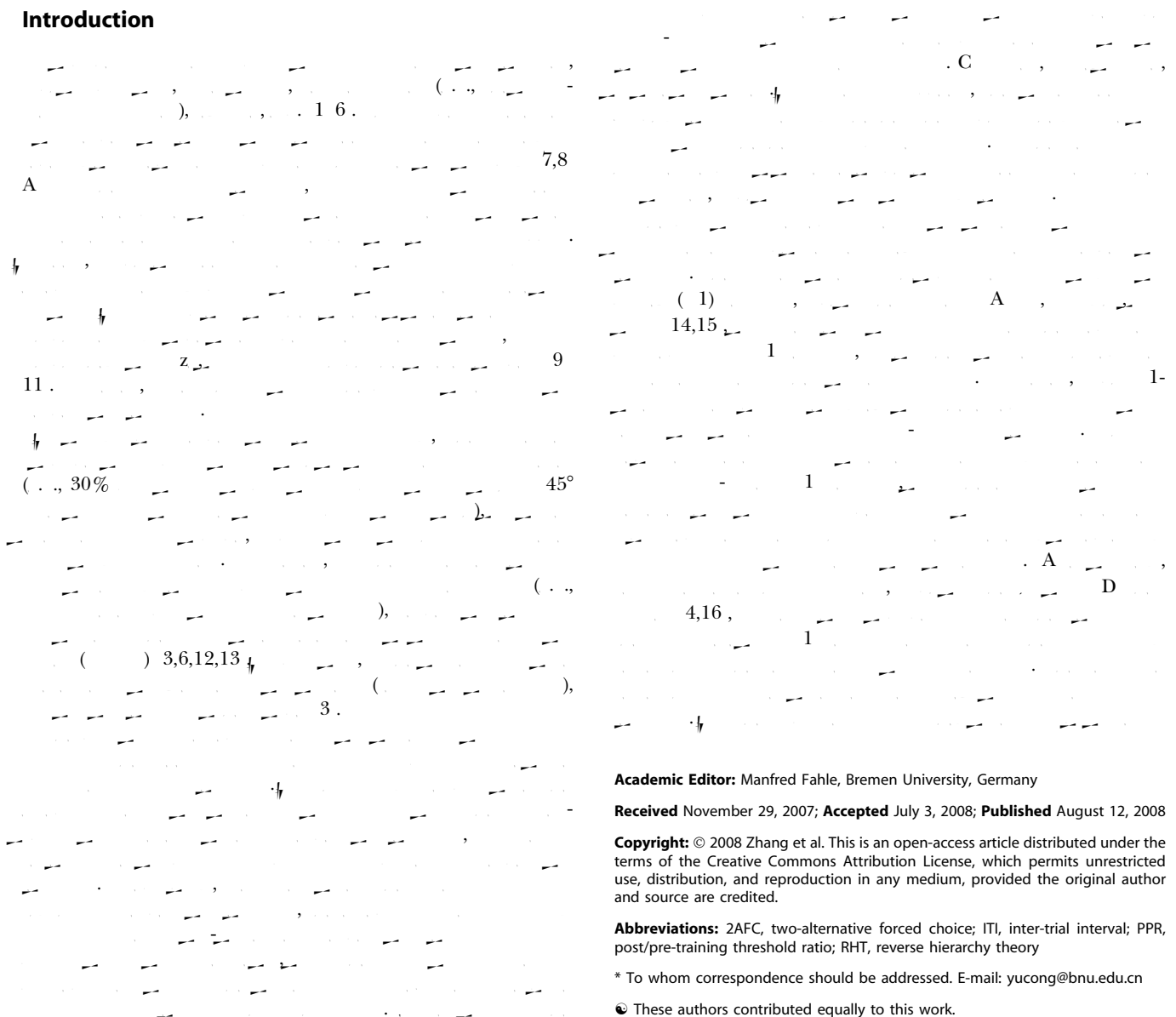
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**Perceptual learning of visual features occurs when multiple stimuli are presented in a fixed sequence (temporal patterning), but not when they are presented in random order (roving). This points to the need for proper stimulus coding in order for learning of multiple stimuli to occur. We examined the stimulus coding rules for learning with multiple stimuli. Our results demonstrate that: (1) stimulus rhythm is necessary for temporal patterning to take effect during practice; (2) learning consolidation is subject to disruption by roving up to 4 h after each practice session; (3) importantly, after completion of temporal-patterned learning, performance is undisrupted by extended roving training; (4) roving is ineffective if each stimulus is presented for five or more consecutive trials; and (5) roving is also ineffective if each stimulus has a distinct identity. We propose that for multi-stimulus learning to occur, the brain needs to conceptually “tag” each stimulus, in order to switch attention to the appropriate perceptual template. Stimulus temporal patterning assists in tagging stimuli and switching attention through its rhythmic stimulus sequence.**

