# **Current Biology**

# **Category-Induced Transfer of Visual Perceptual Learning**

# **Highlights**

- Perceptual learning transferred to features within the same category as the trained
- Category learning of orientations transferred to the opposite visual hemifield
- Category-induced transfer occurred only in the location category learning occurred

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# In Brief

Tan, Wang, et al. find that visual perceptual learning (VPL) of an orientation transfers to untrained orientations within the same category as the trained orientation, but not orientations from a different category. VPL may transfer to a greater degree in a natural environment that is categorically organized than in an experimental room.





# Category-Induced Transfer of Visual Perceptual Learning

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#### SUMMARY

Visual perceptual learning (VPL) refers to a long-term enhancement of visual task performance as a result of visual experience [1-6]. VPL is generally specific for the trained visual feature, meaning that training on a feature leads to performance enhancement only on the feature and those in its close vicinity. In the meantime, visual perception is often categorical [7–10]. This may partially be because the ecological importance of a stimulus is usually determined by the category to which the stimulus belongs (e.g., snake, lightning, and fish) [11]. Thus, it would be advantageous to an observer if encountering or working on a feature from a category increases sensitivity to features under the same category. However, studies of VPL have used uncategorized features. Here, we found a category-induced transfer of VPL, where VPL of an orientation transferred to untrained orientations within the same category as the trained orientation, but not orientations from the different category. Furthermore, we found that, although category learning transferred to other locations in the visual field, the category-induced transfer of VPL occurred only when visual stimuli for the category learning and those for VPL training were presented at the same location. These results altogether suggest that feature specificity in VPL is greatly influenced by cognitive processing, such as categorization in a top-down fashion. In an environment where features are categorically organized, VPL may be more generalized across features under the same category. Such generalization implies that VPL is of more ecological significance than has been thought.

#### **RESULTS**

#### **Experiment 1**

We examined how categorization influences featural specificity of VPL of an orientation detection task (for details, see STAR Methods).

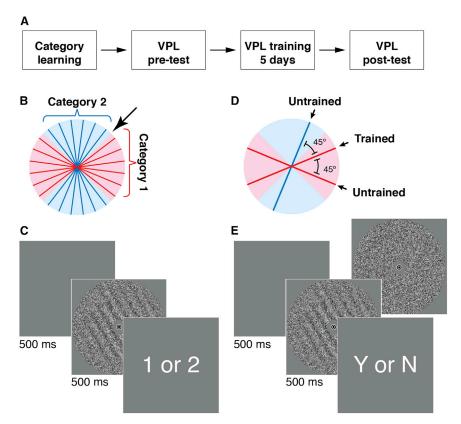
The experiment consisted of 4 stages that were conducted on different days: category learning  $\rightarrow$  VPL pre-test  $\rightarrow$  VPL training (5 days) → VPL post-test (Figure 1A). In the category learning stage, subjects (n = 12) were trained to categorize 12 orientations into category 1 (6 orientations) or 2 (the other 6 orientations). The category boundary orientation was randomly selected from 42.5°, 87.5°, 132.5°, and 177.5° clockwise from the vertical for each subject. Two groups of 6 orientations were separated by the category boundary that centered the range of the orientations (Figure 1B). In each trial, a high S/N ratio (0.2) Gabor was presented at the center of the computer screen. Subjects were asked to report whether the orientation in the Gabor belongs to category 1 or 2 (Figure 1C). Immediately after their response in each trial, subjects were provided with accuracy feedback regarding whether or not the category subjects chose was correct. Training was continued until subjects gave correct responses for the last 5 trials with each of the orientations.

Before and after VPL training (see below), the VPL pre- and post-tests were conducted to measure the detectability for 3 orientations (Figure 1D). These 3 orientations were the trained orientation that was trained in the VPL training stage (22.5° away from the category boundary; trained orientation), an untrained orientation from the trained category (45° from the trained orientation; same category orientation), and an untrained orientation from the untrained category (-45° from the trained orientation; different category orientation). In each trial, after the presentation of a bull's eye fixation, either a Gabor patch with the pre-determined threshold S/N or a 100% noise stimulus was presented. Subjects were asked to report whether or not an oriented structure was presented (Figure 1E).

