



# Perceptual learning on orientation and direction discrimination

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## Abstract

Two experiments were conducted to determine the extent to which perceptual learning transfers between orientation and direction discrimination. Naive observers were trained to discriminate orientation differences between two single-line stimuli, and direction differences between two single-moving-dot stimuli. In the first experiment, observers practiced the orientation and direction tasks along orthogonal axes in the fronto-parallel plane. In the second experiment, a different group of observers practiced both tasks along a single axis. Perceptual learning was observed on both tasks in both experiments. Under the same-axis condition, the observers' orientation sensitivity was found to be significantly elevated after the direction training, indicating a transfer of learning from direction to orientation. There was no evidence of transfer in any other cases tested. In addition, the rate of learning on the orientation task was much higher than the rate on the direction task. The implications of these findings on the neural mechanisms subserving orientation and direction discrimination are discussed. © 1999 Elsevier Science Ltd. All rights reserved.

*Keywords:* Motion; Training; Generalization; Transfer; Specificity; Learning rate

## 1. Introduction

Visual perceptual learning is the increase in visual sensitivity accompanying repeated practice of a visual task. The learning phenomenon has been observed in virtually every visual submodality including orientation and direction of motion. Although many interesting properties of orientation learning (Vogels & Orban, 1985; Shiu & Pashler, 1992; Schoups, Vogels & Orban, 1995) and direction learning (Ball & Sekuler, 1982, 1987), and their similarities (Matthews & Welch, 1997), have been documented, little effort has been devoted to elucidating possible interactions of learning between these two tasks. To address this issue, we investigated the extent to which learning on one task transfers to the other.

One might not expect such cross-task transfer given the fact that learning is quite specific even within each individual task. In particular, since it is known that

learning at one orientation (or direction) does not transfer to the orthogonal orientation (direction) (Vogels & Orban, 1985; Ball & Sekuler, 1987), it appears unlikely that orientation and direction learning would transfer to each other. However, based on physiological properties of the visual cortex, it should be easier to find transfer between orientation and direction than between two orthogonal orientations. Early visual cortical areas are believed to be at least partially involved in learning to discriminate primitive features such as orientation and direction (Gilbert, 1994; Ghose & Maunsell, 1997; Schoups, Vogels & Orban, 1998). Cells in these areas are very sharply tuned to these features, and consequently orthogonal orientations are coded by relatively separate populations of cells. Interactions of learning between orthogonal orientations could only be mediated through synaptic connections, diffusible chemical factors or feedback connections from higher visual areas. On the other hand, there are many cells in the early visual cortex that are simultaneously tuned to both orientation and direction (Hubel & Wiesel, 1968; Albright, 1984), and therefore, learning on one task could have an immediate impact on the

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other. Since direction-selective V1 cells and Type I MT cells are tuned to orthogonal orientation and motion axes, while Type II MT cells prefer the same orientation and motion axis (Albright, 1984), we tested transfer between the two tasks under both the orthogonal-axes and same-axis conditions.

The standard criterion for judging transfer between, for example, two orthogonal orientations is to train observers on one orientation and examine whether the performance at the second orientation has changed. Specificity is assumed if no significant change is detected at the second orientation. With this criterion, learning was found to be specific to the trained orientation or direction (Vogels & Orban, 1985; Ball & Sekuler, 1987). However, a new criterion based on learning rate has been proposed recently that may be a more sensitive measure under certain circumstances (Liu & Weinshall, 1998). According to this criterion, if the learning at the first orientation increases the speed of subsequent learning at the second orientation, then there is transfer across the two orientations. This would be true even if there were no performance improvement at the second orientation immediately after learning at the first orientation. Using this learning rate criterion, evidence of transfer has been found between orthogonal directions of motion previously thought to be independent (Liu & Weinshall, 1998). We have therefore applied both the standard performance criterion and the new learning rate criterion to judge transfer between orientation and direction learning. Independent of the issues of transfer, we also compared the speed of learning on the two visual tasks.

## 2. Methods

### 2.1. Apparatus and stimuli

Stimuli were viewed through a black, circular tube having an inner diameter of 10 cm. The tube extended from the observers' eyes to the computer screen, thereby preventing observers from using external references to determine the orientation or direction of the stimuli. A chin rest helped to stabilise the viewing distance at 57 cm. All responses were made via a Sidewinder 3D Pro joystick (Microsoft Inc.).

The experiment was conducted on a 21" ViewSonic PT180 monitor that was controlled by a psychophysics software package developed in our laboratory (Geesaman & Qian, 1996, 1998) and a Macintosh-compatible PowerTower Pro 225 computer. The vertical refresh rate of the monitor was set to 100 Hz, and the spatial resolution to 1024 pixels by 764 pixels. At this spatial resolution, however, jagged edges and motion discontinuities were visible in stimuli except at some special orientations and speeds. These unwanted artifacts,

which could have been used as cues to orientation and direction, were significantly reduced by an anti-aliasing feature in the software<sup>1</sup>. This rendered the jagged edges and motion discontinuities invisible at the distance from which all stimuli were viewed (57 cm).

