Task-specific perceptual learning on speed and direction discrimination

Tiffany Saffell, Nestor Matthews *

Department of Psychology, Denison University, Granville, OH 43023, USA

Received 31 July 2002; received in revised form 16 December 2002

Abstract

Twenty-two naïve undergraduates participated in a psychophysical experiment designed to elucidate the neural events that allow us to see subtle motion differences. Half of the subjects practiced extensively on a direction-discrimination task while the other half practiced extensively on a speed-discrimination task. The stimulus conditions in the two groups were identical. The results indicated that the learning curves for direction discrimination were significantly steeper than those for speed discrimination. Additionally, the significant practice-based improvements on each motion task did not transfer to the other motion task. The different learning rates and the lack of transfer suggest that the neural events mediating speed discrimination are at least partially independent from those mediating direction discrimination, and vice versa, even under identical stimulus conditions.
© 2003 Published by Elsevier Science Ltd.

Keywords: Perceptual learning; Motion discrimination; Speed discrimination; Direction discrimination; Luminance discrimination

1. Introduction

Visual perceptual learning can be defined as the increase in visual performance associated with extensive practice on a visual task. For example, it is well established that extensive practice can improve our ability to see subtle differences between two directions of motion (Ball & Sekuler, 1987; Matthews, Liu, Geesaman, & Qian, 1999; Matthews & Welch, 1997). However, whether our ability to see subtle speed differences is similarly affected by extensive practice is not known. The present study was conducted to provide this information by comparing perceptual learning on speed discrimination and direction discrimination. More importantly, by using identical stimuli on the speed and direction discriminations, we sought to evaluate different accounts of

the neural events [1] responsible for each task. In particular, the present data have some bearing on whether speed discrimination and direction discrimination are mediated by the same neural events, or by independent neural events. The existing evidence for these two possibilities will be considered in turn.

The evidence that the same neural events mediate speed discrimination and direction discrimination comes from several different lines of investigation. First, psychophysical experiments have revealed various similarities between these two motion tasks for a given stimulus manipulation. The psychophysical similarities include the finding that speed discrimination and direction discrimination covary when the stimulus speed is manipulated (De Bruyn & Orban, 1988), or when the motion-signal strength is manipulated (Festa & Welch, 1997), and that both tasks are unaffected by high-pass

---

* Corresponding author. Tel.: +1-740-587-5782; fax: +1-740-587-5675.
E-mail address: matthewsn@denison.edu (N. Matthews).
URL: http://www.denison.edu/~matthewsn/index.html.

[1] Our use of the phrase "neural events" here is intentionally general. In our usage, a change in "neural events" is meant to encompass either a change in the composition of the task-relevant neural population, or a change in the firing pattern(s) within a given neural population, or both. Because distinguishing among these various neural possibilities is beyond the scope of our research question and psychophysical procedures, we believe that a phrase more specific than "neural events" would be unwarranted.

spatial filtering (Smith, Snowden, & Milne, 1994). Psychophysical data have also indicated that, across participants, speed discrimination and direction discrimination are positively correlated even after controlling for luminance sensitivity and non-specific factors, such as motivation (Matthews, 2002). Additionally, physiological studies have demonstrated that lesions to area MT in the macaque monkey generate impairments on both speed discrimination (Merigan, Pasternak, Ferrera, & Maunsell, 1991; Orban, Saunders, & Vandenbussche, 1995) and direction discrimination (Lauwers, Saunders, Vogels, Vandenbusshe, & Orban, 2000; Newsome & Pare, 1988). Physiological studies have also established that the maximal firing rate of certain cells in the primate visual pathway depends neither on speed alone nor direction alone, but on particular *combinations* of speed and direction (Maunsell & Van Essen, 1983; Mikami, Newsome, & Wurtz, 1986; Perrone & Thiele, 2000, 2001; Rodman & Albright, 1987). Moreover, neural computational work has suggested that a population of such cells (Maunsell & Van Essen, 1983; Mikami et al., 1986; Rodman & Albright, 1987; Perrone & Thiele, 2000, 2001) could reliably estimate stimulus velocity, i.e., the vector incorporating speed *and* direction of motion (Heeger, 1987). Taken together, these psychophysical, physiological, and neural computational findings converge on the possibility that speed and direction discrimination are mediated by the same neural events.

Other studies, however, have suggested that these two motion tasks may be mediated by independent neural events. In particular, there are instances in which a given manipulation differentially affects speed and direction discrimination. For example, one can impair direction discrimination by abruptly changing the dot-density of random dot cinematograms (Watamaniuk, Grzywacz, & Yuille, 1993), or by changing the axis-of-motion from cardinal to oblique (Matthews & Qian, 1999), or by orienting one-dimensional static noise parallel to the axis-of-motion (Burr & Ross, 2002a, 2002b); Speed discrimination is unaffected by each of these manipulations. Conversely, it has been shown that a fixed transcranial magnetic pulse can impair speed discrimination without impairing direction discrimination, even when the visual stimuli are identical on the two tasks (Matthews, Luber, Qian, & Lisanby, 2001). Although the neural substrate of these differences (Burr & Ross, 2002a, 2002b; Matthews et al., 2001; Matthews & Qian, 1999; Watamaniuk et al., 1993) between speed and direction discrimination is not presently known, some physiological evidence suggests that speed and direction tuning are at least partially segregated in the primate cortex. For instance, Lagae, Raiguel, and Orban (1993) identified certain MT cells that retain their direction selectivity over a broad (i.e., 100-fold) range of speeds. Conversely, Cheng, Hasegawa, Saleem, and Tanaka (1994) found that V4 cells, which are not well tuned for

direction, are speed-tuned. It is possible that such cells (Lagae et al., 1993; Cheng et al., 1994), which respond to just one of the two motion attributes (i.e., speed or direction), could generate different limitations for speed and direction discrimination.

