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Reduced direction discrimination sensitivity in visual motion adaptation, and the role of perceptual learning

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ABSTRACT

We investigated visual direction discrimination under the influence of motion aftereffect (MAE). Participants in each experiment first adapted to a horizontally drifting grating before deciding whether a drifting test grating moved to the left or right. A psychometric function was obtained as a function of the velocity of the test. Interestingly, in addition to the horizontal shift of the psychometric function that typified the MAE, the slope of the psychometric function became shallower after adaptation, indicating decreased discrimination sensitivity. However, this decrease was only observed in psychophysically experienced participants. Motivated, but psychophysically inexperienced participants only showed this effect after weeks of perceptual learning. This shallowing effect transferred to the untrained adaptation direction (e.g., from leftward adaptation to rightward), although perceptual learning of improved discrimination could not transfer. When the test duration was lengthened to reduce task difficulty, less training was needed to produce the same effect. These results indicate that, post-adaptation and when steady measurements could be obtained, left-right motion direction discrimination sensitivity was reduced.

1. Introduction

Perceptual adaptation along basic stimulus dimensions such as motion direction, orientation, chromatic and achromatic contrast, and spatial and temporal frequency, is fundamentally important in understanding the neural basis of vision. Adaptation allows one to probe both computational and representational properties along each stage of the visual processing hierarchy. Much progress has been made in elucidating the psychophysical characteristics of perceptual adaptation, particularly motion and orientation adaptation (for a review, see Clifford, 2002).

Encouragingly, important parallels between adaptation in these two modalities have been established that point to a common computational principle that underlies both, e.g., in coding optimization and error correction (Anstis, Verstraten, & Mather, 1998). In fact, this parallel is quantitatively consistent. For example, after adaptation, the neural orientation and direction tuning functions exhibit remarkable similarity in $[0^\circ, 90^\circ]$ for orientation, and in $[0^\circ, 180^\circ]$ for direction. (Here, 0° is the adapting orientation or direction.) Such similarity in coding is called the double-angle representation (Clifford, 2002).

Despite such parallels between motion and orientation and the connections suggested by the double-angle representation, there remain some key differences between the two modalities. In motion discrimination studies, it is common to use stimuli that drift in opposite directions (Thompson, 1981; Newsome & Pare, 1988). The following neurophysiological considerations make such discrimination with opposite directions desirable: The phenomenon of motion opponency, which was found in the primate middle temporal cortex (MT) (Qian & Andersen, 1994; Heeger, Boynton, Demb, Seidemann, & Newsome, 1999), demonstrates the inter-dependent manner in which two opposing motion directions are represented.

Such phenomenon of motion opponency appears to be specific to motion, without an orientation counterpart, as follows. In the context of the double-angle representation, it appears that opposite motion directions correspond to orthogonal orientations. However, unlike opposite motion directions that are linked by opponent neural mechanisms, orthogonal orientations, as far as we know, are not linked by similar mechanisms (De Valois, Yund, & Hepler, 1982; Ringach, Shapley, & Hawken, 2002). Therefore, motion discrimination with opposite directions, which is ecologically important, seems to be unique, without a straightforward counterpart in orientation. Motion discrimination between opposite directions under adaptation, therefore, offers a unique window into the way in which the visual motion system works in the brain.

Blake and Hiris (1993) invented a method to measure MAE strength and, at the same time, measured the psychometric function in direction discrimination of opposite directions. After showing an adapting stimulus of random dots all moving upward, a test stimulus was shown and participants decided whether it moved upward or downward. The dot coherence of the test stimulus was the independent variable for the

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psychometric function. Blake and Hiris (1993) found that this psychometric function shifted horizontally, with the amount of the shift indicating the strength of MAE. The slope of this function, measured from two participants, did not change. This result has important implications in Signal Detection Theory, as argued in Georgeson (2012). Namely, the horizontal shift indicated that MAE was associated with a change in bias, but not sensitivity. According to Georgeson (2012), since MAE was self-evidently perceptual, then the bias was perceptual as well.

Phinney, Bowd, and Patterson (1997) also measured motion discrimination following adaption, although this time they measured fine direction discrimination (a few degrees apart). They found that, along the adapted motion direction, the discrimination threshold was reduced, indicating that adaptation improved angular direction discrimination. Superficially, discriminating motion direction (say, between 32° and 35°) appears to be similar to orientation discrimination. However, tilt adaptation actually leads to decreases, not increases, in orientation sensitivity (Erlikhman, Singh, Ghose, & Liu, 2019).