The experiment was conducted in a well-lit room. Seen through the viewing tube, the screen appeared white and had a constant luminance of 47 cd/m<sup>2</sup>. To eliminate unwanted screen persistence the stimuli always had less luminance, and appeared black against the white background. Although the luminance within the stimuli was modulated slightly by the anti-aliasing software, all stimuli had a minimum luminance of about 0.7 cd/m<sup>2</sup>, resulting in a Michelson contrast of 97%.

Similar to a previous study (Matthews & Welch, 1997), single-stationary-line stimuli and single-moving-dot stimuli were used in the orientation and direction discrimination tasks, respectively. To increase the fairness of the comparison, the trajectory length on the direction task was matched to the line length on the orientation task. Each line stimulus was 2° long and 5 min wide. Each dot stimulus was a 5 × 5-min square that moved at 10 deg/s, traversing in 200 ms (or 20 frames) a distance of 2°.

### 2.2. Observers and experimental procedures

A total of 20 naive adult observers, all with normal or corrected-to-normal vision, were recruited for the two experiments we conducted; ten participated in each experiment. The two experiments were identical in all aspects except that in Experiment 1 the orientation and direction stimuli were along orthogonal axes while in Experiment 2, both were presented along the same axis. In each experiment, five observers trained on the orientation task first and the direction task second, while the other five observers received the opposite order of training. On each task, each observer completed a total of 28 training blocks over five daily sessions, and each block contained 128 trials. Therefore, every observer completed two training phases over ten daily sessions, with the tasks switched on day 6.

All experimental conditions comprised the same sequence of events within a trial. Fig. 1 shows the sequence schematically for Experiment 1. A circular fixation point was presented at the start of each trial. The fixation point disappeared after an observer pulled a trigger on the joystick, leaving the screen blank for

<sup>1</sup> Specifically, anti-aliasing was achieved by first calibrating the monitor for linearity and then letting the luminance of each actual pixel be determined by the proportion of virtual pixels that would have been covered by the stimulus had the resolution of the screen been 16 times greater than the actual resolution. This technique was used for both the stationary line stimuli and the moving dot stimuli.

200 ms before the first stimulus presentation. The first and second stimuli were each presented for 200 ms. This relatively brief stimulus duration was selected so any learning would not likely reflect refinements in the motor processes that control eye movements. The two stimuli in a trial were separated by 600 ms—an inter-stimulus interval sufficiently long to preclude apparent motion between the stimuli. In each trial, one stimulus was presented along a standard oblique axis (i.e. either 45 or 135°) and the other was presented along a nearby test axis, with pseudo-randomization. Observers were required to identify the angular change between the first and second stimuli by rotating the joystick clockwise or counterclockwise. Auditory feedback was provided at the end of each trial. Observers were informed that accuracy was of paramount importance and that reaction time was not being measured. Accurate responses could not be made reliably by using positional cues, as the relative position of the two stimuli was randomised independent of the angular difference (Matthews & Welch, 1997).

To ensure that observers understood the tasks before the training began, each observer first completed a worksheet on which trial sequences were schematically drawn, and then practiced 16 supra-threshold trials consisting of two stimuli that differed by at least 15°. This acquainted the observers with the stimulus sequence and the response while likely leaving initial discrimination thresholds unaltered. Next, the initial baseline performance of each observer on each task was measured with one block of trials. Earlier studies had shown that absolute thresholds on single-dot direction discrimination tasks are higher than those on single-line orientation tasks (Westheimer & Wehrhahn, 1994; Matthews & Welch, 1997). Because it is difficult to fairly compare the slopes of the learning curves that have different starting points, we equated initial dis-

criminability ( $d'$ ) on the two tasks by using two different sets of angular differences determined in a pilot study. The angular differences for the orientation task were 1.1, 1.21, 1.33 and 1.46°, and those for the direction task were 1.3, 1.69, 2.20 and 2.86°; each list forms a geometric series. Although for a few observers these angular differences had to be adjusted slightly before training, we found initial differences in discriminability ( $d'$ ) on the two tasks to be non-significant.

Both the standard performance and the learning rate criteria were applied to judge transfer between orientation and direction learning. With the performance criterion, we compared the performance on one task before (day 1) and after (day 6) training on the other task. With the learning rate criterion, we compared the speed of learning on a given task when that task was trained first (days 1–5) and when that task was trained second (days 6–10). Similar to Matthews and Welch (1997), we found that learning rate can be analysed through linear-regression after log transforming the  $d'$  values and block numbers. Note that although several earlier studies have shown that learning can occur within daily sessions on a variety of perceptual tasks (Ramachandran & Braddick, 1973; Fiorentini & Berardi, 1981; Poggio, Fahle & Edelman, 1992; Karni & Sagi, 1993; Kumar & Glasser, 1993; Beard, Levi & Reich, 1995; Levi, Polat & Hu, 1997), the study most paradigmatically similar to this one (Matthews & Welch, 1997) revealed no evidence for within-session learning. The analyses in the present study were consequently designed to assess perceptual learning across sessions.