Predictions about perceptual learning on speed and direction discrimination depend on whether one hypothesizes that the two tasks are mediated by the same neural events, or different neural events. Specifically, to the extent that speed and direction discrimination are mediated by the same neural events, one would predict comparable learning rates on the two tasks, and transfer-of-learning between the tasks. By contrast, these predictions do not follow from an account based on separate neural events. Accordingly, in the present study we assessed these predictions. To rule out the possibility that any transfer-of-learning could be attributed to non-motion factors, such as motivation, each subject also completed a non-motion task (i.e., luminance discrimination) on the same stimuli that were presented on the motion tasks. To summarize briefly, the results indicated that perceptual learning occurred at a significantly greater rate for direction discrimination than for speed discrimination, and there was no evidence for transfer-of-learning among any of the tasks. We believe these perceptual learning data provide novel evidence that speed discrimination and direction discrimination are limited by at least partially independent neural events.

2. Method

2.1. Stimuli and apparatus

The experiment was conducted on a 21 in. (53.34 cm) ViewSonic P225 monitor that was controlled by a Macintosh G4 computer with a 733 MHz processor and software from the psychophysics toolbox (Brainard, 1997; Pelli, 1997). The vertical refresh rate of the monitor was 120 Hz, and the spatial resolution was 1024×768 pixels. In a well-lit room, subjects viewed the monitor using a chin rest that helped to stabilize head position at 57 cm.

The stimuli were random-dot cinematograms (RDCs) that produced a compelling sense of translational motion. Each RDC consisted of dots that appeared lighter than the dark uniform surround, which had a luminance of 5.83 cd/m². All dots within an RDC were presented at a single luminance, which randomly varied between 19.91 and 89.25 cd/m² across RDCs, thereby creating Michelson contrasts between 54.70% and 87.74%, respectively. Each dot was a 2×2-pixel square ($\approx 5'$ on each side). There were 30 dots ($\pm 16\%$, $\pm 32\%$, $\pm 48\%$, $\pm 64\%$, or $\pm 80\%$, randomly) per RDC, making the mean dot-density ≈ 4.24 dots/deg², as the dots were presented within a circular virtual aperture having a diameter of

3 deg. Dots moving out of the aperture "wrapped around" to the opposite side. Subjects foveally viewed the motion stimuli, and a circular fixation dot (56.91 cd/m^2, 82.26% contrast) in the center of the aperture helped to stabilize eye position.

Each trial comprised two successively presented RDCs. Each RDC was shown for 200 ms (24 frames), and the inter-stimulus interval varied from 500 to 700 ms, randomly. On every trial, two new and unique RDCs were generated. The two always differed from each other in speed, *and* direction, *and* luminance. The speed, direction, and luminance differences were varied independently of each other. Since the RDCs that were presented on the speed, direction, and luminance discrimination tasks were generated from the same algorithm, there were no statistical differences in the RDCs across tasks.

The speed, direction, and luminance differences were arranged such that the mean stimulus values could not be used as the basis for accurate responses. For example, on each trial, the first speed was randomly 6, 7, 8 or 9 deg/s, while the second speed differed randomly *from the first* by ±8%, ±16%, ±24%, ±32%, or ±40%. Consequently, even if a subject could perfectly discern the first speed relative to the mean speed of 7.5 deg/s, there would nevertheless be a 50% chance that the second RDC would be faster (or slower) than the first. Likewise, in the absence of any information about the first speed, perfect comparisons between the second speed and the mean speed would render only chance performance. Thus, subjects were forced to base their speed judgments on information extracted from *both* RDCs. A conceptually similar approach was adopted for the direction differences and the luminance differences. Regarding direction differences, the first direction on each trial was randomly selected from the range ±20 deg from the horizontal (leftward or rightward randomly), and the second direction differed randomly from the first by ±3, ±6, ±9, ±12, or ±15 deg. This prevented subjects from using the mean direction as the basis for correct direction judgments. [2] Likewise, regarding luminance differences, the first luminance on each trail was randomly selected from the range 33.18 to 63.75 cd/m^2, and the second differed randomly from the first by ±8%, ±16%, ±24%, ±32%, or ±40%, making the minimum and maximum dot luminances 19.91 and 89.25 cd/m^2, respectively. This prevented subjects from using the mean luminance as the basis for correct brightness judgments. In short, to reliably make correct responses

on each task, subjects were forced to extract information from the two RDCs presented on each trial. [3]

Several non-motion cues can covary with the speed of motion. One such cue, a "hop-size" cue, arises when the speed difference between two RDCs is achieved solely by varying the distance of the dots' frame-to-frame displacement (i.e., the hop-size). Hop-size cues were eliminated by using two different spatio-temporal configurations to generate the RDCs on each trial. Specifically, one RDC contained dots that "hopped" on each frame (120 Hz), and the other RDC contained dots that "hopped" a larger distance only once every two frames (60 Hz). This two-fold difference in the effective frame rate allows speed differences to be decorrelated from hop-size cues, so long as the speed differences are less than two-fold—which was the case in the present study. Another distance-related cue that can covary with speed is the overall traverse; For a given duration (e.g., 200 ms), a greater distance is traversed at faster speeds than at slower speeds. This distance cue can be eliminated by using limited-lifetime dots (i.e., randomly re-positioning each dot after a given number of frames), and making the mean dot lifetimes proportionally longer (or briefer) for slower (or faster) speeds. Since human subjects are more sensitive to distance cues than to time cues, it is advantageous to eliminate the distance cue and allow the time cue (i.e., mean dot lifetime) to covary with speed (McKee & Watamaniuk, 1994). Accordingly, in one RDC, the lifetime of each dot was randomly selected from a 20-element array of lifetimes that had a mean of 10 frames. In the other RDC, the lifetime of each dot was randomly selected from a different 20-element array that had a mean proportionally longer (or briefer) for speed decrements (or increments). The dot lifetimes in each of these arrays ranged from 6 to 14 frames. A control experiment suggested that subjects were unable to use the time-cues (i.e., the difference in mean dot lifetimes) as the basis for speed judgments (see Section 3). Given those results and the controls on the hop-size and the traverse, subjects were constrained to base their speed judgments on speed differences rather than on cues that covary with speed.