Additional results, this time in increased speed discrimination sensitivity, were found by Hietanen, Crowder, and Ibbotson (2008). They studied speed estimation following adaptation. Radially outward moving dots were used both as adaptor and test stimuli. After adaptation, a stimulus at the same location as the adaptor with a constant speed, and another stimulus on the opposite side of the fixation with a variable speed were presented. Participants decided which of the two moved faster. Hietanen et al. (2008) found that, when the speed of the adapted stimulus was low, discriminability improved post-adaptation.

To summarize, there are theoretical and neurophysiological reasons why motion and orientation adaptation may share similar processing and encoding strategies. Orientation, non-opposing motion direction, and speed adaptation all lead to both shifts in bias and changes in sensitivity. When motion direction discrimination is tested following adaptation using opposing motion directions (what we will refer to as left-right direction discrimination), only a shift in bias has been found, without changes in sensitivity. Why might that be the case?.

Given the dynamic nature of adaptation and its recovery, it is natural to associate discrimination sensitivity with perceptual variation as a function of time. Bex, Bedingham, and Hammett (1999) found increased speed sensitivity during adaptation, and suggested that adaption generally serves to improve a perceiver's sensitivity to the current environment. They discussed, as possible sources of the increased sensitivity, the relationship between sensitivity, perceptual stability, and the time course of adaptation. They considered it unlikely for the sensitivity to be related to different temporal stages in the course of adaptation, because their data did not support such a notion. However, the issue of perceptual stability on a longer temporal scale, a scale comparable to perceptual learning in weeks or months, has not been explored. The current study addressed this issue.

2. Exp. 1: A single session experiment with naïve participants

2.1. Stimuli

The motion stimulus was adopted from Sachtler and Zaidi (1993), and was piloted by authors GE and ZL. Specifically, a vertically oriented sine wave grating moved either leftward or rightward inside a rectangular aperture. The size of the aperture was, in width × height, 10° × 1.25° in visual angles, and the grating's spatial frequency was 0.4 cycles/°. The luminance range of the grating spanned the full range of the display. Fig. 1 (top) shows a static example of the stimulus.

When this grating served as the adaptor, its speed was $5^\circ/s$. When it served as a test stimulus in left-right direction discrimination, its speed had the following three ranges: (1) When direction discrimination was measured without any adaption, the range was $[-1.5, -1.2, -0.9, \ldots, +1.5^\circ/s]$ with a step size of $0.3^\circ/s$. (2) When the adaptor moved to the right, the range was $[-1.0, -0.6, -0.2, \ldots, +3.0^\circ/s]$ with a step size of $0.4^\circ/s$. (3) When the adaptor moved to the left, the range was $[-3.0, -2.6, -2.2, \ldots, +1.0^\circ/s]$ with a step size again of $0.4^\circ/s$. These values were selected in a pilot experiment to attempt to cover the full range of the psychometric function.

2.2. Procedure

The experiment had two parts: 1. discrimination without adaptation, which took about 15 min; and 2. discrimination with adaption, which took about 25 min. The adaptation direction (left or right) for each participant was randomly assigned. These two parts are specified below. Fig. 2 illustrates these two parts.

1. A black stationary fixation dot was shown at the center of the aperture, together with the adaptor for 30 s. In this no adaptation part, the adaptor was simply a middle gray blank screen. A blank, middle gray screen was then shown for 0.5 s, which was the Inter-Stimulus Interval (ISI). Halfway through the ISI, there was a computer beep that alerted the participant that the test stimulus was coming up, and the fixation changed from black to green. The test stimulus was shown for 75 ms, and participants responded whether the test moved to the left or right, without feedback. This 75 ms duration was the same as originally used in Sachtler and Zaidi (1993)