### 3. Results

#### 3.1. Experiment 1: orthogonal-axes case

In this experiment, the stimuli for the orientation and direction tasks were presented along orthogonal axes. We first consider the standard performance criterion for judging transfer between the two tasks. The results are shown in Fig. 2. The left panel plots the mean orientation sensitivities of the five observers before and after they were trained on the direction task in the first five daily sessions. As this was a within-observers analysis, the error bars reflect the 95% confidence intervals after the consistent individual differences were removed<sup>2</sup> (Loftus, 1993; Loftus & Masson, 1994). The overlap in the data indicates that orientation discrimination was

<sup>2</sup> Consistent individual differences, which constitute a source of variability unrelated to the experimental manipulation, were removed by first determining each observer's departure from the grand mean of all observers, then adjusting the observer's scores by that amount. This had the effect of equating the mean performance across observers (Loftus, 1993; Loftus & Masson, 1994).

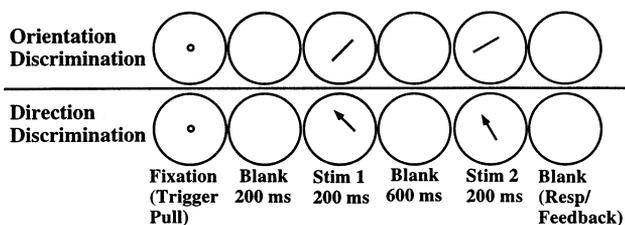


Fig. 1. Trial sequence. The sequence of events on the orientation and direction tasks is shown in the upper and lower rows, respectively. On both tasks, each trial comprised two successively presented stimuli. Observers were required to identify the orientation or direction of the second stimulus to be either clockwise or counterclockwise to the first stimulus. The placement of the two stimuli was randomised so that positional cues would not reliably indicate the orientation or direction change. Immediate feedback on the accuracy of the response was provided after every trial. In Experiment 1, each observer practiced the first task along one oblique axis, and the second task along an orthogonal axis (as shown here). Each observer in Experiment 2 practiced both tasks along a single oblique axis.

## Orthogonal-Axis Case

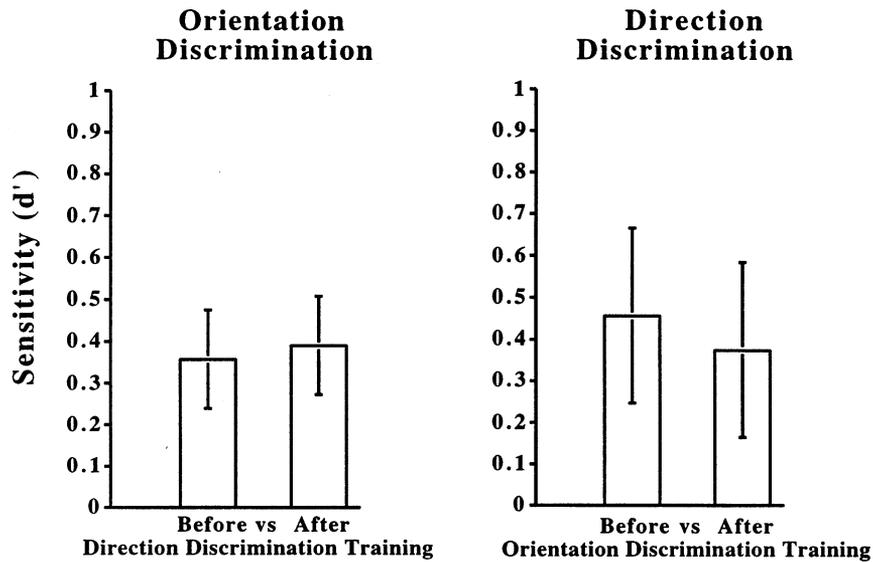


Fig. 2. Analysis of transfer in the orthogonal-axes case using the standard criterion. Left panel: average orientation sensitivity ( $d'$ ) from the five observers who were trained on the direction task during days 1–5. “Before” and “After” represents the orientation sensitivities prior to and following the direction training, respectively. Right panel: average direction sensitivities from the other five observers who were trained on the orientation task during days 1–5. “Before” and “After” represent the direction sensitivities prior to and following the orientation training, respectively. In both panels, consistent individual differences were removed before averaging and the error bars represent the 95% confidence intervals (Loftus, 1993; Loftus & Masson, 1994). No evidence of transfer was found in either case as the 95% confidence intervals for the “Before” and “After” conditions largely overlap.

not significantly affected by the direction training. A similar outcome was found for the other five observers, who practiced the orientation task in the first five daily sessions: Direction discrimination was not significantly different before and after the observers were trained on the orientation task (Fig. 2; right panel). These analyses demonstrate that when the orientation and direction tasks were presented along orthogonal axes, there was no transfer of learning between the two visual tasks based on the standard performance criterion.