2.2. Subjects and tasks

Twenty-two participants were recruited from the Denison University community. All had normal or corrected-to-normal vision.

The stimuli for all tasks are shown schematically in Fig. 1. As mentioned in the preceding section, the same

---

[2] Because the direction task did not require participants to judge whether the motion differed from horizontal, the presence of the monitor's horizontal boundaries provided no information about correct direction judgments.

[3] The speed, direction, and luminance differences tested here were identified in a pilot study on other naïve subjects to determine the range of stimulus values that would likely contain the discrimination threshold for each task.
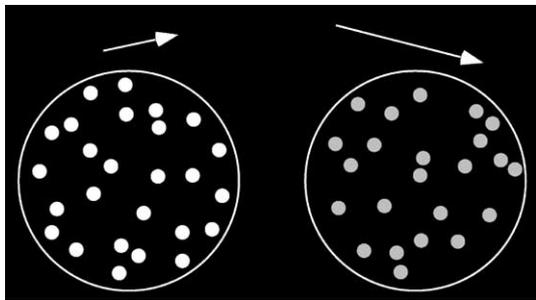
Fig. 1. Schematic of stimuli presented on the speed, direction, and luminance discrimination tasks—two RDCs were shown on each trial. The second RDC always differed from the first in speed, and direction, and luminance. These three attributes were varied independently of each other within each trial block. Across trial blocks, the stimuli were held constant while the task varied from judging the speed ('faster'/'slower'), or the direction ('more upward'/'more downward') or the luminance ('brighter'/'dimmer') of the second RDC relative to the first. In the example shown here, the correct responses would be 'faster', 'more downward', and 'dimmer' on the speed, direction, and luminance tasks, respectively.

computer algorithm generated the RDCs for each task. Consequently, the speed, direction, and luminance discrimination tasks differed solely in the instructions to the subjects. Specifically, in separate trial blocks for each task, subjects indicated how the second stimulus differed from the first; "faster" or "slower" for the speed task, "more upward" or "more downward" for the direction task, and "brighter" or "dimmer" for the luminance task. Subjects responded via a button-press, using one right-hand finger for stimulus increments (i.e., "faster", "more upward", "brighter"), and a different right-hand finger for stimulus decrements (i.e., "slower", "more downward", "dimmer"). The same two right-hand fingers were used across tasks. Subjects were informed that stimulus increments and decrements would occur with equal probability, and that the accuracy (rather than the quickness) of their responses was of paramount importance. To promote accuracy, subjects were encouraged to set their own pace throughout each block, initiating each trial with a left-hand button-press when ready.

The instructions for the direction task, which required participants to judge whether the second direction was more upward or downward than the first, were designed to eliminate a potentially confounding non-motion cue, namely, orientation. Consider a trial on which the second motion trajectory has an orientation that is 3 deg clockwise from the first. If the horizontal component of the motion were from left to right, the correct *directional* judgment on our task would be "more downward". By contrast, if the horizontal component of the motion were from right to left, the correct *directional* judgment on our task would now be "more upward". Note that although the orientation difference has been held constant (3 deg clockwise), the directional difference has changed (from more downward to more

upward). Accordingly, a direction-blind participant with perfect knowledge about orientation (from the trajectories, or the monitor's boundaries, or any other source) would not be able to reliably make correct *direction* judgments. Indeed, an orientation-sensitive-but-direction-blind participant would perform only at chance levels on our direction task. Consequently, our empirical finding that performance on the direction task was always well above chance (see Sections 2.3 and 3) is *not* consistent with the possibility that participants used an orientation-based, direction-blind strategy.

2.3. Initial screening

We sought to establish that the learning in our experiment would be perceptual, rather than conceptual. Accordingly, prior to extensive perceptual training, an initial screening session was conducted to ensure that each subject understood each task, i.e., could perform each task at greater-than-chance levels. [4] The screening session comprised a demonstration phase, practice trials, and threshold estimation. Each of these will be described in turn.

In the demonstration phase, each trial began with a computer-generated voice announcing the correct response before the stimuli were presented. For example, on the speed-discrimination task, the computer-generated voice would announce "The correct answer will be, faster" prior to a trial on which the second stimulus was faster than the first. The difference between the first and second stimuli on each demonstration trial was always the greatest difference from the array of differences that would be tested during actual trials (i.e., ±40% in speed, ±15 deg in direction, ±40% in luminance). Typically, 5–15 demonstration trials were completed before a subject proceeded to the practice trials.

Practice trials were identical to demonstration trials in all aspects, except that the correct response was not announced before each practice trial. During the practice-trial phase, each subject was required to make 10 consecutive correct responses. This performance level, which could occur by chance less than one time in a thousand, ensured that each subject understood each task before proceeding to threshold estimation.

Thresholds were estimated using the method of constant stimuli and were based, for each subject and task, on two 100-trial blocks. Specifically, each trial block comprised 10 randomly ordered presentations of each of the 10 stimulus-difference values (see details in Section 2.1). The 10 stimulus difference values were plotted on

---

[4] Of the 22 participants initially recruited, only one, who was unable to judge even 15-deg directional differences at greater-than-chance levels, did not pass the screening. An additional participant was recruited as a replacement, and passed the screening.

the abscissa of a psychometric function, while the ordinate reflected the proportion of increment responses (i.e., "faster", or "more upward", or "brighter"). A least-squares procedure was then used to fit the data with a sigmoid of the form

$$1/(1 + \exp[-K(X - X_o)])$$

where K and X_o determine the slope and midpoint of the sigmoid, respectively. The correlation between the best-fitting sigmoid and the data, as indexed by the Pearson correlation coefficient (r), was statistically significant ($p < 0.05$) in each case. Because each fit was significant, it was possible to fairly interpolate from the sigmoid each observer's 70% discrimination threshold, which was defined as half the stimulus change required to alter the response rate from 0.30 to 0.70. Mean discrimination thresholds on the speed, direction, and luminance tasks were 10.73% (±1.10 SE), 4.60 deg (±0.58 SE), and 12.59% (±1.15 SE), respectively. These discrimination thresholds are in good quantitative agreement with those from a previous study that used similar stimuli and a different group of naïve subjects (Matthews, 2002).