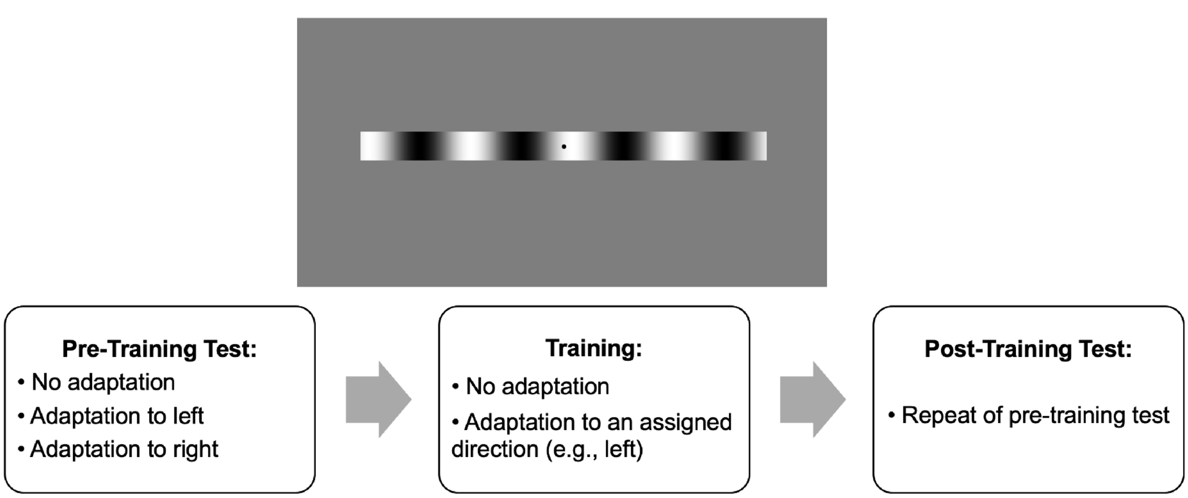

Fig. 1. Top: a static example grating stimulus that was used both as the adaptor and as the test stimulus. The stimulus moved either to the left or right. The central dot is the fixation. **Bottom**: flow-chart of the experimental design on motion direction discrimination with the following steps: pre-training test, training, and post-training test. During training, a fixed adaption direction (left or right) was assigned randomly to a given participant.

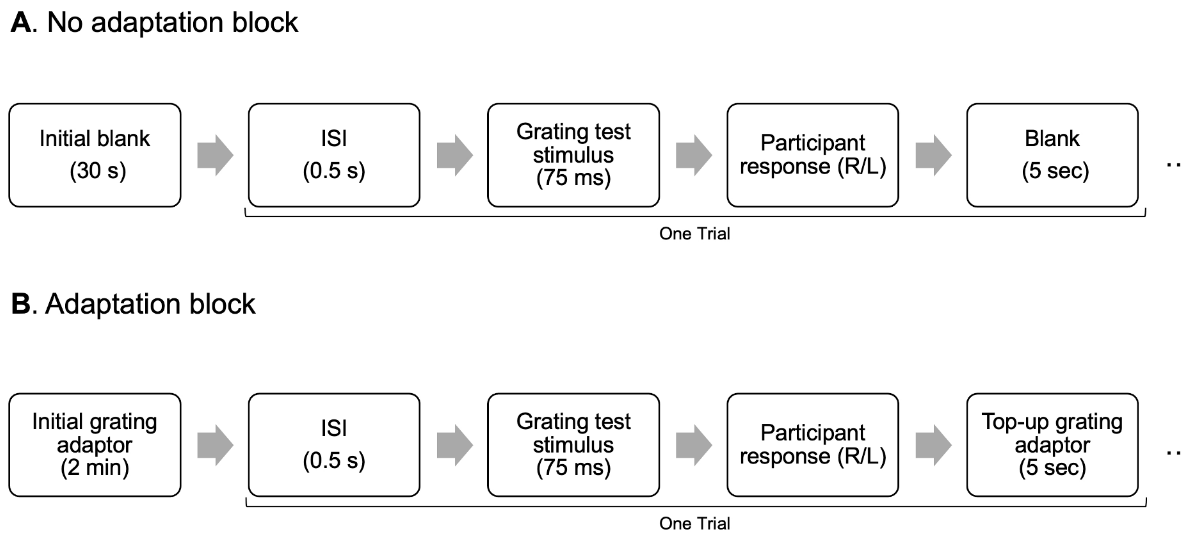

Fig. 2. **A**: illustration of the first part of Experiment 1, when motion direction discrimination was tested without adaptation. **B**: illustration of the second part of Experiment 1, with motion direction discrimination after adaptation.

and was selected in order to minimize eye movements during test stimulus presentation. After the response, the fixation turned black, and the same adaptor was shown for 5 s. Here, again, the adaptor was simply a middle gray blank screen. This was termed top-up adaptation. After the ISI and the computer beep, the fixation turned green, a test stimulus was shown for the participant to respond. All subsequent trials would be identical to the second trial except for the test stimulus, whose speed was randomly sampled from the 11 possible choices in its range. Each of the 11 possible speeds was tested for 20 trials, resulting in 220 trials total.