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## Introduction



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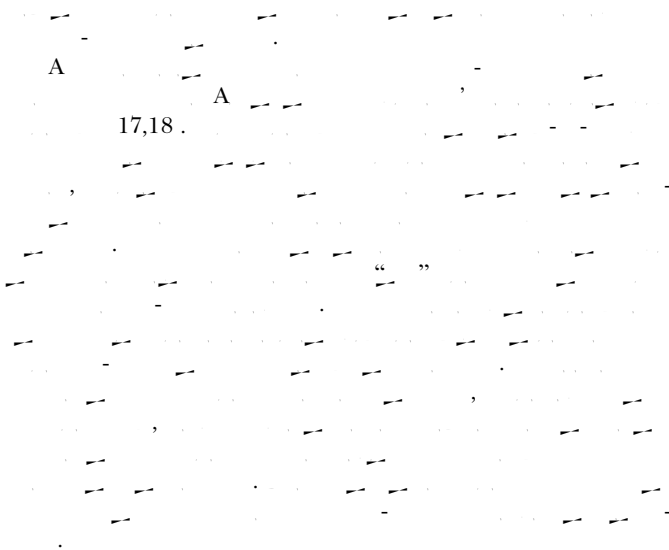
**Abbreviations:** 2AFC, two-alternative forced choice; ITI, inter-trial interval; PPR, post/pre-training threshold ratio; RHT, reverse hierarchy theory

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© These authors contributed equally to this work.

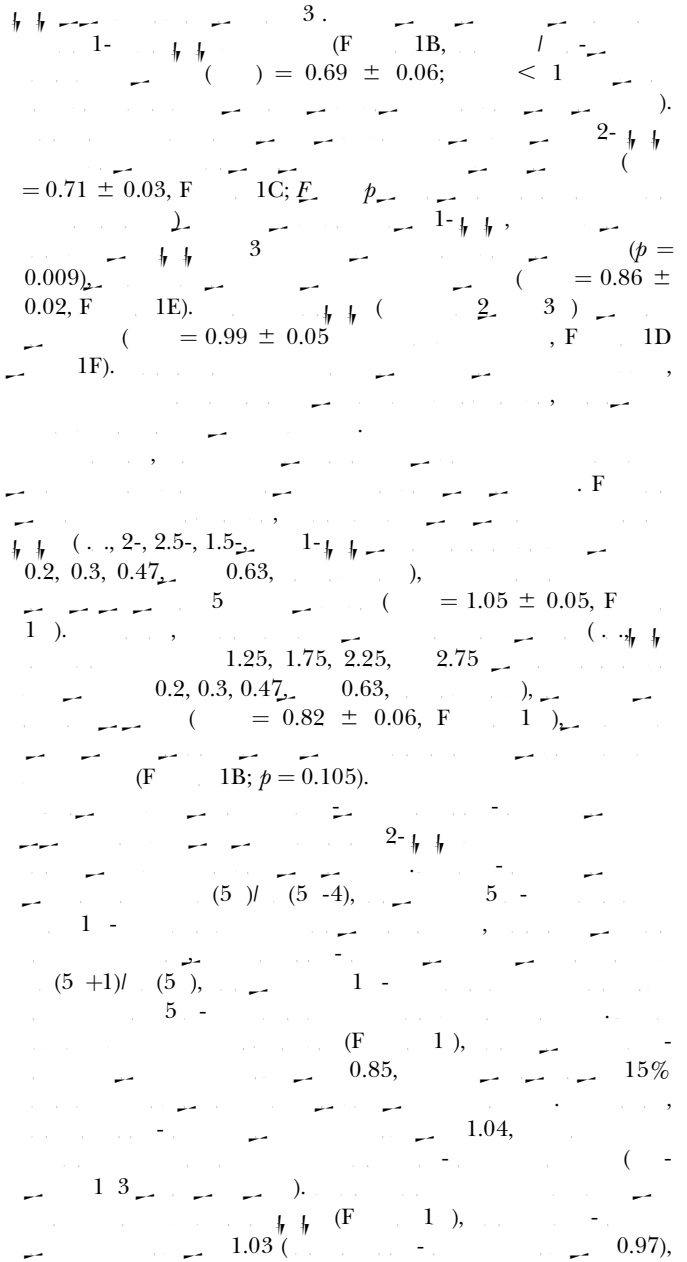
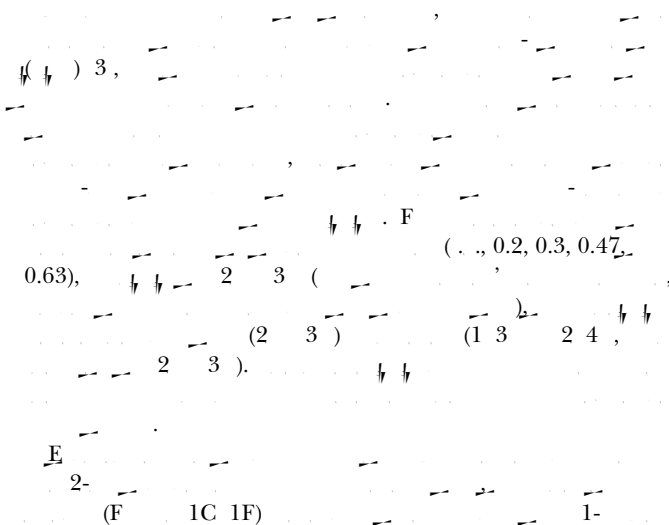
**Author Summary**