At least 1 day after the VPL pre-test, subjects were asked to repeatedly perform the orientation detection task as in the VPL pre- and post-tests, for 5 days of VPL training, whose procedures were identical to the pre- and post-tests (e.g., threshold S/N versus 0 S/N stimulus) except the following two aspects: (1) subjects were asked to perform the task only for the trained orientation and (2) each day, the session consisted of 400 (1 orientation × 20 repetitions × 20 blocks) trials.

Figure 2 shows the mean ( $\pm$  SEM) improvement percentage (% correct in the post-test – % correct in the pre-test) for each of the three tested orientations. A one-way repeated-measures ANOVA with the main factor of orientation (trained, same category, and different category) on the improvement percentages showed that the main factor was significant ( $F_{2.20} = 5.623$ ;





p = 0.012). Post hoc t tests showed that the improvements on the trained and same category orientations were significantly greater than zero (t<sub>11</sub> = 4.245, p = 0.002, q < 0.05 [false discovery rate (FDR)], Cohen's d = 1.279; and t<sub>11</sub> = 3.211, p = 0.009, q < 0.05, Cohen's d = 0.968), whereas the improvement on the different category orientation was not significantly greater than zero (t<sub>11</sub> = 0.162; p = 0.875).

These results indicate the following points. After categorization learning, VPL transferred to the untrained orientation belonging to the same category as the trained orientation, but not to the untrained orientation beyond the category boundary. Given that the same category orientation and different category orientation are both 45° away from the trained orientation, whether transfer to an untrained orientation occurred or not should depend on whether the orientation belonged to the same or different category from the trained orientation. In addition, the results of control experiment 1 (n = 7) with the same procedure as in experiment (exp.) 1 except that there was no category learning showed performance improvement only for the trained orientation (see Figure S1A). We found the same tendency as in experiment 1 when subjects (n = 6) were trained and tested by a 2 forcedinterval choice task in control experiment 2 (see Figure S1B). Around 100% category learning performances for the three orientations rules out the possibility that category learning alone induced transfer of VPL (see Figure S1C). From these results, we conclude that the category learning made VPL of an orientation transfer to another orientation under the same category. We term this transfer as category-induced transfer of VPL (CIT).

Figure 1. Stimuli and Procedures in Experiment 1

(A) Procedures of the whole experiment.

(B) Orientations and category. The arrow points to the orientation as the category boundary, which was randomly selected from 42.5°, 87.5°, 132.5°, and 177.5° clockwise from the vertical for each subject. The orientations in the red zone belonged to category 1, and those in the blue zone belonged to category 2. The orientations here do not precisely reflect those used in the experiment.

(C) The procedure of each trial in the category training.

(D) Three orientations used in the VPL pre- and post-test stages, the trained orientation, an untrained orientation belonging to the same category as the trained orientation (same category orientation), and the other untrained orientation belonging to the other category (different category orientation). The angular difference between the trained orientation and the same category orientation was equal to that between the trained and the different category orientation.

(E) The procedure of each trial in the orientation detection task.

See also Figure S1.

#### **Experiment 2**

Next, experiment 2 tested the location specificity of category learning and CIT.

There were the same and different location conditions (Figure 3A; for details, see STAR Methods). The same location condition (n = 8) consisted of category learning → VPL pre-test → VPL training (5 days) → VPL post-test → location transfer test for category learning. Stimuli for the category learning and the VPL training and tests were all presented 7.5° left from the bull's eve fixation at the center of the display. After the VPL posttest, the location transfer test was conducted to examine whether the category learning transferred to the other visual hemifield. In this test, 10 trials for each of the 12 orientations were conducted at each of the locations at which the category learning had been conducted and the corresponding location in the other visual hemifield. The procedure was otherwise identical to the category learning stage. In the different locations condition (n = 8), the procedures were identical to the same location condition except for the following two aspects. First, the stimuli for the category learning were presented at the opposite visual hemifield to the stimuli for the VPL training and tests (Figure 3A). Second, there was no location transfer test.