2.4. Training paradigm

After completing the initial screening, subjects proceeded to our training paradigm, which comprised seven 1-h daily sessions. The seven sessions consisted of a baseline session (day 1), five training sessions (days 2–6), and a transfer-of-learning session (day 7). Each will be described in turn.

In the baseline session (day 1), each subject completed two 100-trial blocks on each of the three tasks. The speed, direction, and luminance differences that were presented on every trial were set to the subject's 70% discrimination threshold, as measured on each task during the initial screening. Occasionally, a subject's two-block average in the baseline session exceeded 80%, or was below 60%. In these cases, we adjusted the stimulus-difference value to better approximate the desired 70% performance level ($d' = 0.52$). [5] In this way, we eliminated the floor and ceiling effects that would have reduced the potential for perceptual learning.

In the first training session (i.e., day 2), each subject was assigned to either speed training or direction training, according to a block-randomization procedure. Subjects practiced only their assigned task through the five training sessions (days 2–6). Each training session comprised six 100-trial blocks, and the percentage of

correct responses was reported to the subject immediately after each block. Also, discriminability (d') was calculated for each block, and the average of the six blocks was recorded for each subject on each day.

The transfer-of-learning session (day 7) was virtually identical to the baseline session (day 1). The only exception was that, in the transfer-of-learning session, we also conducted a 100-trial control block that measured each subject's sensitivity to the time differences (i.e., differences in dot lifetimes) available on the speed-discrimination task (see Section 2.1). Specifically, RDCs in the time-discrimination control condition comprised *stationary* dots with lifetimes identical to those of the *moving* dots presented on the speed-discrimination task, i.e., proportionately longer (or briefer) for slower (or faster) speeds. The difference in dot lifetimes between the two RDCs on each trial generated different flicker rates. The subjects' task in the control condition was to indicate whether the flicker rate of the second RDC was "faster" or "slower" than that of the first. If the subject had been using these time differences on the speed-discrimination task, one would expect comparable precision on the control condition and the speed-discrimination task.

2.5. Data analysis

It has been shown that perceptual learning on direction discrimination is well described by a power function (Matthews & Welch, 1997). Accordingly, for each subject in the present study, we fit a power function to the data obtained on the training task across the seven daily sessions. The criterion for determining whether the subject demonstrated significant learning was that the Pearson correlation coefficient (r) relating the best-fitting power function to the data had to meet or exceed 0.75, $p < 0.05$.

To determine whether the two tasks generated different learning curves, we planned (a priori) a statistical comparison between the slopes (i.e., the exponents of the power functions) of the direction-trainees and the speed-trainees. To assess transfer-of learning within each group, we planned (a priori) a pre-training versus post-training statistical comparison for each of the three tasks. Subjects who failed to show significant learning on their training task were excluded from that analysis, as mixing learners with non-learners would likely mask any transfer-of-learning effects.

3. Results

The data from the initial screening session are shown in Fig. 2, where there are separate plots for the speed, direction, and luminance discrimination tasks. Two characteristics of the data should be noted. First, it is

---

[5] To compute discriminability (d'), hits and false alarms were operationally defined as increment responses ("faster", "more upward", "brighter") to increment stimuli and decrement stimuli, respectively.
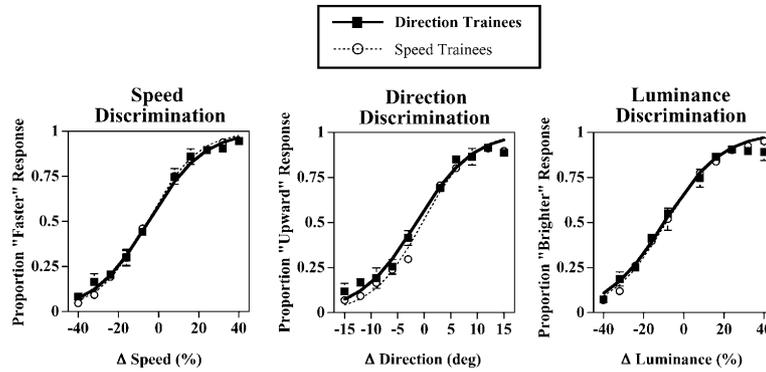
Fig. 2. Psychometric functions from the initial screening session. The left, center and right panels show data from the speed, direction, and luminance tasks respectively. The ordinate of each panel indicates the proportion of increment responses ('faster', 'upward', or 'brighter') and the abscissa indicates the changes in the stimuli. Each datum represents the mean of 2200 judgments (11 subjects per condition × 2 blocks per subject × 100 trials per block). The error bars reflect one standard error of the mean. The data from the 11 subjects assigned to the direction task (solid squares and solid curves) overlap with those of the 11 subjects assigned to the speed task (open circles and dotted curves). This indicates that, on each task, initial performance was comparable in the two groups.

clear from visual inspection that the proportion of increment (i.e., "faster", "upward", "brighter") responses increased in an orderly manner as the stimulus differences changed from large negative values to large positive values. The orderliness of the data implies that our naïve subjects understood the task, and that their limitations were perceptual rather than conceptual. Second, on each task, the performance of subjects assigned to the direction-training condition (solid squares and solid line) was comparable to that of subjects assigned to the speed-training condition (open circles and dotted line). Ensuring that subjects understood the task and that the direction-trainees and speed-trainees initially performed equally was necessary to fairly compare the learning rates from the two groups.