We next applied the learning rate criterion for judging transfer. Fig. 3a shows the orientation learning curves when the orientation task was trained first (left panel) and when the orientation task was trained second, after the direction training (right panel). Every datum point represents the mean of the five observers in each condition, and the error bars reflect one standard error of the mean. As mentioned in Section 2, after log-transforming the  $d'$  values and the block numbers, the learning curves can be well fitted by straight lines and the slopes from linear regression provide a convenient measure of the learning rates. First note that significant learning occurred on the orientation task whether task was practiced first ( $r(26) = 0.933$ ,  $P = 0.01$ ) or second ( $r(26) = 0.837$ ,  $P = 0.01$ ). However, the two learning rates were very similar to each other, independent of the training order. This is confirmed by subtracting the corresponding log-transformed data

points in the two curves and testing the slope of the resulting difference curve which is not significantly different from zero ( $r = 0.333$ , n.s.). Therefore, learning the direction task did not increase the speed of the subsequent orientation learning. Similar results were found for the two direction learning curves shown in Fig. 3b. Again, significant perceptual learning occurred whether the direction task was practiced first ( $r(26) = 0.644$ ,  $P = 0.01$ ) or second ( $r(26) = 0.706$ ,  $P = 0.01$ ). The two learning rates were statistically indistinguishable ( $r = 0.087$ , n.s.), indicating that orientation learning did not increase the speed of subsequent direction learning. We conclude that when the orientation and direction tasks were trained on orthogonal axes, there was no transfer of learning between the two visual tasks based on the learning rate criterion either.

### 3.2. Experiment 2: same-axis case

In this experiment, the stimuli for the orientation and direction tasks were presented along the same axis. The data analyses are very similar to those used in the above orthogonal-axes case. The results, as evaluated by the standard performance criterion, are shown in Fig. 4. The left panel shows the mean orientation sensitivities of the five observers before and after they were trained on the direction task in the first five daily sessions. Unlike the orthogonal-axis case, there is no