Figure 3B shows the results of the VPL tests from the same location condition. A one-way repeated-measures ANOVA with the factor of orientation (trained, same category versus different category) on performance change (% correct in the post-test - % correct in the pre-test) showed a significant main effect ( $F_{2,14}=7.268;\ p=0.007$ ). In post hoc t tests, significantly greater than zero were the improvements on the trained orientation ( $t_7=3.317;\ p=0.016;\ q<0.05;\ Cohen's\ d=1.109$ ) and the same category orientation ( $t_7=2.643;\ p=0.033;\ q<0.05;\ Cohen's\ d=0.934$ ). In contrast, the improvement on

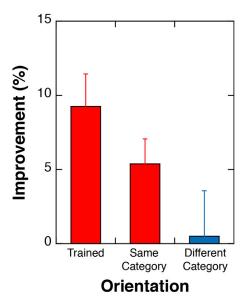


Figure 2. Results of Experiment 1

The mean (± SEM) improvement percentage is shown for the trained orientation, an untrained orientation with the same category as the trained orientation, and an untrained orientation with the different category from the trained orientation. VPL transferred only to the untrained orientation with the same category.

See also Figure S1.

the different category was not significantly greater than zero  $(t_7 = 0.489; p = 0.64)$ . These results show that CIT occurred.

The results of VPL tests from the different location condition differed from the same location condition (Figure 3C). A one-way repeated-measures ANOVA conducted in the same way as in the same location condition showed a significant main effect of orientation ( $F_{2,14}=9.178$ ; p=0.003). Post hoc t tests indicated that only the improvement on the trained orientation was significantly greater than zero ( $t_7=4.389$ ; p=0.003; q<0.05; Cohen's d=1.552). For neither the same category nor different category orientation, the improvement significantly was greater than zero ( $t_7=-1.199$ , p=0.269;  $t_7=0.102$ , p=0.921). These results indicate that no CIT was observed, although VPL of the trained orientation itself occurred.

Changes in *d*'s for the same and different location conditions showed the same tendency as percent correct changes (Figures S2A and S2B).

Figure 3D shows the results of category learning (before VPL) and the location transfer test in the same location condition. The mean ( $\pm$  SEM) correct percentage for the last 10 trials for each orientation of category training in the trained visual hemifield was significantly larger than 50%, the chance level ( $t_7 = 58.92$ ; p < 0.001; Cohen's d = 20.83). Correct percentages of 10 trials for the location transfer test in both the trained and untrained visual hemifields were significantly greater than 50%, the chance level ( $t_7 = 16.90$ , p < 0.001, q < 0.05, Cohen's d = 5.98;  $t_7 = 16.99$ , p < 0.001, q < 0.05, Cohen's d = 6.01). Paired t test showed no significant difference in the mean correct percentage between the trained and untrained visual hemifields ( $t_7 = 0.35$ ; p = 0.733). It is unlikely that 10 trials with no accuracy feedback made categorization learning in the untrained visual hemifield

during the location transfer test. These results indicate that category learning transferred to the other visual hemifield, suggesting that category learning in the current setting is not location specific, as previously found [9, 12–16] (but see [17]). The results also suggest that category learning lasted until after the VPL post-test, assuring that VPL occurred while the categorization remained effective.

The results of experiment 2 collectively indicate that, although the categorization learning was not location specific, for CIT to occur, the stimuli for the categorization learning and VPL had to be presented at the same location.

#### **DISCUSSION**

A visual feature trained in most VPL experiments is very simple and not categorically organized. The reliance of VPL studies on simple features has led researchers to question the generalizability of these findings beyond the experimental setting. It is not clear whether a VPL paradigm is applied to our everyday life. The present finding of CIT-VPL suggests that VPL indeed plays an important role in adapting to or surviving an environment. CIT-VPL indicates that encountering or working on a visual feature from a category increases sensitivity to features under the same category, which may in turn lead to better detection of an object under the category. Another study has also found that VPL of a grating orientation transfers orientations of a natural object [18]. Thus, in a natural environment, VPL may occur in a more generalized and useful way than most experiments of VPL have shown.

Two previous studies have developed methods to reduce or eliminate location specificity [19–21]. However, these methods may not be directly related to the current finding. First, these led to the reduction or elimination of *location* specificity in VPL rather than *feature* specificity. Second, the results are not category dependent.