When a person learns to judge several stimuli in succession, like baseball pitches arriving at various speeds and spins, judgments may improve with practice only if these stimuli are presented in a fixed temporal sequence, rather than in a random order. These contrary effects suggest the need for proper stimulus coding for multi-stimulus learning in the brain. We studied how the temporal order of the stimuli affects the encoding, consolidation, and retrieval stages of perceptual learning that describe the basic stimulus coding rules throughout the learning process. We also studied why fixed stimulus sequences are required for multi-stimulus learning. Our results suggest that for multi-stimulus learning to occur, the brain needs to identify or tag each stimulus conceptually or semantically, so that the neural activity specific to each stimulus can be properly attended to. This high-level conceptual process adds to the current understanding of the mechanisms underlying perceptual learning and may have important implications for sensory training and rehabilitation.

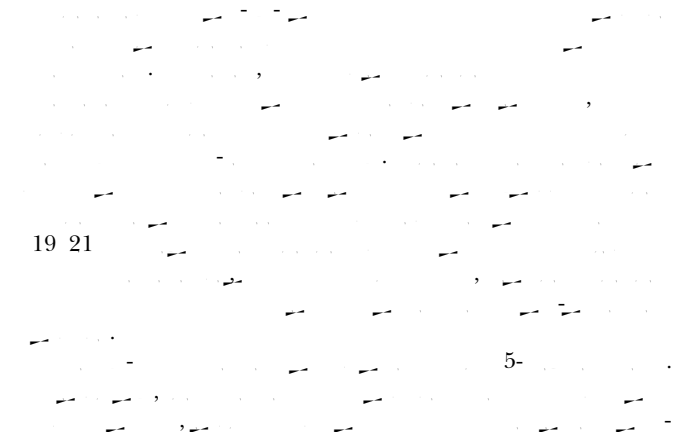


**Results**

**The Role of Stimulus Rhythm in Temporal Patterned Practice**



**Roving Interferes with Consolidation During Perceptual Learning**





**Figure 1.** Effects of Stimulus Rhythm and ITI on Perceptual Learning of Multiple Contrast Discrimination

(A) Illustration of a 2AFC trial in a contrast discrimination task. The observers judged which interval contained the higher contrast stimulus.

(B) Learning effects under the 1-s constant ITI condition from our previous study [3]. In this and other plots throughout the paper, data points below the red diagonal lines indicate learning. Error bars indicate s.e.m.  $\Delta C$  indicates contrast threshold.

(C and D) Learning effects under 2-s constant ( $F_{1,5} = 89.9, p < 0.001$ ; repeated measures ANOVA) and jittered ( $F_{1,5} = 0.08, p = 0.789$ ) ITI conditions,

respectively. In these and later plots, the gray dashed line indicates the mean PPR.

