

Perceptual Learning of Grate Orientation Discrimination in Cats

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Abstract: Perceptual learning of orientation discrimination was investigated using cats. Two adult cats (Cat 1 and 2) were trained to monocularly discriminate between two static striped sinusoidal grates with 30° orientation difference. After greater than 80% correct performance was reached, cats were then required to monocularly perform a discrimination between two grates with consecutively shifting orientation difference (2°, 4°, 6°, 8°, 10°, 12°, 16°, 20°, 24°, 30°). The staircase method (two correct-down and one error-up) was applied throughout the training to track the threshold of orientation difference that cats could detect. The performance of detecting grates with varied orientation difference was measured respectively for both trained and untrained eyes before and after training. Our results showed that the learning effect of discrimination for grates with a fixed orientation difference transferred completely from the trained eye to the untrained eye, whereas the inter-eye transfer for detecting grates with gradually reducing orientation difference was almost nonegrates. The two opposite learning effects in the same subject strongly suggest that different information processing mechanisms might mediate the learning processes.

Key words: Perceptual learning; Orientation discrimination; Cat

猫对方位辨别的知觉学习

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摘要: 观察了猫对光栅方位辨别的知觉学习。两只成年猫 (cat 1 和 cat 2) 先单眼辨别方位差为 30 度角的两个正弦光栅以获得食物奖赏。当辨别正确率达 80% 以上后, 猫开始学习用单眼辨别夹角连续变化的两个正弦光栅, 采用二进一递进训练方法 (two-correct down/one-error up staircase method, 即猫连续两次辨别正确, 则待辨别的两个光栅的方位差降低为原来的 0.9 倍; 如果辨别错误一次, 则方位差增加至原来的 1.1 倍) 追踪猫可辨别的光栅方位差。在训练前后分别检测训练眼和非训练眼对不同方位差 (2°, 4°, 6°, 8°, 10°, 12°, 16°, 20°, 24°, 30°) 光栅辨别的正确率。结果显示: 对于固定方位差光栅的辨别学习, 学习效果能完全传递给非训练眼; 但对方位差连续减小的光栅辨别, 两眼间几乎没有传递。提示固定方位角和连续变化方位角光栅的辨别学习可能由不同的信息处理机制介导。

关键词: 知觉学习; 方位辨别; 猫

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Human perceptual learning, including orientation discrimination, motion perception, contrast detection and spatial frequency discrimination has been well documented (Karni & Sagi, 1991; Rivest et al, 1997;

Gray & Regan, 1998; Lages & Treisman, 1998; Matthews & Qian, 1999; Niebauer & Christman, 1999; Matthews et al, 2001; Grove & Regan, 2002; Sowden et al, 2002; Vimal, 2002; Sally & Gurnsey,

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2003). The long-lasting improvement through learning has been shown to be highly specific to stimulus parameters, retinal locations and even the eye employed during task performance. Such specificity of learning was generally interpreted as evidence for plasticity at early stages of cortical information processing, such as in the primary visual cortex (Karni & Sagi, 1991; Gilbert, 1994; Doshier & Lu, 1999). However, the neural mechanism underlying such perceptual learning is poorly understood though great progress has been made in psychological paradigms (Doshier & Lu, 1998, 1999). A major difficulty with this issue may lie in the limitation of applying powerful research approaches, such as electrophysiological recording or brain lesions, on humans. To our knowledge, so far no one has paid attention to the domestic cat and asked whether a cat can perceptually learn visual tasks, although there have been widespread and detailed investigations on cat visual pathways. We chose cats as subjects in the current study because, if perceptual learning can happen in the cat brain similarly to the human brain, it would be an ideal animal model for probing the underlying neural mechanism to perceptual learning. Previous studies proved that cats can discriminate orientation differences of single lines, bars or sinusoidal gratings (Vandenbussche & Orban, 1983; De Weerd et al, 1990; Zablocka & Zernicki, 1996; Sprague et al, 1996). They can also detect objects or signals with varied luminance, contrast, spatial frequency, size, patterns and moving directions or speeds (Berkley et al, 1978; Peck et al, 1979; Pasternak & Merigan, 1980; Blake & Petrakis, 1984; Blake et al, 1986; Vandenbussche et al, 1986; Zernicki, 1991; Zablocka & Zernicki, 1991; Burnat & Zernicki, 1997). It is therefore reasonable to ask the question about the visual perception in cats' brains. The present experiment aims to see if cats characterize visual learning plasticity similar to that of human beings.