How does CIT-VPL occur in visual information processing? Here is one possibility (see Figure S3): training of classifying orientations into two categories makes the two category units in the category stage of visual processing. The unit for one category is activated when an orientation belonging to the category is presented. Results of experiment 2 and other studies indicate that category learning is not location specific and therefore occurs in a relatively higher-level stage [9, 12–16] (but see [17]). Although an orientation is being trained for a detection task, the unit of the orientation at a location-specific feature stage is activated and provides input to the category stage. Then, at the category stage, the unit for the category to which the trained orientation belongs is activated and provides top-down signals to the units for all of the orientations within the category at the feature stage. This may cause learning of the orientations within the category. This model may account for the result that stimuli for category learning and VPL need to be presented at the same location although category learning is not location specific. Future research may help to build a more detailed model.

High specificity of VPL termed "the curse of specificity" [22] could hinder VPL from being used as an effective clinical tool to cure or reduce visual degradation or declination due to injuries, eye diseases, and aging. However, VPL training either followed by category training or conducted in an everyday

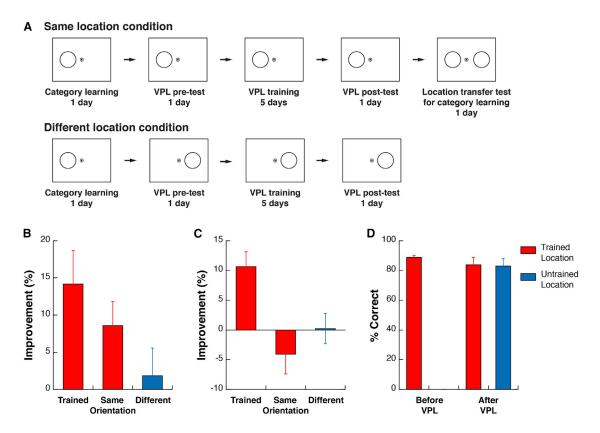


Figure 3. Procedures and Results of Experiment 2

(A) The stages of the experiment. Circles represent stimuli.

(B) The mean (± SEM) improvement (%) for the VPL trained orientation (trained), an untrained orientation belonging to the same category as the trained orientation (same), and an untrained orientation beyond the category of the trained orientation (different) in the same location condition. Stimuli for category learning and for VPL were presented at the same location.

(C) The mean (± SEM) improvement (%) in the different locations condition in which stimuli for category learning and for VPL were presented in different visual hemifields.

(D) The mean (± SEM) correct % in the category learning (before VPL) in the left visual hemifield and location transfer test (after VPL). The red bars represent the correct percentages in the last 10 trials of the category training (before VPL) and in the location transfer test (after VPL) in the same location as in the category training. Similar high correct mean percentages were obtained from the data for each of the first 3 and 5 trials for the location transfer test in both the trained and untrained visual hemifields. The blue bar represents the correct percentage in the location transfer test (after VPL) when the stimuli were presented in the different visual hemifield than in the category training.

See also Figures S2 and S3.

environment may greatly reduce the curse of specificity on the trained feature and would be a strong clinical tool.

How would CIT-VPL occur for VPL of a discrimination task? Although VPL of orientation detection may as well be associated with the peak enhancement of tuning curves of the trained orientation, VPL of fine-grained discrimination of orientations may be associated with sharpening of the slopes of tuning curves of orientations surrounding the discriminated orientations [23, 24]. If categorization of orientations assimilates the shapes of tuning curves of orientations within the same category at the category stage, the sharpening of tuning curves of orientations surrounding the discriminated orientations may spread to those of orientations within the same category. This may lead to CIT-VPL of orientation discrimination. Future research needs to test this possibility.

It has been reported that transfer of VPL can occur due to prolonged training at threshold [25]. This raises the question as to whether CIT-VPL simply originates from the possibly heavy exposure to a wide range of orientations (though they were above threshold) during the phase of learning categories. Note that the untrained orientations belonging to the same category and different category from the VPL trained orientation had the same angular distance from the trained orientation and were exposed to subjects as frequently as the trained orientation during the category training. If the amount of exposure to an orientation during the phase of learning categories had determined transfer, it should have occurred not only with the untrained orientation belonging to the same category but also with the untrained orientation belonging to the different category. However, transfer occurred only with the orientation with the same category. Thus, mere exposure to these orientations cannot explain CIT-VPL.