(E and F) Learning effects under 3-s constant ( $F_{1,5} = 84.8, p < 0.001$ ) (E) and jittered ( $F_{1,5} = 0.08, p = 0.786$ ) ITI conditions (F).

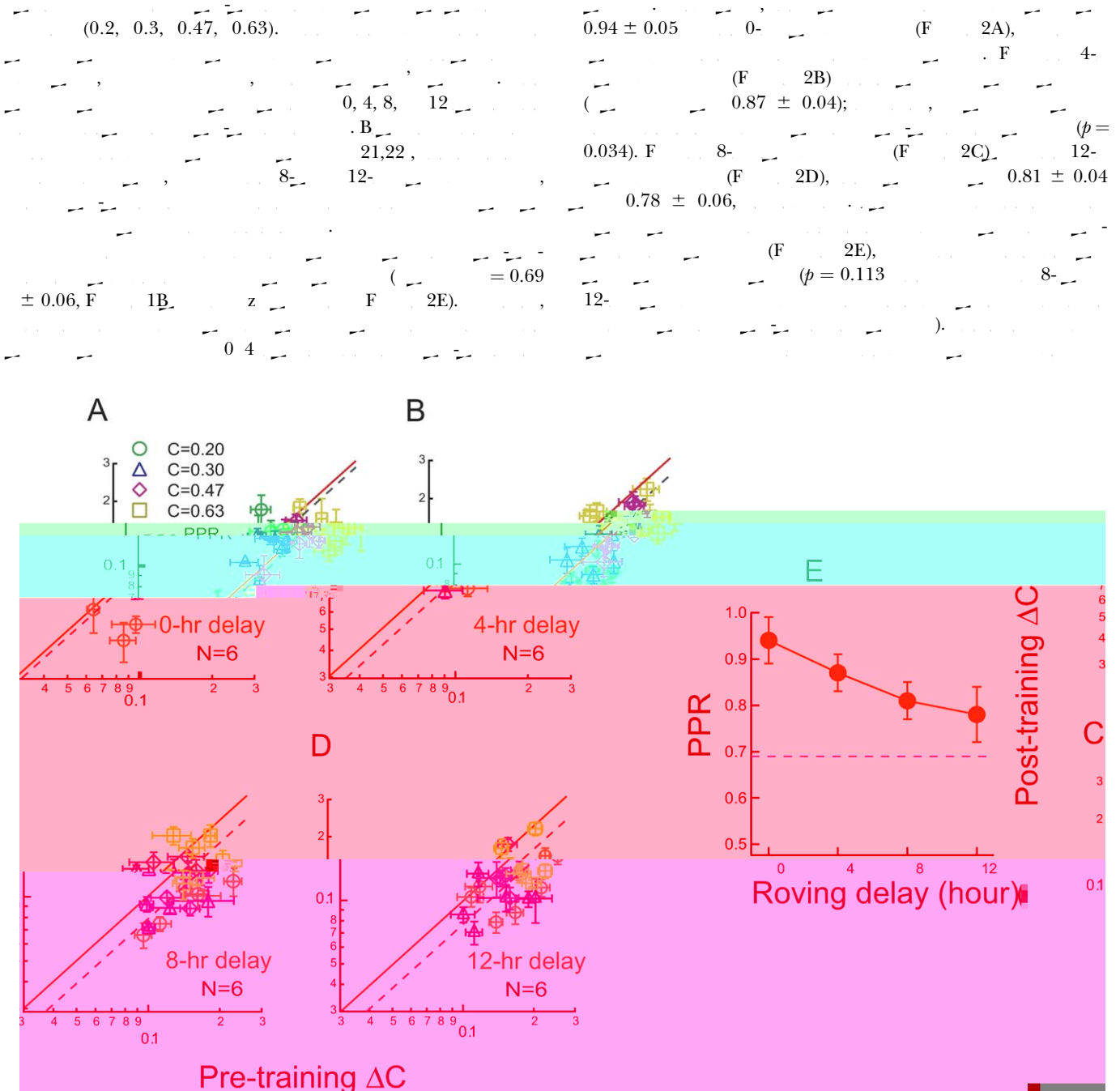
(G) Post- versus pre-training contrast thresholds with an uneven rhythm (neighboring ITIs = 2, 2.5, 1.5, and 1 s;  $F_{1,5} = 1.22, p = 0.320$ ).