### Orthogonal-Axis Case

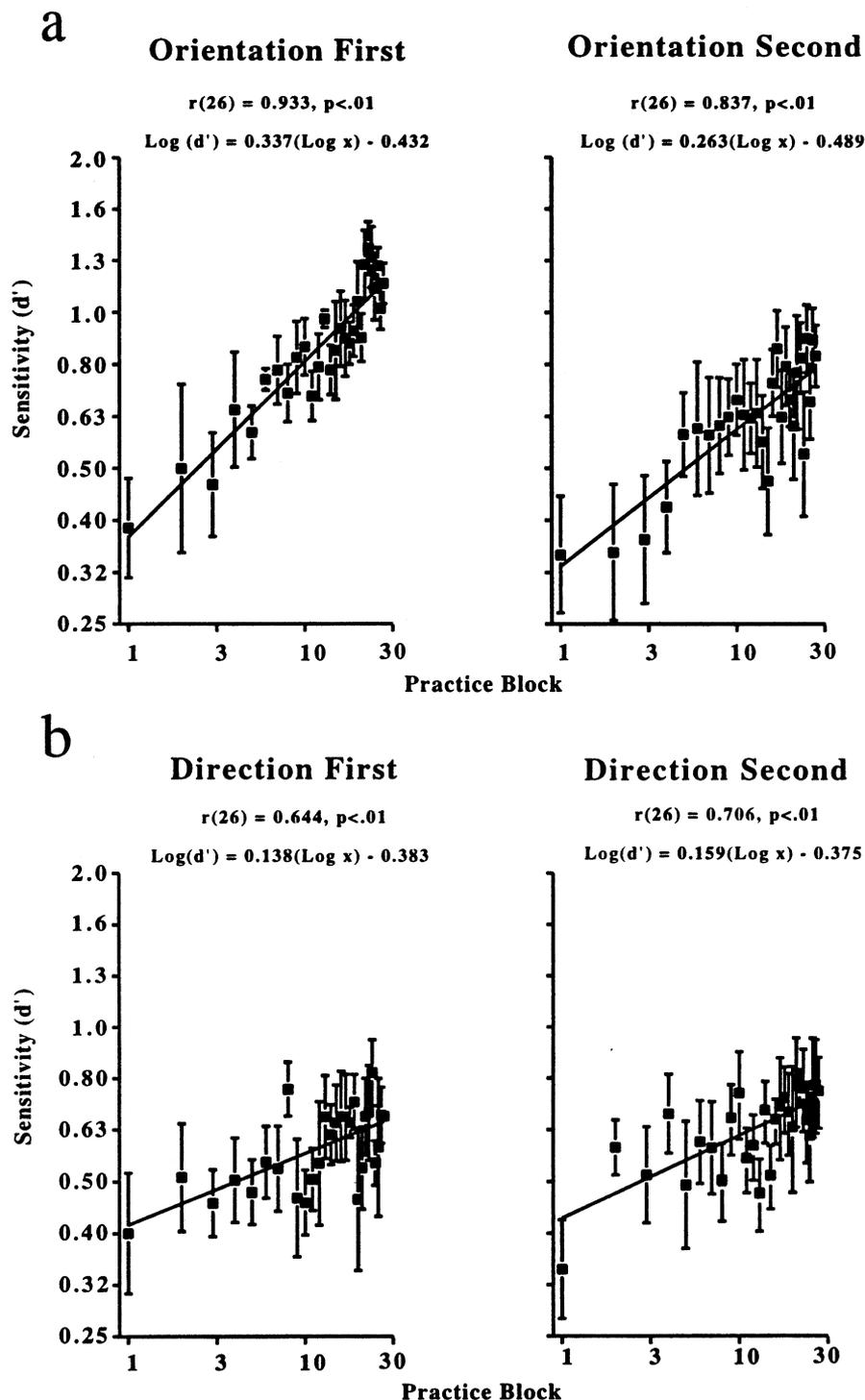


Fig. 3. Analysis of transfer in the orthogonal-axes case using the rate criterion. Each panel represents data averaged over the five observers in each condition, and the error bars indicate one standard error of the mean. (a) Orientation learning-curves when the orientation task was trained first (days 1–5) on five observers (left panel), and when trained second (days 6–10) on the other five observers (right panel). Orientation sensitivity improved significantly but the two rates were statistically indistinguishable. (b) Direction learning-curves when the direction task was trained first (days 1–5) on five observers (left panel), and when trained second (days 6–10) on the other five observers (right panel). Direction sensitivity improved significantly but the two rates were statistically indistinguishable. Therefore, there was no evidence for transfer in either case.

## Same-Axis Case

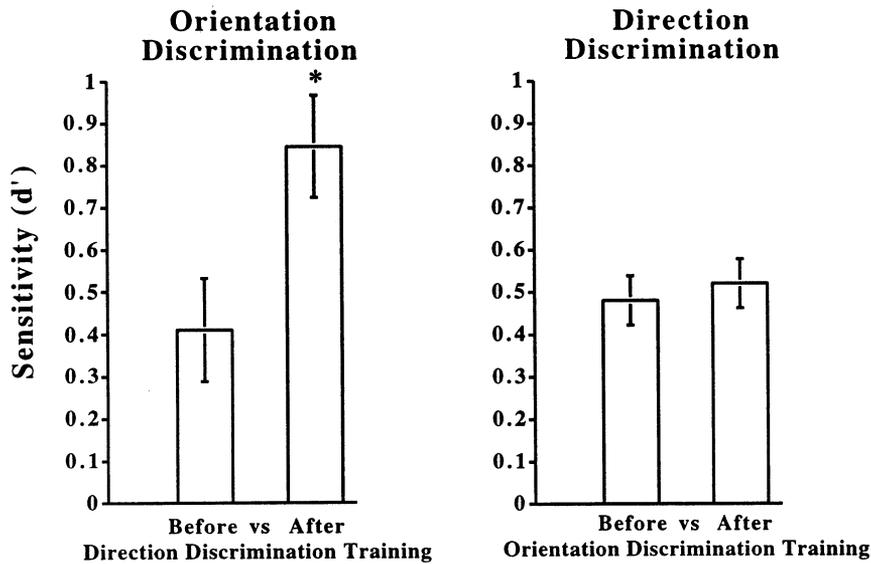


Fig. 4. Analysis of transfer in the same-axis case using the standard criterion. Left panel: average orientation sensitivity ( $d'$ ) from the five observers who were trained on the direction task during days 1–5. Right panel: average direction sensitivity from the other five observers who were trained on the orientation task during days 1–5. The conventions here are the same as for the orthogonal-axis case (Fig. 2). Unlike Fig. 2, the left panel shows that direction learning transferred to orientation discrimination.

overlap between the two error bars representing the 95% confidence intervals. Therefore, in the same axis condition, orientation sensitivity was significantly improved immediately after the direction training. This conclusion was further confirmed by a within-observers  $t$ -test which revealed that orientation discrimination after the direction training was significantly higher than before the training ( $t(4) = 5.03$ ,  $P = 0.01$ , two-tailed). As we used the convention of  $d' = 1$  corresponding to 84% correct, the mean performance improvement seen in the left panel of Fig. 4 represents a change from 65% correct to 80% correct. In contrast, the right panel of Fig. 4 shows that the mean direction sensitivity was not significantly different before and after the orientation learning. This is indicated by the large overlap of the two 95% confidence intervals. We conclude that when the orientation and direction stimuli were presented along the same axis, direction learning transferred to orientation discrimination but not vice versa, according to the standard performance criterion.

The learning curves for the orientation and direction tasks in this experiment are shown in Fig. 5a and b, respectively. In both parts (a) and (b), the average results from the observers who practiced the task first (left panel) and from the observers who practiced the task second (right panel) are plotted side by side. The error bars represent one standard error of the mean. In Fig. 5a, orientation sensitivity improved significantly whether the orientation task

was trained first ( $r(26) = 0.855$ ,  $P = 0.01$ ) or second ( $r(26) = 0.579$ ,  $P = 0.01$ ). In addition, learning occurred at a significantly faster rate when the orientation task was practiced first (left panel) than when it was practiced second (right panel). However, the learning rate criterion for judging transfer cannot be applied here because the two curves have significantly different starting points—the datum point at block 1 in the right panel was much elevated due to the immediate transfer from direction learning to orientation discrimination (see Fig. 4, left panel). Most likely, the slower learning seen in the right panel merely reflects the fact that there is more saturation and less room for improvement, and thus should *not* be taken as evidence that direction learning slowed subsequent orientation learning. In the current experimental paradigm, if the standard performance criterion revealed a significant transfer, then the learning rate criterion cannot be fairly applied.