In conclusion, the results of the experiments of the current study suggest that feature specificity in VPL is greatly influenced by cognitive processing, such as categorization in a top-down fashion. If VPL is effectively combined with categorization, the

curse of specificity in VPL may be relatively easy to overcome and VPL would be a stronger clinical tool.

#### **STAR**\*METHODS

Detailed methods are provided in the online version of this paper and include the following:

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#### SUPPLEMENTAL INFORMATION

Supplemental Information can be found with this article online at https://doi. org/10.1016/j.cub.2019.03.003.

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#### **AUTHOR CONTRIBUTIONS**

Q.T. and T.W. designed experiments. Q.T. and Z.W. collected data. Q.T., Z.W., Y.S., and T.W. analyzed data. Y.S. and T.W. wrote the paper.

#### **DECLARATION OF INTERESTS**

The authors declare no competing interests.

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### **STAR**\*METHODS

#### **KEY RESOURCES TABLE**

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and Algorithms		
MATLAB 2015b	The MathWorks	https://www.mathworks.com/
RStudio	RStudio	https://www.rstudio.com/
R-3.3.3	The R Foundation	https://www.r-project.org/
Psychtoolbox 3.0.13	[26]	http://psychtoolbox.org/

#### **CONTACT FOR REAGENT AND RESOURCE SHARING**

Further information for resources should be directed and will be fulfilled by the Lead Contact, Takeo Watanabe (takeo\_watanabe@brown.edu).

#### **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

All participants employed in the current study were young healthy humans with normal or corrected-to-normal vision. Twelve (7 females) subjects participated in Experiment 1, 9 subjects (4 females) in Control Experiment 1 and 6 subjects (3 females) in Control Experiment 2 (originally 7 subjects but one subject was an outlier and excluded from data analysis) and 16 subjects in Experiment 2. They were naive about a VPL experiment. Their ages ranged between 18 and 26 years old. All participants gave their written informed consent to participate. All experimental procedures were approved by the institutional review board at Brown University.

#### **METHOD DETAILS**

#### **Experiment 1**

#### Stimuli and apparatus

Experiments were conducted in a dimly lit room. Stimuli were presented on a 19-inch Pure Flat Sony Trinitron CRT monitor, with a spatial resolution of 1024 × 768 pixels and a refresh rate of 100 Hz. Subjects viewed the stimuli from a distance of 57 cm. Their head position was stabilized using a chinrest. Oriented Gabor patches (spatial frequency = 1 cycle/degree, contrast = 100%, Gaussian filter sigma = 2.5°; random spatial phase) were presented within an annulus subtending 0.75° to 5°. The central circle and the background were gray with the mean luminance of the annulus. The Gabor patches were spatially masked by a noise pattern using a pixel substitution method. Noise fields were generated from a sinusoidal luminance distribution at a given signal-to-noise (S/N) ratio. For example, in the case of a 10% S/N ratio, 90% of the pixels of the Gabor patch were replaced with a noise pattern. The mean background luminance was 33 cd/m², and the maximum luminance of the display was 67 cd/m².

#### Category learning task

The category boundary orientation was randomly selected from 42.5°, 87.5°, 132.5° and 177.5° clockwise from the vertical for each subject. Two groups of 6 orientations were separated by the category boundary that centered the range of the orientations (Figure 1B). The 12 orientations of Gabors were evenly spaced (15° apart). As in Figure 1C, subjects performed a modified two-alternative forced-choice task, in which a high S/N ratio (20%) patch in a certain orientation was presented. Each trial started with a 500-ms fixation interval. Then, a stimulus was presented for 500 ms and was followed by a response interval. Subjects were asked to report whether the orientation in a Gabor belongs to Category 1 or Category 2, by pressing the '1' or '2' button on a keyboard, respectively. A high pitch beep followed a correct response while a low pitch beep followed a wrong response. The order of the presentations of 12 orientations was randomly determined for each subject. Training was terminated when subjects gave correct responses for the last 5 trials with each of the orientations. It took around 15 min for each subject to complete the categorization training.