(H) Post- versus pre-training contrast thresholds with a lengthening rhythm (neighboring ITIs = 1.25, 1.75, 2.25, and 2.75 s;  $F_{1,5} = 8.22, p = 0.032$ ).

(I) A summary of the learning effects in (B–H). Each bar represents the mean PPR over all four contrast conditions and all observers in the corresponding plot, as indicated along the x-axis. Previous result with 1-s ITI (blue colored) [3] was also plotted here for reference.

(J and K) Averaged within- and between-session contrast threshold changes under 2-s constant and jittered ITI conditions (see C and D), respectively, for each reference contrast and the overall means across all reference contrasts. Each data point represents one interleaved staircase run, and each session contains five consecutive runs.

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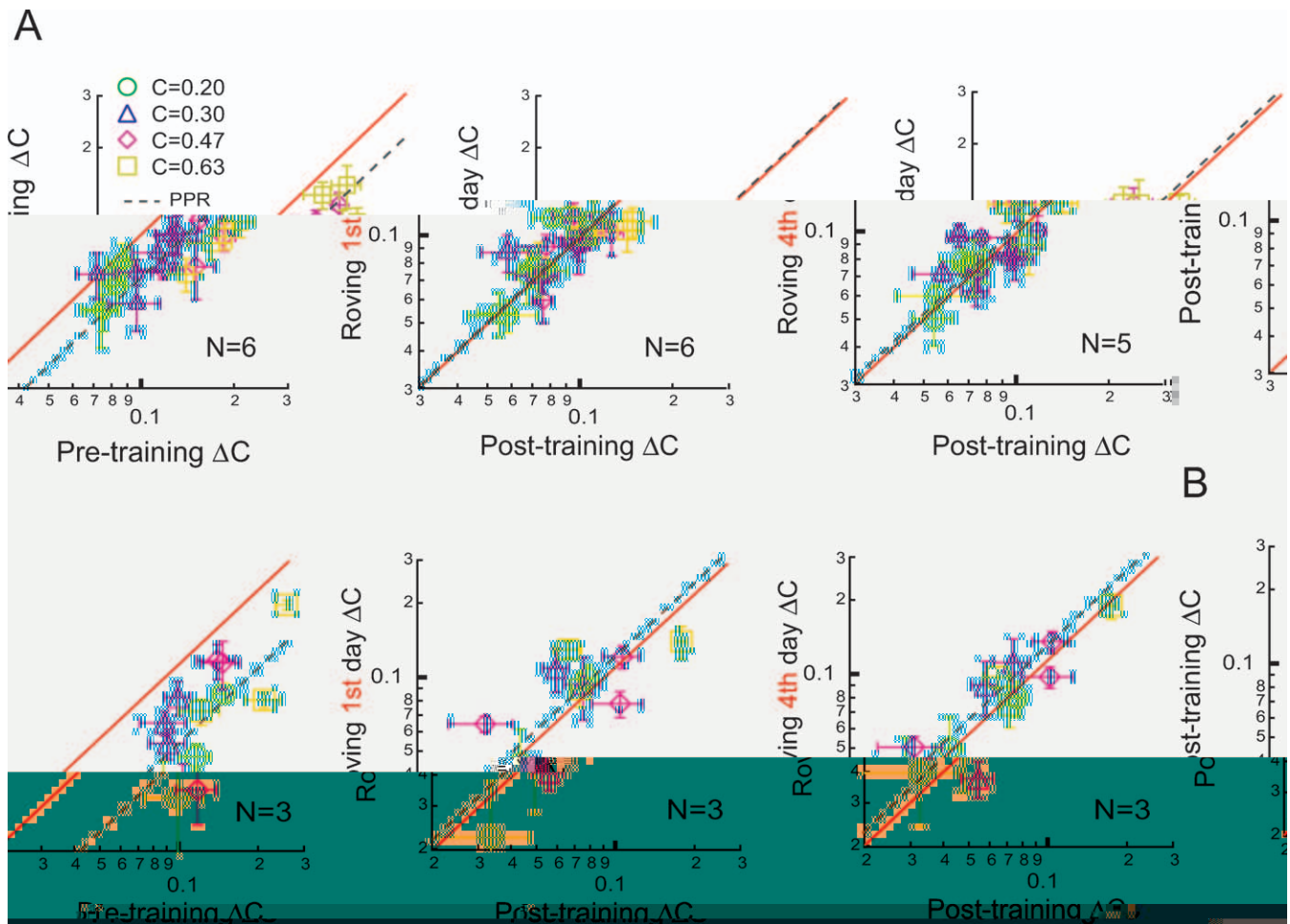


