Perceptual Learning: Sharing and Keeping Learned Improvements within a Category

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Perceptual learning is highly specific for the trained feature with limited generalization. A new study shows broad transfer of perceptual learning for features belonging to the same category, but no transfer for features of different categories.

For a non-expert, looking at an X-ray image reveals not much more than the presence of many shades of grey. For a radiologist, however, the greys will easily form complex structures, which allow, for example, the detection of early signs of cancer. This remarkable ability comes from the simple fact that our perceptual abilities are not constant, but depend crucially on practice. Having viewed thousands of X-rays, a radiologist has trained his visual system to see meaningful structures which the non-trained observer fails to see. The process of training and practicing our senses to improve perceptual abilities is called perceptual learning and holds for all sensory modalities [1–4].

Research in visual perceptual learning uses simple stimuli characterized by very simple, basic features such as orientation, direction of motion, or contrast [2]. The idea is that the physical properties of simple features can easily be fully controlled, characterized, and manipulated, which is much more difficult when using natural or anthropogenic scenes as the example of X-ray images [5].

A fundamental and surprising property of visual perceptual learning is the specificity of what is learned. In a typical visual perceptual learning experiment, participants are trained over several sessions to discriminate or to detect a simple feature, such as the orientation of a line, or of a noise field (Figure 1). The gain in performance measured before and after the training marks the amount of learning. For example, when subjects have learned a 45° orientation, there is no gain for an oriented structure of 90°, a phenomenon often denoted as the "curse of specificity" [6]. Why perceptual learning shows such specificity has triggered a substantial body of research. Because training on visual tasks can be used to treat forms of abnormal vision, such as amblyopia, this limited transfer is highly undesirable: it would be much more useful if generalization were as broad as possible [6].

A new study by Tan *et al.* [7], reported in this issue of *Current Biology*, now shows that orientation specificity of visual perceptual learning is absent when, prior to training, participants had learned to classify different orientations into two orientation categories. As a result of this prior learning, the typically observed feature specificity became replaced by a specificity for categories, but with category-induced transfer of learned gains in perceptual performance with features within a category.

The work of Tan *et al.* [7] starts from the apparent way that visual perception and decision-making operates largely at a categorical level but not on simple features [8]. In everyday life, we rely on categories to judge ecological importance and chances of survival [9]. To know when to run when seeing a potentially dangerous animals, we do not have to know its precise striping pattern, but simply that it is a tiger. In contrast, visual perceptual learning experiments have tended to employ simple features, rather than categorically organized ones: how categorization of features affects learning and specificity of learning was not known.

To address these questions, in their study Tan *et al.* [7] first trained subjects in a category learning task to classify 12 different orientations of a small Gabor patch into two categories divided by a boundary arbitrarily set for each individual (Figure 1). As a next step, the participants underwent a typical visual perceptual learning task, where they were trained over several days to detect an oriented structure in a noise field (Figure 1). By changing the signal-to-noise ratio, the detection can be made more or less difficult. Before and after the training, the detectability for three different orientations was measured: for the orientation that was trained in the visual perceptual learning training (22.5° away from the category boundary, denoted trained orientation); for an untrained orientation from the trained category (45° from the trained orientation, denoted same category orientation); and for an untrained orientation from the untrained category (–45° from the trained orientation, denoted different category orientation).

Tan *et al.* [7] found that the gain for the trained orientation transferred to non-trained orientations belonging to the same category, but there was specificity — there was no transfer to non-trained orientations belonging to a different category. Both non-trained orientations were 45° away from the trained orientation; however, whether there was transfer or not depended on whether the non-trained orientation belonged to the same category as the trained one. After categorization, subjects were able to better detect oriented features in a noisy environment without having trained it, given that the feature was of the same category. The authors called this novel phenomenon category-induced transfer.

Besides specificity for orientation, another fundamental specificity in visual perceptual learning is location specificity [2]. Learning a feature at a specific

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location within the visual field does not transfer to other locations. In a second experiment, therefore, Tan *et al.* [7] tested location specificity of both the learning of a category and the category-induced transfer. To evaluate a possible location-specificity of category learning, they repeated the experiment as described above, but additionally tested whether category learning transferred to a different location in the other visual hemifield. They found that category learning in contrast to feature learning was not location specific, as it transferred to another visual hemifield.