On the other hand, it was possible to fairly apply the learning rate criterion to the direction learning curves in Fig. 5b. This is because the initial performances for the observers who practiced the direction task first (left panel) and for those who practiced the direction task second (right panel) were not significantly different from each other (see also Fig. 4, right panel). The two learning rates were found to be statistically indistinguishable ( $r = -0.069$ , n.s.) although significant learning occurred whether direction discrimination was practiced first (left panel,  $r(26) =$

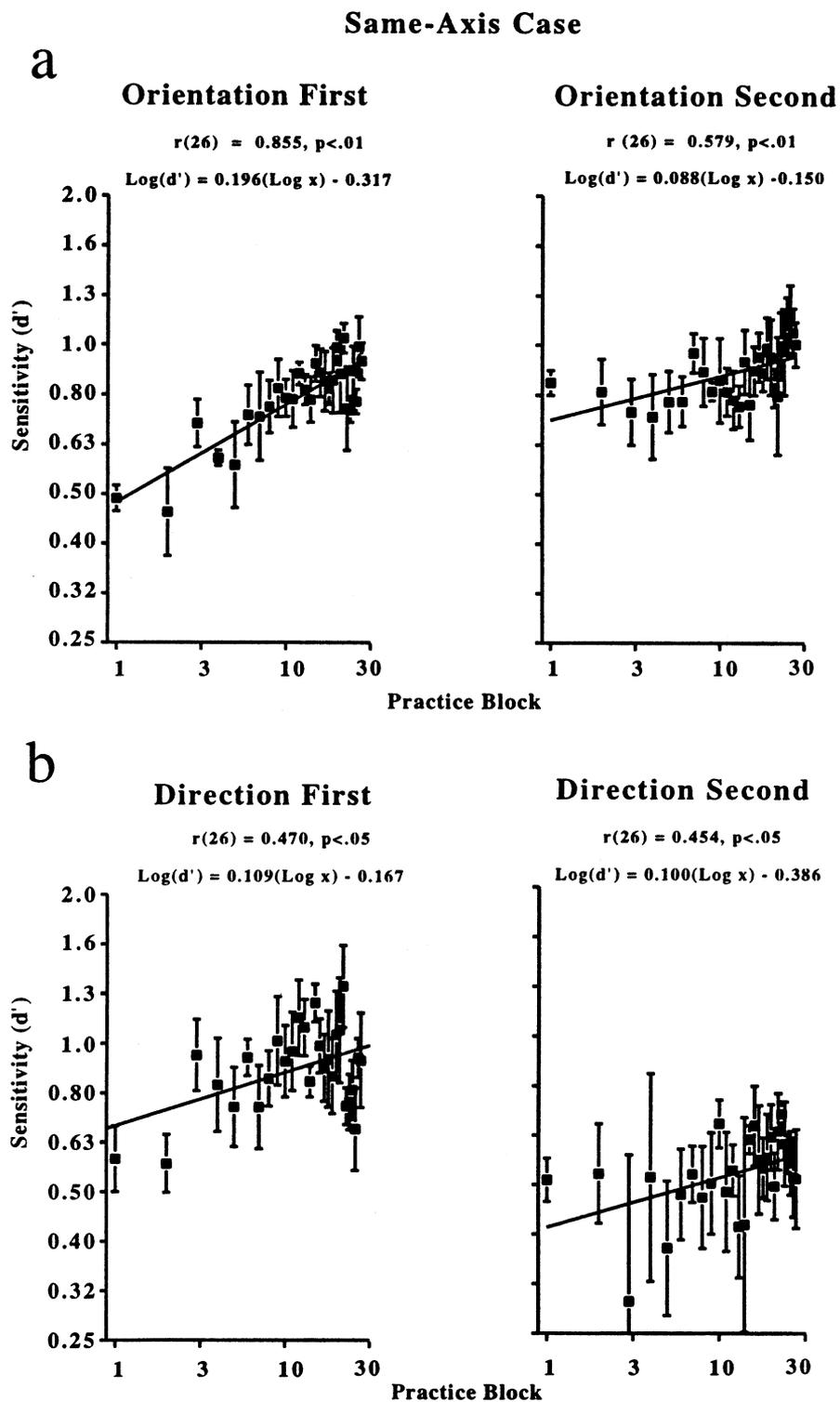


Fig. 5. Analysis of transfer in the same-axis case using the rate criterion. (a) Orientation learning curves when the orientation task was trained first (days 1–5) on five observers (left panel), and when trained second (days 6–10) on the other five observers (right panel). (b) Direction learning curves when the direction task was trained first (days 1–5) on five observers (left panel), and when trained second (days 6–10) on the other five observers (right panel). The conventions here are the same as in Fig. 3. Note that the rate criterion cannot be fairly applied to the orientation learning curves in part (a) because the starting points of the two curves are different due to the transfer shown in the left panel of Fig. 4.