**Figure 2.** The Effects of Roving After Each Training Session on Perceptual Learning

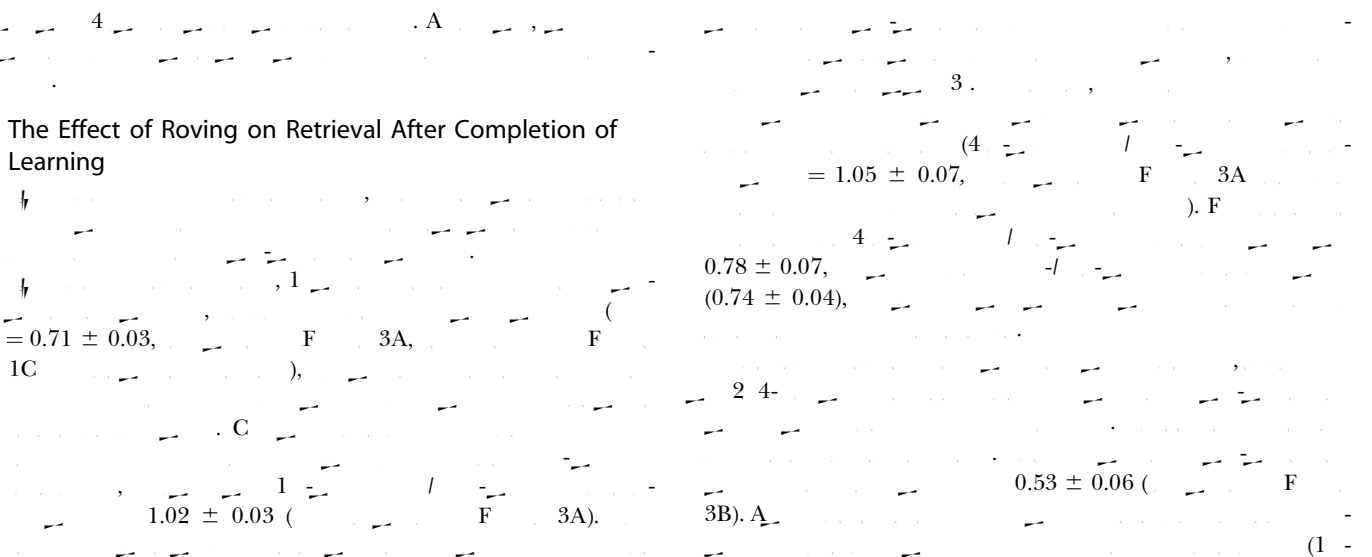
(A–D) Post- versus pre-training contrast thresholds in practice conditions in which each regular temporal-patterned training session was followed by roving interference after a delay of (A) 0 h ( $F_{1,5} = 1.48, p = 0.278$ ), (B) 4 h ( $F_{1,5} = 10.6, p = 0.022$ ), (C) 8 h ( $F_{1,5} = 42.0, p = 0.001$ ), and (D) 12 h ( $F_{1,5} = 13.1, p = 0.015$ ).

(E) PPR as a function of the delay of roving interference. The horizontal line indicates the PPR in regular temporal-patterned training without followed roving interference (Figure 1B).

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**Figure 3.** The Effects of Stimulus Roving After Learning  
 (A) Stimulus roving immediately after completion of temporal-patterned training. The left panel shows pre- versus post-training thresholds. The middle panel shows first roving session versus post-training thresholds ( $F_{1,5} = 0.24, p = 0.647$ ). Notice that the y-axis in the left panel becomes x-axis in the middle and right panels. The right panel shows the fourth (last) roving session versus post-training thresholds ( $F_{1,4} = 0.49, p = 0.520$ ; only five observers finished all four roving sessions).  
 (B) Same as (A) except that roving sessions started 2–4 wk after temporal-patterned training. The left panel shows pre- versus post-training thresholds. The middle panel shows first roving session versus post-training thresholds ( $F_{1,2} = 0.46, p = 0.570$ ). Notice that the y-axis in the left panel becomes x-axis in the middle and right panels. The right panel shows the fourth (last) roving session versus post-training thresholds ( $F_{1,2} = 2.36, p = 0.264$ ).  
 doi:10.1371/journal.pbio.0060197.g003