2. This part was almost identical to Part 1, except that: the initial 30 s blank adaptor was replaced by a grating adaptor with a fixed motion direction and speed that lasted for 2 *min*. The subsequent top-up adaptor in each trial was also this same grating with the same velocity.

Each participant was provided with written instructions on the computer display, and could ask questions to the research assistant conducting the experiment. At the beginning of the experiment, the research assistant also provided feedback to the participant during the easy trials, when the speed was fast and its direction easier to see. Such verbal feedback was to ensure that the participant understood the task.

The no-adaptation condition was always run first to avoid any lingering adaptation effect to performance in Part 1 from Part 2. Also, since Part 2 always followed Part 1, any performance decrement from Part 1 to 2 could not be due to any learning. Such decrement would be unlikely due to fatigue either since Part 1 was only 15 min.

2.3. Apparatus

The experiment was run on a Sony Triniton CRT monitor, which was gamma-corrected, with a resolution of 1440×900, and a refresh rate of 60 *Hz*. Participants viewed the stimuli binocularly from a chin rest, with a viewing distance of 70*cm*. The test room was lit only by the CRT display and a dim LED lamp behind the participant. Participants adapted their eyes to the dark room before starting the experiment.

2.4. Participants

Fifty-three psychology undergraduate students from the University of California Los Angeles (UCLA) participated for partial course credit. This study was approved by the UCLA IRB. All participants in this and subsequent experiments in the current study gave informed consent.

2.5. Results

We used the nonlinear fitting function *nlinfit* of MatLab (MathWorks Inc., Natick, MA) to fit each participant's psychometric function to a cumulative Gaussian, with two free parameters: mean μ and standard deviation σ. The lapse and guess rate used in the fitting function were fixed at zero for simplicity.

Fig. 3 shows the 53 participants' psychometric functions, with the no adaptation condition in the top row, and the adaptation condition in the bottom row (left- and right-adaptations not separated). Fig. 4 shows summarized results with the MAE as the μ difference between the adaptation and no-adaptation conditions on the left, and the σ difference on the right. Since $1/\sigma$ is defined as the direction discrimination sensitivity, which is the slope of the psychometric function at the Point of Subjective Equality (PSE), any difference in $1/\sigma$ would indicate discrimination sensitivity change from pre- to post-adaption. No such change in discrimination sensitivity was found ($z = 1.17, p = 0.24$, two-tailed Wilcoxon ranked sign test, which will be used throughout the current study)(some participants' data could not be included in the analysis because their $\sigma \rightarrow \infty$). Yet, the MAE was apparent: the $\Delta\mu$ analysis gave rise to $z = 5.65, p = 1.65e-8$.

Such analyses demonstrated that the MAE reflected in the data was not indicative of the discrimination performance. This is because MAE was associated with the discrimination bias in the task, whereas discrimination performance here was associated with the sensitivity. As can be seen in Fig. 3, the discrimination performance from the participant pool as a whole was poor. Therefore, we could not rule out the possibility that the lack of discrimination sensitivity change was due to the overall poor performance. The next experiment aimed to collect data from more dedicated participants, and with more sessions in an attempt to obtain more stable data.

3. Exp. 2: A three-session experiment with more dedicated participants

3.1. Participants

This experiment was identical to Exp.1 except that the participants were seven research assistants in the laboratory of author ZL. These participants, including author SK, had no prior experience in any low-level psychophysical experiments. They ran the two-part experiment three times in separate days, and the adaptation direction was randomized each time.