To test a possible location-specificity of the category-induced transfer, Tan *et al.* [7] ran another experiment, where the locations for category learning and for visual perceptual learning were different. In a first step, the categories were learned in the left hemisphere. Then, in contrast to the first experiment, during the training sessions to improve detectability, the stimuli were presented in the right hemifield. Under these conditions, although subjects improved their performance for the trained orientation, the previously observed category-induced transfer was lost. This indicates that while the categorization learning itself is not location specific, category-induced transfer requires that the stimuli for the categorization and for visual perceptual learning are presented at the same location.

There is a long-lasting debate about the anatomical sites in the brain that mediate the changes in perception induced by visual perceptual learning. Is this happening in early stages of processing such as primary visual cortex (V1), which is characterized by neurons that are narrowly-tuned and have spatially localized receptive fields? This bottom-up route is easily compatible with the high specificity of visual perceptual learning [10]. Alternatively, higher-order stages and decision areas with very large and broadly tuned neurons might have a top-down influence on early stages of processing [11]. For a long time, therefore, understanding the processes that create or eliminate specificity of visual perceptual learning has been considered a key for understanding the neural basis of visual perceptual learning [12–16].

Many approaches have been taken to understanding the conditions that lead to

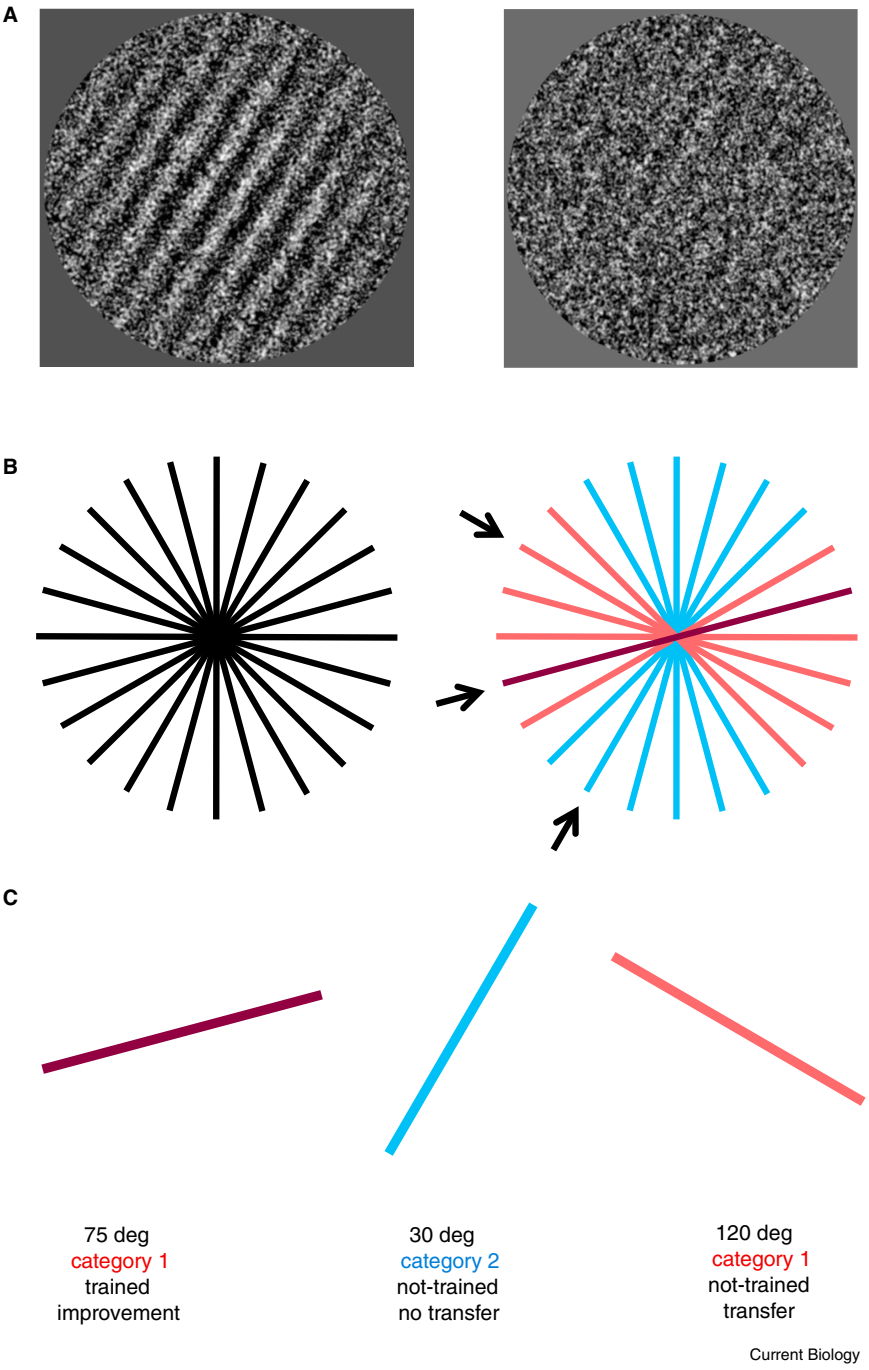

Figure 1. Oriented structures as features and categories.
Orientations are presented as oriented Gabor patches with different signal-to-noise-ratios to vary difficulty of detection (A). During category learning, twelve evenly distributed orientations (here depicted as lines for convenience) had to be categorized into two different categories as marked by different colors (B). To induce visual perceptual learning (visual perceptual learning), one orientation was trained in a detection task (dark red). Afterwards, detection performance was re-assessed for the trained and for two non-trained orientations, one belonging to the trained (red), the other to the non-trained category (blue; arrows in B mark the three tested orientations). The training-induced gain in performance transferred to other orientations of the same category (category-induced transfer), but not to orientations of the non-trained category, although both non-trained orientations differ by ±45° from the trained one. Angles of orientations are given in degrees from the vertical (C).