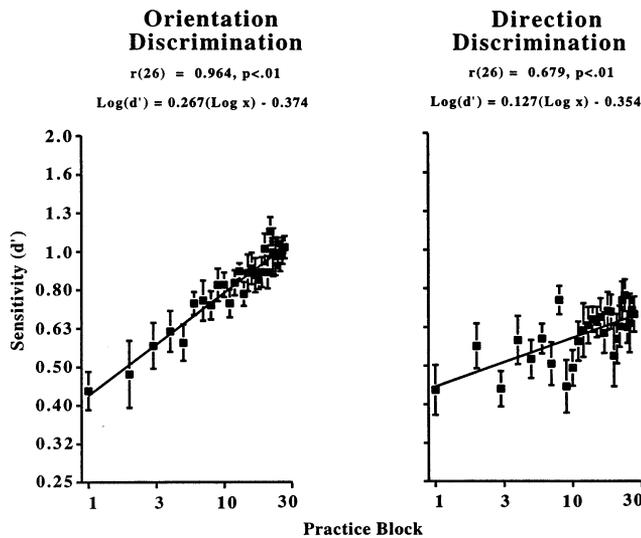


Fig. 6. Task-specific learning rates. The left panel shows the mean orientation sensitivity ( $d'$ ) for the ten observers in Experiments 1 and 2 who were first trained on orientation discrimination. Mean direction sensitivity is similarly plotted in the right panel for the other ten observers, who were first trained on direction discrimination. There are 1280 trials in each datum point. The orientation learning proceeded at a significantly faster rate than direction learning. The conventions here are the same as in Fig. 3.

0.470,  $P = 0.05$ ) or second (right panel,  $r(26) = 0.454$ ,  $P = 0.05$ )<sup>3</sup>. We conclude that the orientation learning did not affect the rate of subsequent direction learning, and that there was no evidence of transfer based on the learning rate criterion.

### 3.3. Task-specific learning rates

Regardless of the issue of transfer, Experiments 1 and 2 suggest that the practice-based improvements in orientation discrimination and direction discrimination occurred at different rates (see Figs. 3 and 5). This was true despite the fact that the initial difficulties of the two tasks were made equal by adjusting the angular differences (see Section 2). A formal comparison of the task-specific learning rates is shown in Fig. 6. The left panel reflects the mean sensitivity of the ten observers in both Experiments 1 and 2 who were first trained on the orientation discrimination. In the right panel, mean direction sensitivity is shown for the other ten observers, who were first trained on the direction discrimination. The data from the second phase of training in both experiments were excluded from this analysis to prevent any distortions of

learning rate caused by transfer. Fig. 6 indicates that orientation sensitivity ( $d' = 0.435$ ) and direction sensitivity ( $d' = 0.434$ ) were virtually identical when training began. However, orientation sensitivity increased at a significantly faster rate than direction sensitivity, as the slope of the difference curve is significantly different from zero ( $r(26) = 0.626$ ,  $P = 0.01$ ).

## 4. Discussion

The purpose of the present study was to determine the extent to which perceptual learning would generalise between orientation discrimination and direction discrimination. Motivated by the physiological properties of V1 and two types of MT cells (Albright, 1984), we investigated the cases when the two tasks were presented along orthogonal axes and when they were presented along the same axis. Every observer was trained on both the orientation and direction tasks, one task after another. This two-training-phase design allowed us to apply the learning rate criterion for judging transfer whenever the standard performance criterion failed to reveal a transfer. We found that under the performance criterion, direction learning transferred significantly to orientation discrimination along the same axis. This transfer could be mediated by the type II MT cells, which prefer the same orientation and motion axis (Albright, 1984). No evidence of transfer was found in any other conditions. We also found that observers learned the orientation task much faster than the direction task even though the difficulties of the two tasks were initially equated.

The observed transfer from direction to orientation along the same axis is unlikely due to some non-specific aspects of learning (such as task understanding), since non-specific learning would transfer equally well from orientation to direction and would also transfer under the orthogonal-axes condition; neither was observed. Another possible explanation for our results is that the direction stimuli also contain orientation information when integrated over time. Consequently, direction learning might actually involve refinements of both direction and orientation mechanisms, and therefore transfer to the orientation task. One could further argue that the lack of transfer from orientation to direction is because stationary orientation stimuli do not contain motion. While we cannot rule out this possibility, it is unlikely for the following reasons. First, if both direction and orientation information were employed for learning the direction task, then the extra information would likely make the direction learning faster than the orientation learning. The opposite was observed in our experiments. Second, if the direction learning depended significantly on an orientation component, then some transfer from orientation learning to direction discrimination *would* be expected. This was again not the case.