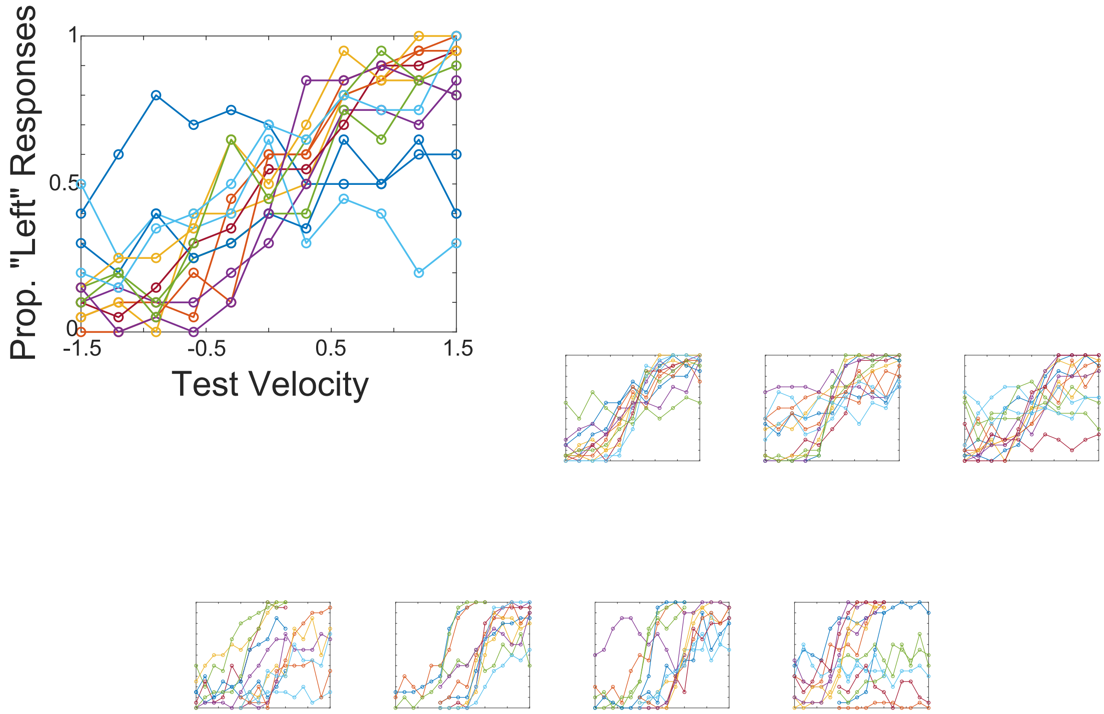

Fig. 3. Exp. 1 results. **Top**: Unfitted psychometric functions in the non-adapt condition of 53 naïve participants, randomly divided into four groups to avoid clustering: No. 1 – 13, 14 – 26, 27 – 39, and 40 – 53. **Bottom**: the psychometric function counterparts of the same participants in the adaptation condition. In each panel, there were both left-adapt and right-adapt psychometric functions. The blown-up panel at top-left is meant to be more legible. Subsequent figures will also use this style of plot representation.