transfer and generalization after perceptual learning. For example, previous research had demonstrated that transfer is critically affected by initial training conditions, such as training in more than one condition, reducing visual adaptation, or training at different difficulty levels [12–16]. In addition, mere exposure to repetitive stimulation using an oriented stimulus has been shown to result in improved discrimination over a wide range of orientations [17]. In their cleverly designed experiments, Tan *et al.* [7] were able to create a novel paradigm that links feature learning to category learning. Their results imply a close interaction between category learning and visual perceptual learning. Category learning is assumed to involve higher processing stages [9], so the findings of Tan *et al.* [7] can best be explained by a crucial role of top-down influences arising from higher category-processing stages. Given that category learning was not location specific, in this scenario, it is conceivable that after an orientation has been allocated to a category, the training of this orientation connects to the category-processing units, thereby eliminating its location specificity.

Historically, the use of simple features like orientations goes back to the seminal work of Hubel and Wiesel [18], who suggested that single neurons are triggered by basic features relevant for perception. There is a controversial debate about the use of natural scenes versus artificial stimuli [5,19]. The findings of Tan *et al.* [7] provide the first lines of evidence for perceptual learning under more generalized conditions getting close to natural, everyday environments. In fact, analysis of neural processing by means of voltage-sensitive dye imaging has shown that natural scenes create different states of neural dynamics compared to those seen when using simple stimuli [20]. Extrapolating from the new work of Tan *et al.* [7], therefore, a next logical step would be to use natural scenes for visual perceptual learning that contain both features and categories. It is conceivable that further research into this direction might show quite different properties of visual perceptual learning, with a broader generalization than observed so far. The latter would be a highly desired prerequisite for a broader use of visual perceptual learning applications in rehabilitation and clinical interventions.

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Olfaction: Mosquitoes Love Your Acid Odors

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Mosquitoes use their sense of smell to find humans. A new study shows that the ionotropic receptor 8a (IR8a) plays a primary and non-redundant role in human host-seeking behaviors.

Humans are smelly. To female *Aedes aegypti* mosquitoes, the human scent is absolutely wonderful, offering the promise of a delicious blood meal full of nutrients to support egg production. Mosquitoes have existed since before the dawn of humans, and mosquitoes that evolved to feed on human blood have