<sup>3</sup> The comparatively low mean performance of the group of observers who practiced direction discrimination second (Fig. 5b, right panel) is attributable to the anomalously low performance of one observer, particularly on blocks 3, 4, 5, and 14. However, the outcome of our statistical tests did not depend on whether data from this observer were included or excluded. For methodological consistency then, we chose to include those data.

Finally, since opposite directions of motion share the same orientation axis, transfer between opposite directions would be observed if the direction learning depended on a common orientation component. Yet, contrary to this expectation, Ball and Sekuler (1987) failed to find such transfer. Of course, one could avoid all these difficulties by assuming that although both direction and orientation mechanisms were activated by the direction stimuli, only the direction mechanism contributed to the direction task. However, the observed direction-to-orientation transfer would then imply that the task-irrelevant, passive stimulation of the orientation mechanism during the direction discrimination training could cause orientation learning. This is questionable since earlier studies suggest that passive stimulation is not sufficient for perceptual learning (Shiu & Pashler, 1992; Ahissar & Hochstein, 1993), even when stimulus–response relationships perfectly covary on different tasks (Ahissar & Hochstein, 1993).

We speculate that the observed direction-to-orientation transfer along the same axis might imply that at a certain stage in the visual pathway, orientation processing depends on direction processing. As a further speculation, the asymmetry of transfer might also be related to the fact that most direction selective cells are orientation selective while there are many orientation selective cells that are not direction selective in the visual cortex.

The observed transfer from direction to orientation may be somewhat surprising because, except in Beard et al. (1995), most previous studies found that visual learning is task specific (Shiu & Pashler, 1992; Ahissar & Hochstein, 1993; Fahle & Morgan, 1996; Fahle, 1997). For example, Shiu and Pashler (1992) found no transfer of learning between a brightness task and an orientation task. Likewise, Ahissar and Hochstein (1993) found that learning on a local orientation pop-out task did not improve a subsequent global orientation discrimination performed on the same set of stimuli. We would like to suggest that the lack of transfer in some previous studies may be explained by the fact that the tasks used in those experiments were not strongly physiologically related even though they might appear conceptually similar. Indeed, the local orientation pop-out and the global orientation discrimination tasks in Ahissar and Hochstein (1993) must be mediated by separate neuronal populations tuned to very different spatial scales. In contrast, the orientation and direction stimuli we used were matched in trajectory length and could have activated partially overlapping neuronal populations tuned to both orientation and direction.

Except the one-way transfer mentioned above, we did not find evidence for transfer in any other conditions examined. We would like to point out, however, that any null results should be interpreted with caution. It has been reported recently that by making a discrimination task easier a previously null result on transfer can be

turned positive (Liu, 1995; Ahissar & Hochstein, 1997). Therefore, we are open to the possibility that more instances of transfer between orientation and direction might be found under different sets of experimental parameters. We also failed to reveal any transfer with the learning rate criterion in the current study. This is in agreement with a previous report of ours (Matthews, Liu & Qian, 1998) that used the same rate criterion in an interleaved training paradigm for the two tasks (instead of the sequential training paradigm used here). As we mentioned in Introduction, the learning rate criterion has been found to be more sensitive in detecting transfer between orthogonal directions of motion than the standard performance criterion (Liu & Weinshall, 1998). The relative merits of the two criteria under different situations remain to be determined. It should be emphasised that the learning rate criterion is not applicable whenever a transfer is found by the standard performance criterion because such a transfer will distort the learning rate estimation. Finally, the failure to reveal transfer with the learning rate criterion could be specific to the experimental parameters we used.

Consistent with previous studies in which motion stimuli were also presented at a speed of 10 deg/s (Westheimer & Wehrhahn, 1994; Matthews & Welch, 1997), we found initial absolute thresholds to be approximately  $0.7^\circ$  lower for orientation discrimination than for direction discrimination. To control for this difference, we used two different sets of angular separations for discrimination such that the initial discriminability ( $d'$ ) on the two tasks was virtually identical. Nevertheless, subsequent training of the two tasks resulted in a much faster learning rate on the orientation task than on the direction task. The difference in both the initial threshold and the learning rate between the two tasks might be attributable to the difference in stimulus energies: In each frame, the orientation stimuli contained an entire line while the direction stimuli contained only a single dot. Alternatively, one might speculate that the difference between the two tasks could be due to the fact that the visual cortex contains more orientation selective cells than direction selective cells. Both explanations predict that the initial threshold and the learning rate for multiple-moving-dot stimuli should be superior to those for single-moving-dot stimuli because the multiple-dot stimuli contain more stimulus energy and would activate more visual cortical cells. However, Matthews and Welch (1997) found the opposite to be true. Further investigation is required to determine the origin of the task-specific learning rates and initial thresholds.

In summary, we have demonstrated that direction learning transfers significantly to orientation discrimination along the same axis. This is consistent with a partial overlap between the sensory responses constraining these

two visual tasks. We also found that orientation learning proceeded at a much higher speed than the direction learning even when the initial difficulties of the two tasks were equated. Determining whether a more general pattern of transfer will emerge between orientation and direction learning requires further exploration of the parameter space.

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