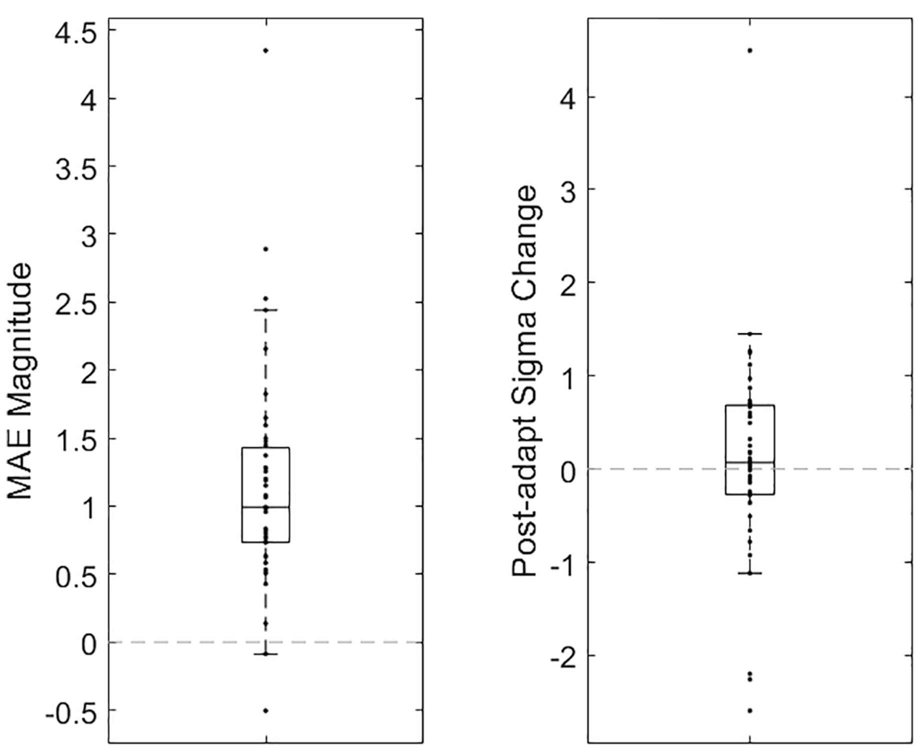

Fig. 4. Left: Exp. 1's Motion Aftereffect (MAE) or $\Delta\mu$, measured as the difference of the means of the fitted Gaussians between the adaptation and no-adaptation conditions. The plot shows both the mean MAE and all participants' MAE's as a scatter plot. The extent of the box is the 25th and 75th percentiles, respectively, with the horizontal line inside representing the median. The whiskers extend to most extreme points that are not outliers, defined by the Matlab boxplot functions and corresponding to roughly 2.7 standard deviation units. **Right**: Similar as the left panel, except $\Delta\mu$ is replaced by $\Delta\sigma$, where σ is the standard deviation of the fitted Gaussian function. These data are from 43 of the 53 participants, because the remaining 10 participants' data could not be fitted with a psychometric function. Their $\sigma\rightarrow\infty$, which means a flat function with the μ practically undetermined.

3.2. Results

To visualize the performance, Fig. 5 shows the final session's psychometric functions for each inexperienced participant. It should be apparent that, out of the seven participants, four (bottom row) had less than perfect fitting psychometric functions. This suggests that, even after three sessions, participants as a whole still could not give rise to regular shaped psychometric functions.

We then averaged each participant's σ's and, separately, μ's across their runs (after taking into consideration whether each run was left- or

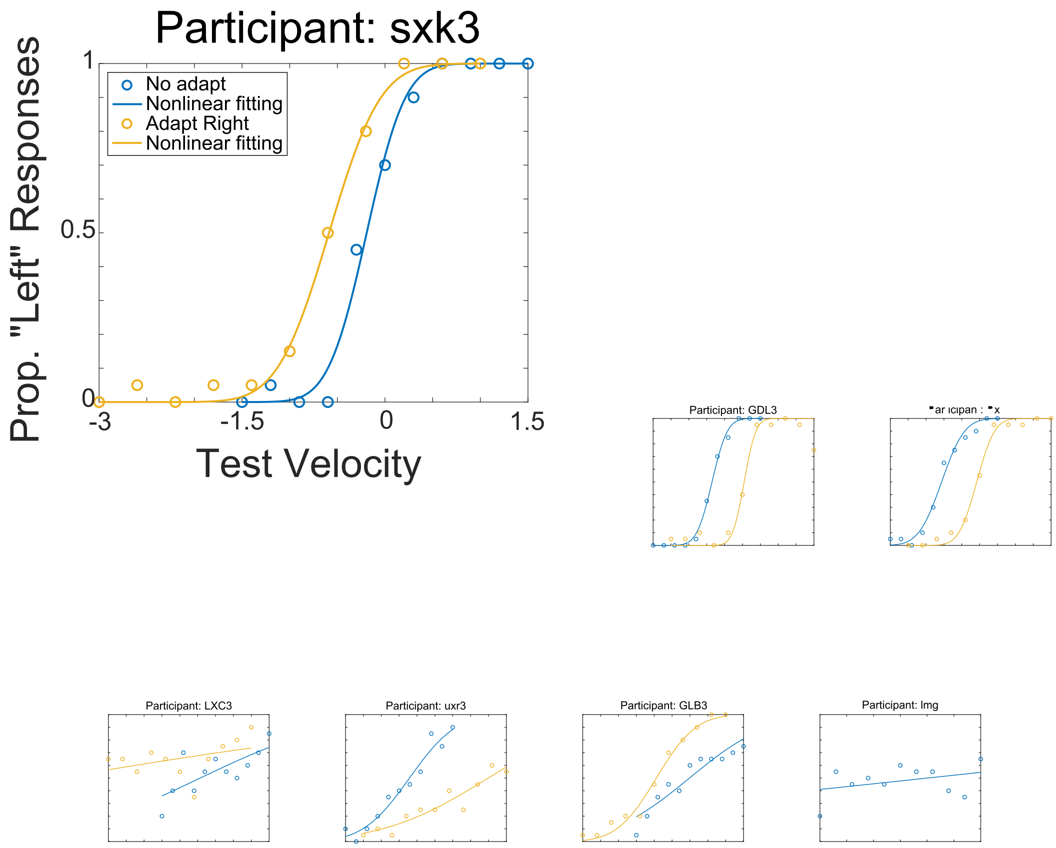

Fig. 5. Exp.2's final session of the seven participants' psychometric functions in the no-adapt (blue or darker curves) and adapt (yellow or lighter curves) conditions. There was no consistent pattern between the slopes of the two psychometric functions across panels. Apparently, some participants still had difficulty, even in the third try, to obtain a regular psychometric function. This can be seen in the last panel, from the 7th participant. This single psychometric function was the only one possible to obtain from model fitting. The other psychometric function is effectively flat, with $\sigma \rightarrow \infty$ and an uncertain bias μ.