#### Yes-or-no orientation detection task of VPL

A yes-or-no orientation detection task was conducted on one orientation (trained) for the VPL training stage and on three orientations for test stages. These 3 orientations were; the trained orientation that was trained in the VPL training stage ( $22.5^{\circ}$  away from the category boundary), an untrained orientation from the trained category ( $45^{\circ}$  from the trained orientation), and an untrained orientation from the untrained category ( $-45^{\circ}$  from the trained orientation). As shown in Figure 1E, in each trial, subjects performed a yes-or-no orientation detection task for VPL, in which either a Gabor patch with an individually predetermined threshold S/N ratio (described below) or a noise (0% S/N ratio) was presented. Each trial started with a 500-ms fixation interval. After a 500-ms stimulus presentation, letters Y and N were displayed, one on the left and the other on the right to the fixation, randomized across trials. Subjects were asked to



report whether the display contains a grating or not, by pressing the button of Y or N. Subjects were instructed to fixate on a bull's eye fixation presented against a gray disk (0.75° radius) throughout each trial. The next trial started immediately after the subject's response. No feedback regarding the accuracy of a subject's response was provided.

In the VPL pre- and post-test stages, there were 60 (3 orientations x 20 repetitions) trials, whose order was counterbalanced for each subject. Each test stage took approximately 8 min. The VPL training stage consisted of 400 (1 orientation x 20 repetitions x 20 blocks) trials for each day. There was a small time break between blocks. Each day the training session took 40 to 50 min. The training stage lasted 5 days.

#### Threshold measurements

Before the pre-test, the S/N ratio threshold for each of the three orientations used for training and/or the pre- and post- tests was measured using a standard 2-down-1-up staircase rule, which converges to a 70.7% accuracy rate. The threshold for each orientation was measured in each block. The initial S/N ratio was set to 25%. The step size of the staircase was 0.05 log units. Each block ended after 10 staircase reversals—typically about 40 trials. The geometric mean of the last six reversals was taken as the S/N ratio threshold for that block.

#### Control Experiment 1 (with no category learning)

The procedures were the same as in exp. 1 except that there was no category learning. See Figure S1A.

#### Control Experiment 2 (with a 2 interval forced choice detection task)

The experimental procedures were identical to exp. 1 except that a 2IFC task was used in the VPL training and the VPL pre- and post-tests. One interval was presented with a Gabor patch (same as in exp. 1) with certain S/N ratio, and the other interval was presented with a stimulus that contains only noise. In the 2IFC task, subjects determined during which interval an orientated structure (Gabor patch) was presented. Each trial started with a 500-ms fixation interval. This was followed by two 50-ms stimulus intervals separated by a 300-ms blank inter-stimulus interval. Subjects were asked to press the '1' key on the keyboard if they saw an oriented structure in the stimulus presented in the first interval and to press '2' key if they saw an oriented structure in the second interval. Subjects were instructed to fixate on a white bull's-eye fixation point presented against a gray disk (0.75° radius) throughout each trial. The next trial started immediately after the subjects' response. No feedback regarding subjects' accuracy was provided to subjects. Each of the S/N thresholds for each of the three orientations (as in exp. 1) was measured in a block. The S/N threshold was determined using a standard 2-up-1-down staircase rule, which converges to an accuracy of about 70.7%. The initial S/N ratio was set to 25%. The step size of the staircase was 0.05 log units. Each block ended after 10 reversals, which yielded approximately 40 trials for each block. The geometric mean of the last six reversals was calculated as the S/N threshold for that block. During the pre- and post-tests, the threshold for each of the three orientations (trained, same category and different category orientations) was measured for 3 blocks, resulting in 9 blocks in total during tests. The order of the orientations was randomized across blocks. During the training, S/N thresholds for the trained orientation were measured for 15 blocks. See Figure S1B for the results.

#### **Experiment 2**

There were the same location condition and different location condition in each of which a different group of participant took part, as shown in Figure 3A. Only in the same location condition, the location transfer test for the category learning was conducted after the 4 stages such as the category learning, VPL pre-test, training and post-test stages.