The comparison of learning rates is shown in Fig. 3. The most striking feature of the figure is that the mean discriminability (d') of the 11 direction-trainees (solid squares and solid line) grew markedly, while that of the 11 speed-trainees (open circles and dotted line) remained relatively flat. Indeed, after determining the best-fitting power function for each subject, we found that the slopes from the direction-trainees significantly exceeded those from the speed-trainees ($F(1, 20) = 9.581$, $p = 0.006$). Since the performance of each group on the first daily session approximated 70% discrimination ($d' = 0.52$), neither floor nor ceiling effects can account for the significantly lower learning rate of the speed-trainees.

The two groups also differed with respect to the number of trainees who demonstrated significant learning. Specifically, 8 of the 11 direction-trainees produced learning curves with slopes significantly greater than zero, while the remaining three produced slopes that were non-significantly positive. By contrast, of the 11 speed-trainees, only four produced learning curves with slopes significantly greater than zero, two
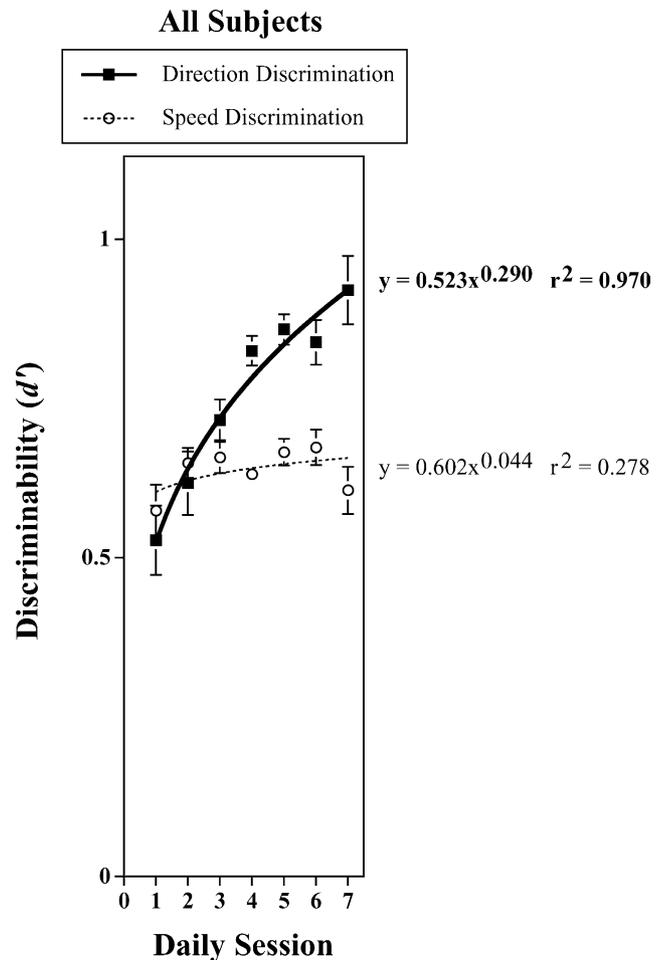

Fig. 3. Learning curves for speed and direction discrimination (all subjects). Mean discriminability (d') of the 11 direction-trainees (solid squares and solid curves) and the 11 speed-trainees (open circles and dotted curves) is plotted for each daily session. The error bars here, and in all remaining figures, reflect one standard error of the mean after consistent individual differences were removed (Loftus, 1993). For each group, the equation for the best-fitting power function and proportion of variance explained (r^2) are shown. The slope of the direction curve is clearly steeper than that of the speed curve.
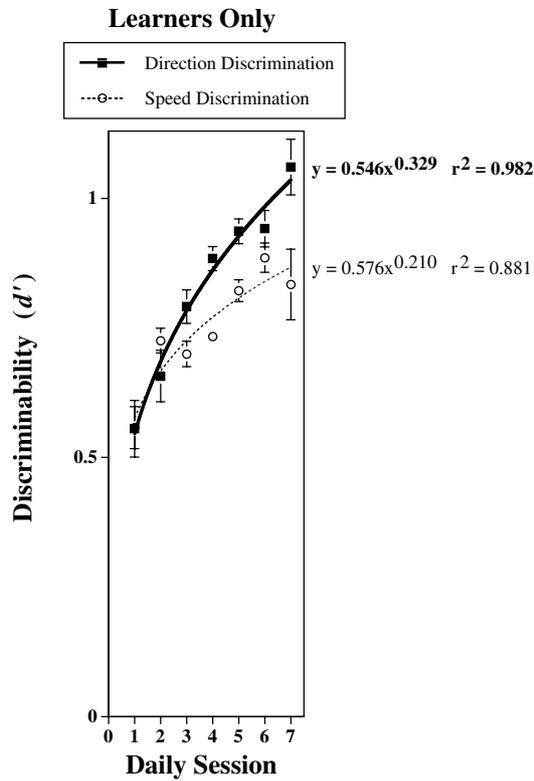
Learners Only

Fig. 4. Learning curves for speed and direction discrimination (significant learners only). Mean discriminability (d') for the trainees who showed significant learning is plotted for each daily session (conventions are the same as in Fig. 3). Although the difference in slopes here is not as distinct as in Fig. 3, the direction curve is still clearly steeper than the speed curve.
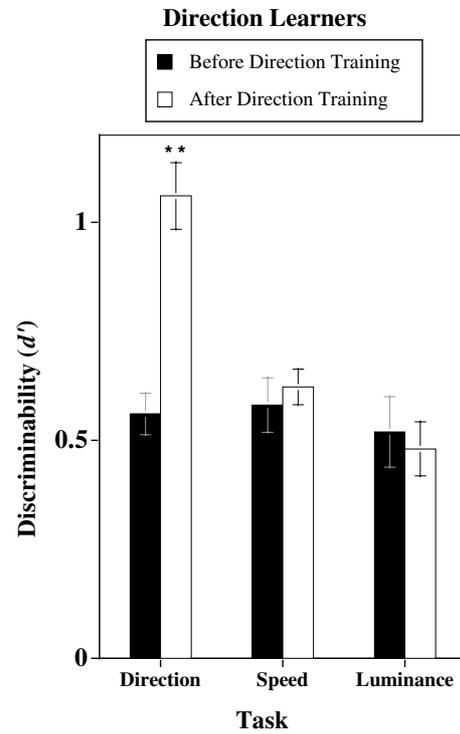
Direction Learners