right-adapted). Some sessions had to be skipped because no σ and μ could be estimated because the psychometric function was effectively flat with $\sigma \rightarrow +\infty$ and μ completely unreliable. As a result, one of the participants' had only one σ and one μ available from the last session (Fig. 5). From the remaining six participants' data, every one showed a reliable horizontal shift of the psychometric function from no adaptation to adaption, giving rise to a statistically significant MAE, after the left and right adaptations were properly aligned ($T = 0, \alpha = 0.05$). Five of the six participants showed a greater σ for the adaptation than no adaptation condition. However, since $n = 6$, all participants had to show the same sign of the difference for the effect to be statistically significant. Consequently, the reduction of $1/\sigma$ as a result of adaptation was not statistically significant ($T = 4 > 0, \alpha = 0.05$).

Nevertheless, given that five of the six participants showed that their discrimination sensitivity was reduced from pre- to post-adaptation, the effect may be statistically significant if more participants were tested. We also note that, for the 7th participant, the $\sigma \rightarrow +\infty$ was for the adaptation condition, and not for the no adaptation condition. That is to say, the seventh participant showed the same trend as the rest of the five out of six participants.

In addition, if we look at participant's SXK's σ's from all three sessions (Fig. 6), numerically these are: [no adaptation, adaptation] = [0.77, 0.73], [0.24, 0.44], and [0.32, 0.43], respectively. From the first to second session, discrimination sensitivity improved. However, from the second to the third session, the no-adaptation σ worsened even though the adaptation σ remained steady. In addition, in both the second and third sessions, the discrimination sensitivity without adaptation remained higher (or σ was lower) than that with adaptation. This single participant's data offered promise and suggested the need for stable performance, probably because the overall performance was still improving.

We subsequently collected data from authors GE and ZL, who were both psychophysically experienced, but had little experience with this specific experiment. As shown in Fig. 6, both showed a very clear pattern of higher sensitivity for the no-adaptation than adaptation conditions. This raised an intriguing question, i.e., whether the effect of reduced discrimination sensitivity as a result of adaptation could be found only for participants with more psychophysical experience than three sessions of measurements. After all, the experimental parameters were adopted from Sachtler and Zaidi (1993) whose participants were psychophysically experienced. The next experiment tested this hypothesis.

4. Exp. 3: A perceptual learning experiment

The time duration of this experiment was eight weeks, chosen because one UCLA quarter was 10 weeks. This experiment was conducted using a typical perceptual learning procedure with the following three components: 1. pre-training tests, 2. training, and 3. post-training tests, as follows.

1. Psychometric functions in the following three conditions, no adaptation, adaptation to the left, and adaptation to the right were obtained in separate days.
2. The no adaptation, and one of the two adaptation conditions (left or right was randomly assigned to, but fixed for, each participant during the entire training), were alternatively run in separate days.
3. At the end, the untrained adaptation condition was run in two separate sessions (except for one participant who ran only once) to