1 Material and Method

1.1 Subjects and animal care

The subjects for this experiment were two young adult male cats (age: 1–3 years old; body weight: 2.2–3 kg) which were examined ophthalmoscopically before experiments and had no apparent optical or retinal problems that would impair their visual function. The cats were housed in one room and maintained on a 12 h light/dark cycle with water available *ad libitum*. Each cat received a food reward only through practicing a learning task for approximately 2 h on each weekday,

but received enough food on weekends. All animal treatments were strictly in accordance with the National Institute of Health's Guide for the Care and Use of Laboratory Animals.

1.2 Training apparatus

The training apparatus was similar to that used by Vandenbussche & Orban (1983), De Weerd et al (1990) and Orban et al (1990) (shown in Fig. 1: A, B). Briefly, cats performed a required discrimination task between gratings displayed on a fixed displayer (Cathode Ray Tube, CRT) and acquired food rewards by pushing the correct nose key. The distance from the CRT to the eyes was 57 cm.

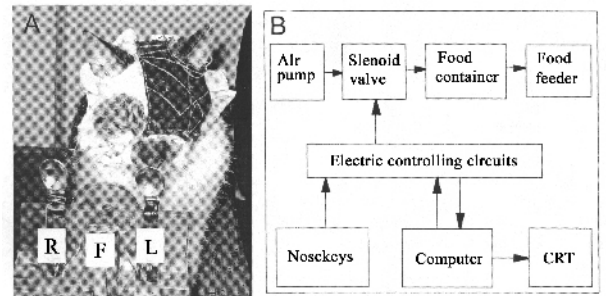


Fig. 1 Training apparatus and rewarding system

A: showing right (R) and left (L) nosekeys and food feeder (F); B: showing the automatic rewarding system. When the cat detects gratings displayed on a monitor (CRT) and pushes the correct nosekeys, the electric controlling circuits will trigger the Slenoid valve open and the air pump will push some food from food container to food feeder.

1.3 Stimuli and experimental procedure

All visual stimuli were circular grating-containing light spots with a diameter of 18 cm (equivalent to 18° visual acuity) and mean luminance of 19 cd/m². The program to generate the stimuli was written in MATLAB, using the extensions provided by the high-level Psychophysics Toolbox (Brainard, 1997) and low-level VideoToolbox (Pelli, 1997). At first, cats were trained to monocularly (the other eye was covered with a special mask) discriminate between two sinusoidal gratings with the same spatial frequency (0.4 c/deg), same contrast (80%) and fixed orientation difference (30°) (Fig. 2: A, B). The gratings slanted 15° clockwise and anti-clockwise away from the vertical axis for Cat 1, and from the horizontal axis for Cat 2. The two differently oriented gratings randomly presented on the CRT with an interval of four seconds. For Cat 1 (Fig. 2A), if the upward end of the grating tilted clockwise, pushing the right nose-key would trigger a food reward, while if tilted anti-clockwise, pushing the left nose-key would be rewarded. For Cat 2 (Fig. 2B), if

the right end of the grate tilted clockwise, pushing the left nose-key would trigger a food reward. If tilted anti-clockwise, pushing the right nose-key would be rewarded. The duration of each signal presentation was set at 4.35 seconds with a response denied period (RDP) of 0.35 seconds during which nose-key pushing triggered no food reward. The response time was defined as the time from the end of the RDP to the action of nose-key pushing. In each daily training session, each cat was subjected to 800 – 1000 trials arranged in 8 – 10 blocks. Each block contained 100 trials. There was a 5 – 10 minutes rest between blocks. After over 80% of discriminations with the trained eye at 30° orientation were correct over six consecutive days, the performance at different orientations (2°, 4°, 6°, 8°, 10°, 12°, 16°, 20°, 24°, 30°) was measured (500 – 600 trials for each orientation difference) for both eyes. The tests for trained and untrained eyes were conducted on alternate days. On each day, tests for different orientations (2 – 3 blocks of 50 trials per block for each orientation) were arranged randomly. To familiarise untrained eyes with the learning task, 3 – 5 blocks (50 trials/block) of pre-test adaptation, using alternating orientation differences, were given on the first day of testing. Orientation perceptual learning for the trained eye was carried out using the 2-correct-down/1-error-up staircase method. Using this method the orientation to be discriminated in the subsequent trial was either reduced to 90% of that in the former trial if the cat made two correct judgments or increased to 110% if the cat made a single error. This psychophysical algorithm tracks a threshold orientation difference value that corresponds to a performance accuracy level of about 70.7%. The mean discriminable threshold orientation difference was calculated each day to build a learning curve for monitoring the learning process. After more than two months of learning using the staircase method, when the learning curve reached a plateau, the percentage of correct performances at different orientations (2°, 4°, 6°, 8°, 10°, 12°, 16°, 20°, 24°, 30°) was re-examined for both the trained and untrained eyes as described above.