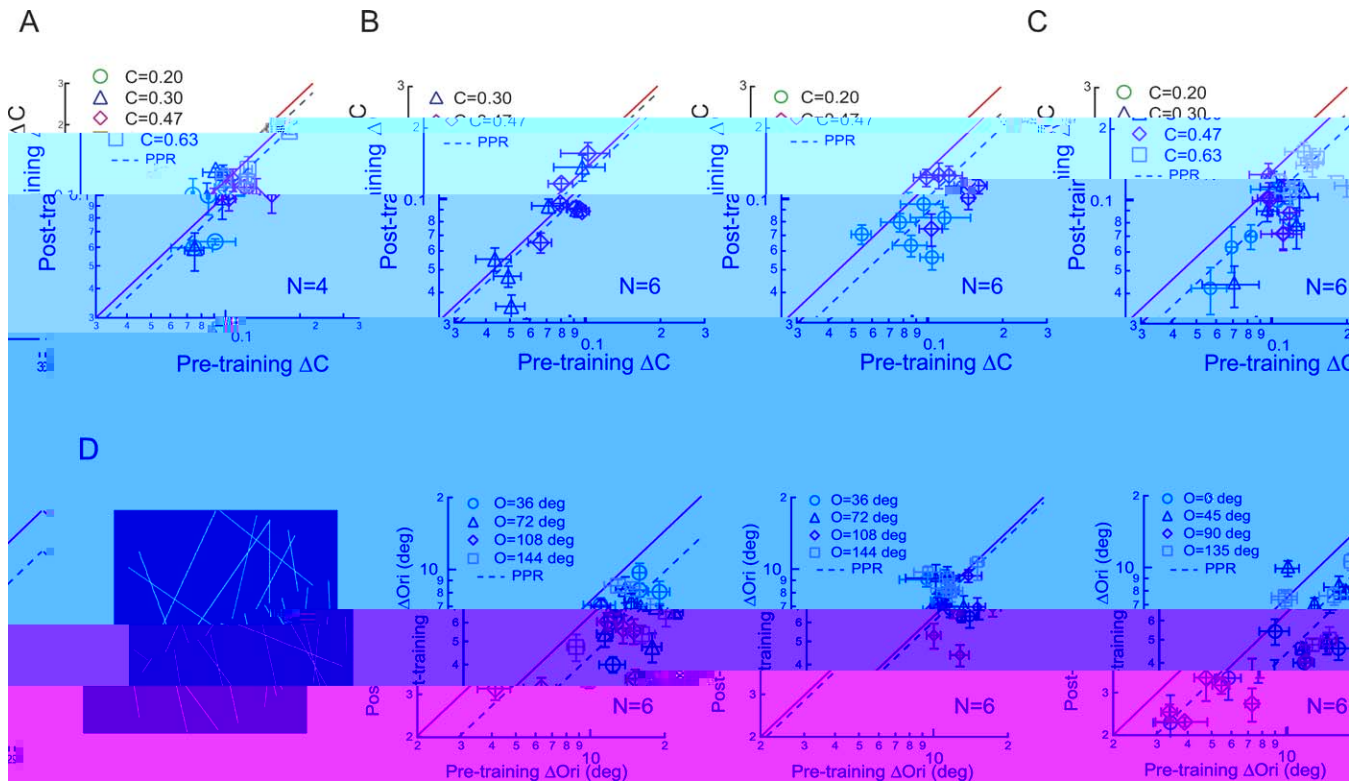
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How Many Trials Form a Useful “Block” for Learning?