Fig. 5. Transfer for direction-learners. Across all conditions shown here, the stimuli were identical, as was the level of statistical power. The black columns and white columns respectively reflect discriminability (d') before and after direction training. On the direction task (left), discriminability (d') increased significantly after direction training. By contrast, on the speed (center) and luminance (right) tasks, discriminability (d') was unaffected by direction training.

produced non-significantly positive learning curves, and five showed declines in discriminability (d') across the daily sessions. Interestingly, there also were task-specific tendencies even among those trainees who demonstrated significant learning. In particular, although an ANOVA indicated that the slopes of the eight significant direction-learners did not differ statistically from those of the four significant speed-learners, there was a tendency for steeper slopes among the direction-learners. This can be seen in Fig. 4, where the difference in slope is evident despite virtually identical discriminability (d') on the first daily session. Taken together, the data in Figs. 3 and 4 suggest that substantially more learning occurred on direction discrimination than on speed discrimination.

We next assessed transfer-of-learning. Since transfer-of-learning would not be likely from subjects who failed to demonstrate learning on their training task, our analysis included only those trainees who demonstrated significant learning. Mean pre-training (black columns) and post-training (white columns) discriminability (d') for the eight direction-learners is shown in Fig. 5. Despite the fact that the stimuli were identical across all conditions in the figure, it is clear from visual inspection

that post-training performance exceeded pre-training performance only on the trained task, i.e., direction discrimination. ANOVAs confirmed that the difference between pre- and post-training discriminability (d') for these subjects was significant on the direction task ($F(1, 7) = 25.021$, $p = 0.002$), and non-significant on the speed and luminance tasks. In fact, of the eight direction-learners, four showed post-training declines in speed discrimination, and four showed post-training declines in luminance discrimination. These data indicate that the learning was task-specific.

Further evidence for task-specific learning can be seen in Fig. 6 (conventions are the same as in Fig. 5), where the mean pre- and post-training discriminability (d') is plotted for the four speed-trainees who demonstrated significant learning. Again, despite the fact that the stimuli were identical across all conditions in the figure, it is clear from visual inspection that post-training performance exceeded pre-training performance only on the trained task, i.e., speed discrimination. ANOVAs confirmed that the difference between pre- and post-training discriminability (d') for these subjects was significant on the speed task ($F(1, 3) = 73.392$, $p = 0.003$), and non-significant on the direction and luminance
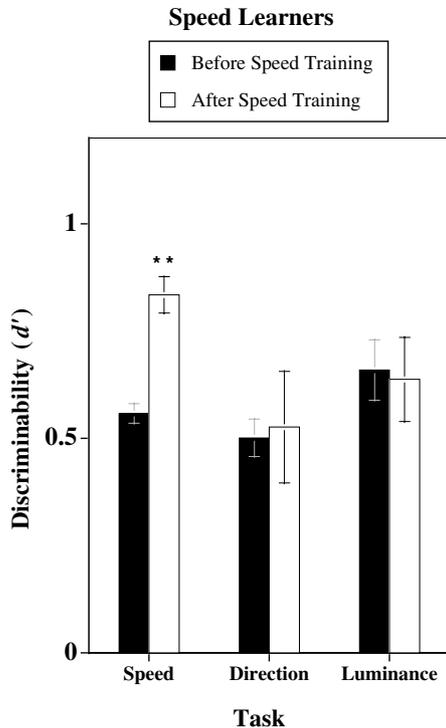
Speed Learners

Fig. 6. Transfer for speed-learners. Across all conditions shown here, the stimuli were identical, as was the level of statistical power. The black columns and white columns respectively reflect discriminability (d') before and after speed training. On the speed task (left), discriminability (d') increased significantly after speed training. By contrast, on the direction (center) and luminance (right) tasks, discriminability (d') was unaffected by speed training.

tasks. In fact, of the four speed-learners, two showed post-training declines in direction discrimination, and two showed post-training declines in luminance discrimination. Taken together, the data in Figs. 5 and 6 provide little evidence for transfer-of-learning, and suggest instead that the learning was task-specific.

As we mentioned above, one would not expect transfer-of-training from participants who failed to show practice-based improvements on the trained task. In principle however, such transfer is possible, and would be consistent with the hypothesis that the speed and direction tasks are mediated by shared neural events. To explore this possibility, we considered the data shown in Table 1. Visual inspection of the data

from the non-trained tasks indicates that the post-training means never exceeded the pre-training means. Therefore, like the learners, the non-learners failed to show transfer-of-training.

Finally, as noted in Section 2, a time-discrimination control condition was necessary to establish that subjects had based their speed judgments on speed, and not the co-varying time differences (i.e., dot-lifetime differences) available in the stimulus. Time discriminability in the control condition was measured on the final daily session, and compared to speed discriminability from that session. We found that for each of the 22 subjects, time discriminability (mean $d' = 0.18$, ± 0.02 SE) was worse than speed discriminability (mean $d' = 0.60$, ± 0.02 SE), and that this difference was statistically significant ($F(1, 21) = 120.8$, $p < 0.0001$). The comparatively poor precision with which subjects judged time differences in the control condition would not have been sufficient to sustain the much greater precision with which speed differences were judged on the speed-discrimination task. This finding, coupled with the fact that the traverse of the slower-moving dots equaled that of the faster-moving dots (see Section 2), implies that subjects based their speed judgments on speed, not distance or time.