1.4 Data analysis

The correct performance at each orientation (2°, 4°, 6°, 8°, 10°, 12°, 16°, 20°, 24°, 30°) was evaluated using the mean percentage of correct performances across 10 – 12 testing blocks of 50 trials per block. Data for the trained and untrained eyes were tested for significance before and after learning using *t*-tests (independent, two-tailed). All mean values were expressed as mean \pm standard deviation.

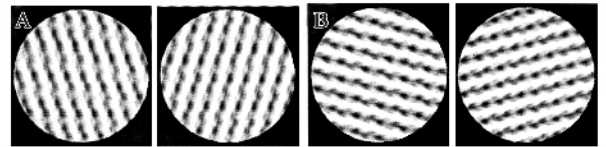


Fig. 2 Sinusoidal gratings for discrimination

A: Two gratings (oriented $\pm 15^\circ$ from Y-axes) with 30° orientation difference for Cat 1; B: Two gratings (oriented $\pm 15^\circ$ from X-axes) with 30° orientation difference for Cat 2.

2 Results

The two cats could successfully discriminate between two sinusoidal gratings with a fixed orientation tilted $\pm 15^\circ$ from the vertical or horizontal axes after seven to eight months of intensive training. A slow but steady improvement was evident in both cats, which was shown by the transformation from an initial random choice to greater than 80% correct responses after approximately 25 weeks of learning (Fig. 3).

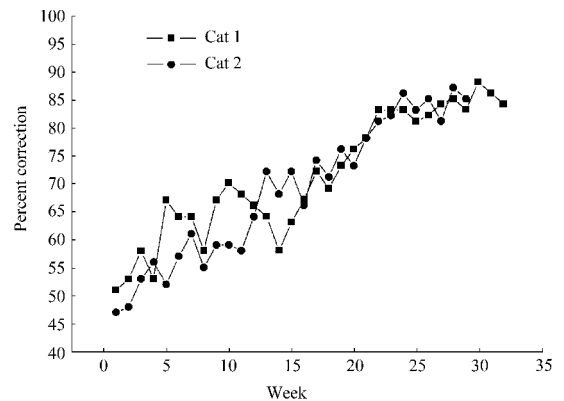


Fig. 3 The learning process of detecting gratings with 30° orientation difference in Cat 1 and Cat 2

After discrimination was over 80% correct during six consecutive days, performance at varied orientations (2°, 4°, 6°, 8°, 10°, 12°, 16°, 20°, 24°, 30°) was tested for both trained and untrained eyes. The performance in the trained eye and untrained eye of both cats was comparable (Fig. 4: A, B). *T*-tests showed no significant difference in correct performance at each orientation between the trained and untrained eyes ($P > 0.05$). The comparable performance in both eyes of each cat indicates that the learning effect of differentiating gratings with a fixed orientation (30°) can transfer completely from the trained eye to the untrained eye. In addition, the learning effect was not specific to the trained orientation difference. After cats succeeded in detecting gratings with a 30° orientation differ-

ence, the performance at smaller orientation differences (6° , 8° , 10° , 12° , 16° , 20° , 24°) was also considerably improved. Therefore, the learning effect at 30° orientation difference was transferred to other orientations. From Fig. 4, we can see that the smaller the difference from the trained orientation, the less the learning effect was transferred, and vice versa.

Orientation perceptual learning for the trained eye was carried out for approximately 70–90 days. Learning changes to the angle threshold (the orientation difference that can be detected at 70.7% correct performance) are shown in Fig. 5. There was an obvious learning effect. The final angle threshold that could be detected decreased from 15° to 7.6° in Cat 1, and from 14.1° to 6.4° in Cat 2. Typically, learning was fast during the first 10–20 days of training and was slower

in the following days.