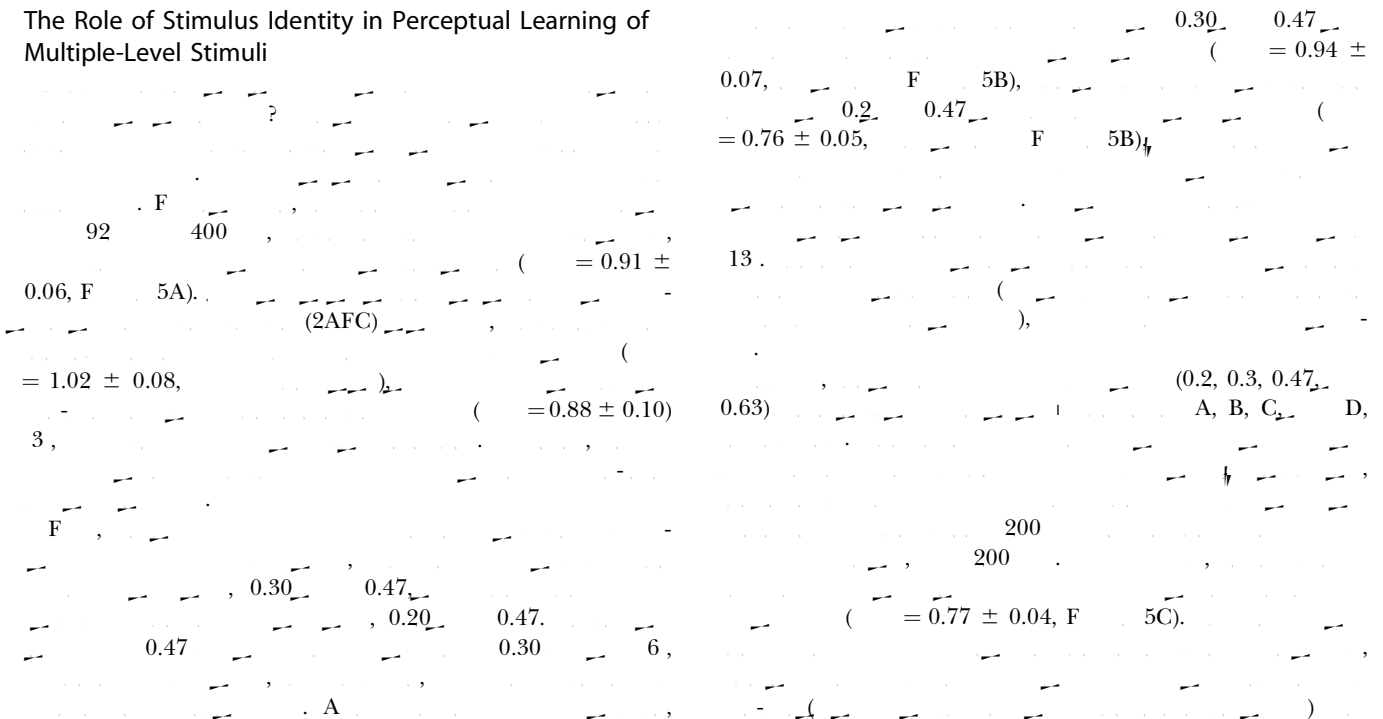
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**Figure 5.** Cases in Which Learning was Undisturbed by Stimulus Roving (Except (A))  
 (A) Post- versus pre-training contrast thresholds for four roving contrasts with longer stimulus duration at 400 ms ( $F_{1,3} = 3.29, p = 0.167$ ).  
 (B) Post- versus pre-training contrast thresholds for (left) a more similar pair of roving contrasts (0.30 and 0.47;  $F_{1,5} = 0.79, p = 0.414$ ) and (right) a more distinct pair of roving contrasts (0.20 and 0.47;  $F_{1,5} = 23.2, p = 0.005$ ).  
 (C) Post- versus pre-training contrast thresholds for four roving contrasts with pre-trial letter cues for their temporal identities ( $F_{1,5} = 34.7, p = 0.002$ ).  
 (D) Perceptual learning of orientation discrimination for illusory line stimuli (far left). Post- and pre-training orientation thresholds were compared for (middle left) the temporal patterning condition ( $F_{1,5} = 27.7, p = 0.003$ ), (middle right) roving condition ( $F_{1,5} = 0.61, p = 0.472$ ), and (far right) roving conditions with four cardinal or oblique orientations ( $F_{1,5} = 40.8, p = 0.001$ ). Thresholds for cardinal orientations (green and purple symbols), were lower than those for oblique orientations (blue and yellow symbols), showing a classical oblique effect.  
 doi:10.1371/journal.pbio.0060197.g005

The Role of Stimulus Identity in Perceptual Learning of Multiple-Level Stimuli



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### Discussion

#### Stimulus Coding Rules for Perceptual Learning

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