4. Discussion

This psychophysical study was designed to elucidate the neural events that mediate speed discrimination and direction discrimination. One group of 11 naïve subjects extensively trained on a speed discrimination task, while another group of 11 naïve subjects completed the same training regimen on a direction-discrimination task. The stimulus conditions and initial discriminability (d') were also held constant across the tasks. There were two main findings. First, the learning curves for direction discrimination were significantly steeper than those for speed discrimination. Second, a comparison of pre- and post-training performance indicated that the perceptual learning was task-specific; significant practice-based improvements in direction discrimination did not transfer to speed discrimination, and significant practice-based improvements in speed discrimination did not

Table 1
Transfer data for non-learners

	Speed task		Direction task		Luminance task	
	Pre	Post	Pre	Post	Pre	Post
Speed trainees	0.584	0.528	0.529	0.331	0.480	0.332
Direction trainees	0.588	0.528	0.453	0.545	0.553	0.426

The pre- and post-training discriminability (d') means on all tasks are shown for the participants who failed to demonstrate significant improvement on their trained task. Neither the speed-trainees (top row) nor the direction trainees (bottom row) showed transfer-of-training to any non-trained task.

transfer to direction discrimination. [6] Below we consider what the present findings imply about the neural events mediating these two motion tasks.

The finding that the learning curves for direction discrimination were significantly steeper than those for speed discrimination is difficult to reconcile with the possibility that the two tasks are mediated by the same neural events. The lack of evidence for transfer-of-learning is also contrary to what would be expected if the same neural events mediated the two tasks. However, we note that the lack of transfer from speed discrimination to direction discrimination could be because the practice-based improvements on speed discrimination were modest, even among subjects who met the criterion for significant learning. Additionally, it is possible that training on either of the present tasks created a type of learning not detectable by our paradigm. In particular, Liu (1999) and Liu and Weinshall (2000) have shown that training on one task can alter the *rate* at which a second task is learned. We cannot rule out this possibility, since the present paradigm involved measuring learning rates only on the training task. Nevertheless, we emphasize that no transfer-of-learning was found in our pre- versus post-training tests, and one would expect such tests to reveal at least partial transfer if the same neural events were mediating the two tasks. That fact coupled with the difference in learning rates renders the present findings consistent with previous studies that have reported differences between speed and direction discrimination (Burr & Ross, 2002a, 2002b; Matthews et al., 2001; Matthews et al., 1999; Watamaniuk et al., 1993).

A previous perceptual-learning study by Shiu and Pashler (1992) is conceptually similar to the present study. In that study (Shiu & Pashler, 1992), participants made either brightness judgments or orientation judgments about line stimuli that differed from each other both in luminance and orientation. Those results, like the present results, indicated that the perceptual learning was task-specific, rather than stimulus-specific; Practice on the brightness task did not improve performance on the orientation task, even though the same stimuli were used on both tasks. Although neither that study (Shiu & Pashler, 1992) nor the present study can identify the specific neural change(s) underlying the practice-based improvements, we now consider two possible neural correlates of perceptual learning.

On the one hand, perceptual learning could reflect changes in the tuning curves of individual neurons. For example, perceptual learning on orientation discrimination has been correlated with changes in the slope of neuronal tuning curves, and such changes are specific to the neurons most likely to code the trained orientation (Schoups, Vogels, Qian, & Orban, 2001). Alternatively, perceptual learning could arise from changes in the weights between various neural populations that contribute to a participant's decision, without assuming any retuning of individual neurons (Dosher & Lu, 1998). Evidence that various neural populations become differentially active in a task-specific manner comes from a recent fMRI study on human participants who viewed linearly moving dots superimposed on radially moving dots (Watanabe et al., 1998). At all times the stimuli were constant, while the task required the participants respond to the linear motion, or the radial motion, or to passively view the stimuli. Relative to the passive viewing condition, activity increased significantly in areas V1 and MT+ when participants attended linear motion, yet the increase was limited to area MT+ when participants attended radial motion. Watanabe et al.'s (1998) study, therefore, demonstrates that different neural populations can be become active when the motion task is varied under constant stimulation, although that study did not assess the neural events responsible for speed and direction discrimination.

The neural events responsible for speed and direction discrimination have been the specific focus of several other imaging studies. Those studies, however, unlike the present study, either addressed speed discrimination (Corbetta, Miezen, Dobmeyer, Shulman, & Petersen, 1990; Orban et al., 1998) or direction discrimination (Cornette et al., 1998) separately, or investigated both discriminations but under very different stimulus conditions (Huk & Heeger, 2000). Future imaging studies that investigate these two motion tasks within subjects and under identical stimulus conditions, might localize neural events that distinguish speed discrimination from direction discrimination. In principle, though, some neural events that distinguish speed discrimination from direction discrimination could be, indistinguishable to neuro-imaging techniques. That is, even given identical stimulus conditions and stimulus-driven neural responses, speed discrimination and direction discrimination could be limited by task-specific *pooling strategies* performed on the same set of same hemo-dynamic events. If this were the case, then imaging studies would fail to reveal the dissociation between speed and direction discrimination that has been suggested by the present psychophysical data.

Acknowledgements

---

[6] Since the learning was task-specific, it is unlikely that non-motion factors, such as motivation, can account for the improvements. Accordingly, the results from our luminance discrimination task, which was designed to control for non-motion factors, are now unnecessary.

References

Ball, K., & Sekuler, R. (1987). Direction specific improvements in motion discrimination. *Vision Research, 27*, 953–965.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*, 433–436.

Burr, D. C., & Ross, J. (2002a). Direct evidence that "speedlines" influence motion mechanisms. *Journal of Neuroscience, 22*(19), 8661–8664.

Burr, D. C., & Ross, J. (2002b). Direct evidence that 'speed lines' aid perception of motion direction. *Vision Sciences Society Abstracts, 2*(260), 94.

Cheng, K., Hasegawa, T., Saleem, K. S., & Tanaka, K. (1994). Comparison of neuronal selectivity for stimulus speed, length, and contrast in the prestriate visual cortical areas V4 and MT of the macaque monkey. *Journal of Neurophysiology, 71*, 2269–2280.