In order to see if the learning effect could be transferred between the trained and untrained eyes, the percentage of correct performance at different orientations (2° , 4° , 6° , 8° , 10° , 12° , 16° , 20° , 24° , 30°) was re-tested after learning (Fig. 6: A, B). A significant improvement in performance at orientation differences larger than or equal to the final angle threshold (6° , 8° , 10° , 12° , 16° , 20° , 24° , 30°) was observed for the trained eye ($P < 0.05$) but not for the untrained eye ($P > 0.05$). However, performance at orientation differences below the angle threshold (2° , 4°) showed little or no change after learning and was almost the same for both eyes ($P > 0.05$). The results above indicate that the learning effect was robust, but that there was almost no inter-eye transfer.

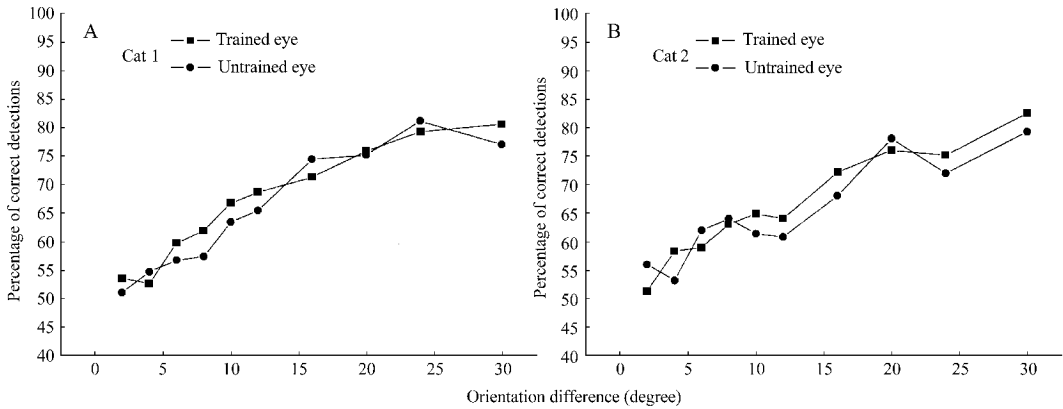


Fig. 4 Performance (percentage of correct detections) of detecting gratings of different gradient orientation (2° , 4° , 6° , 8° , 10° , 12° , 16° , 20° , 24° , 30°) measured for both trained and untrained eyes before learning using the staircase method

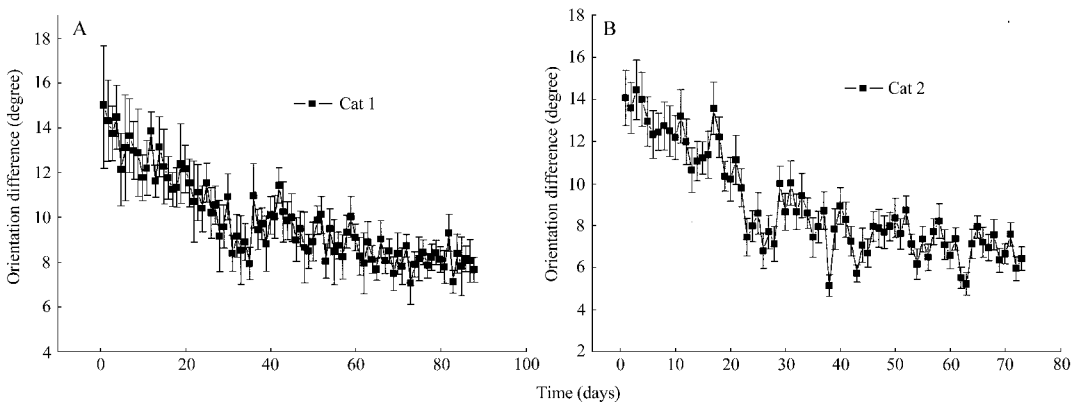


Fig. 5 The angle threshold (orientation difference that can be detected at 70.7% correct performance) change with learning in Cat 1 (5A) and Cat 2 (5B)