#### Same location condition

In this condition, in all of the category learning stage, VPL pre-test, VPL training and VPL post-test stages, stimuli were all presented 7.5° left from the central bull's eye fixation. Except for the location of stimuli, the other aspects of procedures of the category learning, VPL pre-test, training and post-test stages were identical to exp. 1. In the location transfer test for category learning, the same procedures as in the category learning stage were conducted except the following aspects. First, only 10 trials for each of the 12 orientations were given to subjects at the location at which the category training was conducted (7.5° left from the central bull's eye fixation) or on the opposite side (7.5° right from the bull's eye fixation). Second, trials with 12 orientations at 2 locations were conducted in a counterbalanced manner without providing subjects with accuracy feedback to avoid subjects from further improving category learning during the location transfer test.

#### **Different locations condition**

In the category learning stage, stimuli were consistently presented 7.5° left from the central bull's eye fixation. In contrast, in the VPL pre-test, VPL training and VPL post-test stages, stimuli were consistently presented 7.5° right from the central bull's eye fixation. There was no the location transfer test for category learning. This was because we considered the possibility that presentations of Gabors 7.5° right from the bull's eye fixation during the VPL training and test stages could influence the transfer of the category learning.

#### **QUANTIFICATION AND STATISTICAL ANALYSIS**

Only behavioral data were collected in all experiments.

#### **Experiment 1**

For categorization training, subjects were asked to press the '1' key on a keyboard if the orientation in the Gabor belongs to Category 1 and the '2' key if it belongs to Category 2. Training was continued until subjects gave correct responses for the last 5 trials with each

of the orientations. Before and after VPL training, the VPL pre-test and post-test were conducted to measure the detectability for 3 different orientations. In each trial, an orientation detection task was conducted. Either a Gabor patch with the pre-determined threshold S/N or a 100% noise stimulus was presented. Subjects were asked to press the Y key on a keyboard if an oriented structure was presented and the N key if an oriented structure was not presented. There were 60 (3 orientations x 20 repetitions) trials, whose order was counterbalanced for each subject. Improvement percentage (% correct in the post-test - % correct in the pre-test) for each of the three tested orientations was calculated. A one-way repeated-measures ANOVA with the main factor of orientation (Trained, Same Category, and Different Category) was conducted on the improvement percentages. Post hoc t tests examined whether or not the improvements on each of the three orientations was significantly larger than zero. The false discovery rate (q) was set to 0.05. To measure effect sizes, Cohen's d was calculated as mean difference/standard deviation. Basically the same statistical analysis was conducted with data in Control Experiment 1 (see Figure S1A).

In Control Experiment 2, S/N ratio thresholds were measured in the pre- and post- tests, as mentioned above. Improvement was defined by (threshold in pre-test – threshold in post-test)/(threshold in pre-test).

#### **Experiment 2**

There are two conditions, the same location and different location conditions, in which category training and VPL training were conducted at the same and different locations, respectively. The statistical analyses to test any difference in performance improvement among the three orientations in each condition were identical to those of exp. 1. We also applied t tests to examine whether each of the mean correct percentages for the last 10 trials for category training in the trained visual hemifield and the mean correct percentages of 10 trials for the location transfer test for category learning in the trained and untrained visual hemifields was greater than 50%. Paired t test was also applied to examine whether there was any significant difference in the mean correct percentage between the trained and untrained locations for the location transfer test.

In addition to % correct, d' was also calculated from the number of trials in which subjects pressed the Y key when an oriented structure was really presented (hit) and the number of trials in which subjects pressed the Y key when an oriented structure was not presented (false alarm).

$$d' = Z_{FA} - Z_{Hit}$$

where FA and Hit refer to the false alarm and hit rates, respectively, that correspond to right-tail probabilities on the normal distribution. Z<sub>FA</sub> and Z<sub>Hit</sub> denote the z-scores that correspond to these right-tail p values represented by FA and Hit, respectively.

Then mean d' changes for each of the three orientations (trained, same category, different category) was calculated by (d' in posttest - d' in pre-test)/(d' in pre-test) x 100 across the subjects, for each of the same and different location conditions. See Figures S2A and S2B.

#### **DATA AND SOFTWARE AVAILABILITY**

Data and custom-built MATLAB programmed scripts are available upon request.