Corbetta, M., Miezen, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1990). Attentional modulation of neural processing of shape, color and velocity in humans. *Science, 248*, 1556–1559.

Cornette, L., Dupont, P., Rosier, A., Sunaert, S., Van Hecke, P., Michiels, J., Mortelmans, L., & Orban, G. A. (1998). Human brain regions involved in direction discrimination. *Journal of Neurophysiology, 79*, 2749–2765.

De Bruyn, B., & Orban, G. A. (1988). Human velocity and direction discrimination measured with random dot patterns. *Vision Research, 28*, 1323–1335.

Dosher, B. A., & Lu, Z. L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proceedings of the National Academy of Sciences, 95*(23), 13988–13993.

Festa, E. K., & Welch, L. (1997). Recruitment mechanisms in speed and fine-discrimination tasks. *Vision Research, 37*, 3129–3143.

Heeger, D. J. (1987). Model for the extraction of image flow. *Journal of the Optical Society of America A, 4*, 1455–1471.

Huk, A. C., & Heeger, D. J. (2000). Task-related modulation of visual cortex. *Journal of Neurophysiology, 83*, 3525–3536.

Lagae, L., Raiguel, S., & Orban, G. A. (1993). Speed and direction selectivity of macaque middle temporal neurons. *Journal of Neurophysiology, 69*, 19–39.

Lauwers, K., Saunders, R., Vogels, R., Vandenbusshe, E., & Orban, G. A. (2000). Impairment in motion related tasks is unrelated to amount of damage to superior temporal sulcus motion areas. *Journal of Comparative Neurology, 420*, 539–557.

Liu, Z. (1999). Perceptual learning in motion discrimination that generalizes across motion directions. *Proceedings of the National Academy of Sciences USA, 96*(24), 14085–14087.

Liu, Z., & Weinshall, D. (2000). Mechanisms of generalization in perceptual learning. *Vision Research, 40*(1), 97–109.

Loftus, G. R. (1993). A picture is worth a thousand *P* values: on the irrelevance of hypothesis testing in the microcomputer age. *Behavior Research Methods, Instruments and Computers, 25*, 250–256.

Matthews, N. (2002). Correlations among speed, direction, and luminance discrimination thresholds. Investigative Ophthalmology and Vision Science Supplement 42, #1428.

Matthews, N., Luber, B., Qian, N., & Lisanby, S. H. (2001). Transcranial magnetic stimulation differentially affects speed and direction judgments. *Experimental Brain Research, 140*, 397–406.

Matthews, N., Liu, Z., Geesaman, B., & Qian, N. (1999). Perceptual learning on orientation and direction discrimination. *Vision Research, 39*(22), 3692–3701.

Matthews, N., & Qian, N. (1999). Axis-of-motion affects direction discrimination, not speed discrimination. *Vision Research, 39*, 2205–2211.

Matthews, N., & Welch, L. (1997). Velocity-dependent improvements in single-dot direction discrimination. *Perception and Psychophysics, 59*, 60–72.

Maunsell, J. H. R., & Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *Journal of Neurophysiology, 49*, 1127–1147.

McKee, S. P., & Watamaniuk, S. N. J. (1994). The psychophysics of motion perception. In A. T. Smith, & R. J. Snowden (Eds.), *Visual motion detection* (pp. 85–114). San Diego: Academic Press.

Mikami, A., Newsome, W. T., & Wurtz, R. H. (1986). Motion selectivity in macaque visual cortex. I. Mechanisms of direction and speed selectivity in extrastriate area MT. *Journal of Neurophysiology, 55*, 1308–1327.

Merigan, W. H., Pasternak, T., Ferrera, V., & Maunsell, J. H. R. (1991). Permanent deficits in speed discrimination after MT/MST lesions in macaque monkeys. *Society for Neuroscience Abstracts, 17*, 8.

Newsome, W. T., & Pare, E. B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *Journal of Neurophysiology, 8*, 2201–2211.

Orban, G. A., Dupont, P., De Bruyn, B., Vandenberghe, R., Rosier, A., & Mortelmans, L. (1998). Human brain activity related to speed discrimination tasks. *Experimental Brain Research, 122*, 9–22.

Orban, G. A., Saunders, R. C., & Vandenbussche, E. (1995). Lesions of the superior temporal cortical motion areas impair speed discrimination in the macaque monkey. *European Journal of Neuroscience, 7*, 2261–2276.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision, 10*, 437–442.

Perrone, J. A., & Thiele, A. (2000). Predicting the optimum speed tuning of MT neurons from their spectral receptive fields. *Society for Neuroscience Abstracts, 26*, 399.3.

Perrone, J. A., & Thiele, A. (2001). Speed skills: measuring the visual speed analyzing properties of primate MT neurons. *Nature Neuroscience, 4*(5), 526–532.

Rodman, H. R., & Albright, T. D. (1987). Coding of visual stimulus velocity in area MT of the macaque. *Vision Research, 27*, 2035–2048.

Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature, 412*(6846), 549–553.

Shiu, L. P., & Pashler, H. (1992). Improvement in line orientation discrimination is retinally local but dependent on cognitive set. *Perception and Psychophysics, 52*(5), 582–588.

Smith, A. T., Snowden, R. J., & Milne, A. B. (1994). Is global motion really based on spatial integration of local signals? *Vision Research, 34*, 2425–2430.

Watamaniuk, S. N., Grzywacz, N. M., & Yuille, A. L. (1993). Dependence of speed and direction perception on cinematogram dot density. *Vision Research, 33*, 849–859.

Watanabe, T., Harner, A. M., Miyauchi, S., Sasaki, Y., Nielsen, M., Palomo, D., & Mukai, I. (1998). Task-dependent influences of attention on the activation of human primary visual cortex. *Proceedings of the National Academy of Sciences, 95*(19), 11489–11492.