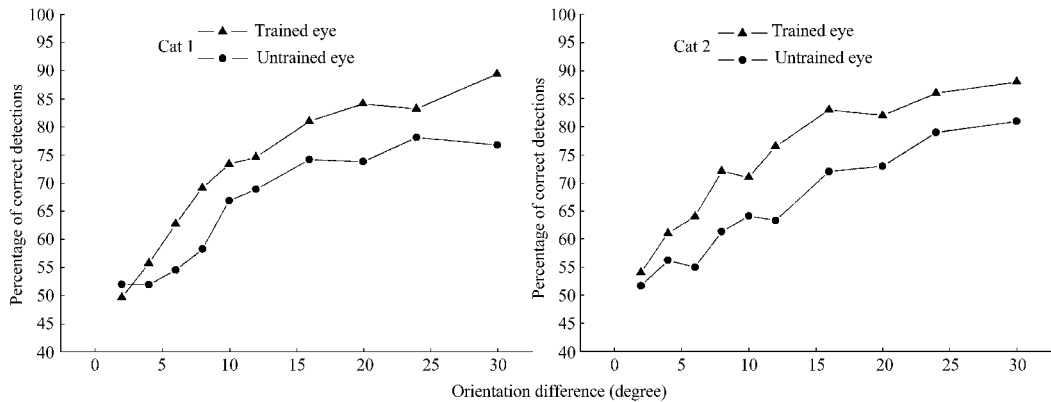


Fig. 6 Performance (percentage of correct detections) of detecting gratings with different gradient orientations (2° , 4° , 6° , 8° , 10° , 12° , 16° , 20° , 24° , 30°) measured for both trained and untrained eyes after learning using the staircase method

3 Discussion

A considerable number of studies in human subjects have shown that interocular transfer is a universal phenomenon in perceptual learning of various tasks, such as orientation discrimination (Fiorentini & Berardi, 1981; Schoups et al, 1995; Schoups & Orban, 1996) and the detection of motion direction (Ball & Sekuler, 1987). These studies seem to agree that perceptual learning takes place at a stage in the visual pathway where binocular convergence of visual input has occurred—i.e., at a stage higher than layer 4 of the primary visual cortex. Specificity to the trained eye is a very rare case in human subjects. Contrary to this, Fahle (1994) once reported an eye-specific effect in a vernier-acuity learning task. Karni & Sagi (1991) found that texture discrimination learning was specific not only for background orientation but also for retinal input of the trained eye. Thus they suggested that perceptual learning could only occur at a site where binocular inputs still remained separate to each other. Our data from two cats indicated that discrimination between gratings with fixed orientations could be transferred completely from the trained to the untrained eye, which was in accordance with previous studies of the cat (Ganz et al, 1972; Zernicki, 1991). However, detection of gratings with gradually reducing orientation difference showed almost no interocular transfer. The learning specificity for the trained eye suggested that a different cortical region, or information processing mechanism, might mediate the learning plasticity. In fact, information processing task dependency is not a rare thing. Vazquez et al (2000) made an observation on line-orientation detection in human

and nonhuman primates, using two different kinds of tasks (fixed and continuous discrimination tasks). The orientation of the reference stimulus did not change across trials in the former task but shifted randomly from trial to trial in the latter. It was shown that the fixed and continuous discrimination tasks were different. Both the human and nonhuman primates used different behavioral strategies to complete each task. Another study combined the techniques of PET (Positron Emission Tomography), selective lesions and single-cell recording, to show that orientation identification and successive orientation discrimination activated varied cortical loci in different temporal modulations in both human and nonhuman primates (Orban & Vogels, 1998). Therefore, the opposite learning effects observed in this experiment may also indicate that different processing circuits or modulations underlie the two different learning processes. Subsequent research is needed to distinguish between these two learning plasticities for further electrophysiological or brain imaging studies, aimed at finding clues of the potential neuronal correlations.

So far, the neural mechanism of perceptual learning still remains unknown. Limited studies in monkeys indicate that although substantial improvement in orientation discrimination is shown specific to the trained orientation and retinal location, only minor changes were found in the orientation tuning curves of V1 neurons with receptive fields at trained positions (Schoups et al, 2001). However, a significant increase in visually evoked response and narrowed orientation tuning of trained neurons in the region of V4 was unexpectedly observed recently in macaque monkeys who received the same learning task as above (Yang & Maunsell,

2004). Therefore, it is hard to identify where visual perceptual learning really occurs. Further studies are needed to explore the location of the loci and the neural mechanisms that mediate visual perception.

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