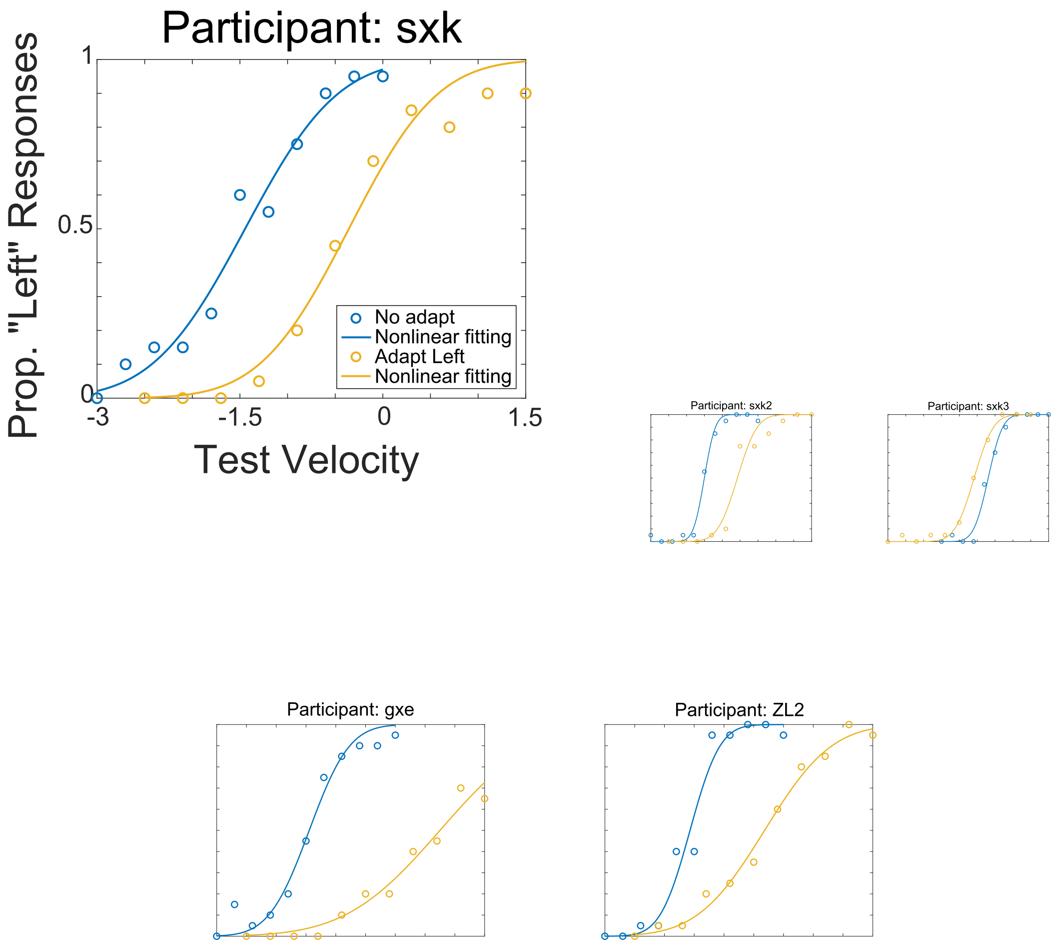

Fig. 6. Exp.2's psychometric functions with (yellow or lighter curves) and without adaption (blue or darker curves) for author SK in her three sessions in the top row, and for authors GE and ZL in the bottom row. For GE and ZL, the slope of the no adaptation curve is clearly steeper than that of the adaptation curve.

ensure reliable measurements of the corresponding μ's and σ's. The purpose was to test whether learning in the no-adaptation and trained adaptation conditions could transfer to the untrained adaptation condition.

4.1. Participants

Eleven UCLA undergraduate students participated for partial research credits. Two of the students, including author SK, had participated in Exp. 2 above. The average total number of sessions each participant ran was 24. Eight of these participants were no longer available for any further data collection after the school quarter, but the remaining four continued in the following quarter. These four participants continued their training, similarly as before, in the originally assigned trained adaptation condition, and in the no-adaptation condition, five sessions each. At the end, they ran two sessions of the untrained adaptation condition, and each of which was preceded by a no-adaptation condition. The duration of this continued training and testing was also eight weeks. The purpose was two fold: (1) to test whether any systematic difference of the standard deviation σ between the no-adaptation and trained adaptation conditions could eventually diminish, and (2) to test whether some non-learning participants could eventually learn. The average total number of sessions for each of these four participants was 14.

4.2. Results

4.2.1. Comparing σ between adaptation and no adaptation conditions

We were most interested in the question whether direction discrimination sensitivity ($1/\sigma$) under motion adaptation was reduced as compared with the no-adaptation sensitivity, after participants were sufficiently trained. We first looked at each participant's final session's σ in the following three conditions: no-adaptation, adaptation along the trained direction, and adaptation along the untrained direction. Fig. 7 shows the scatter plot of the 11 participants, plus the data from authors GE and ZL (who were psychophysically experienced). The scatter plot compares the σ's between the no adaption σ along the x-axis and adaption σ along the y-axis (trained and untrained). For both the trained and untrained conditions, the majority of the corresponding data points are above the 45° line. This indicates that the σ with adaptation was greater than without adaptation, with statistical significance ($\alpha = 0.05, T = 15 < 17_{critical-value}(n = 13)$ for the trained, and $T = 6 < 10_{critical-value}(n = 11)$ for the untrained condition).

Note that since both the trained-adaptation and no-adaptation conditions went through the same durations of training, their σ difference could not be due to more training in one condition over the other. On the other hand, for the untrained adaptation condition, its psychometric function also became shallower, as compared to the no adaptation condition. This transfer of reduced discrimination sensitivity relative to the no adaptation condition will be compared with the result below when little transfer of perceptual learning was found from the trained to the untrained conditions. Taken together, these results indicate that the

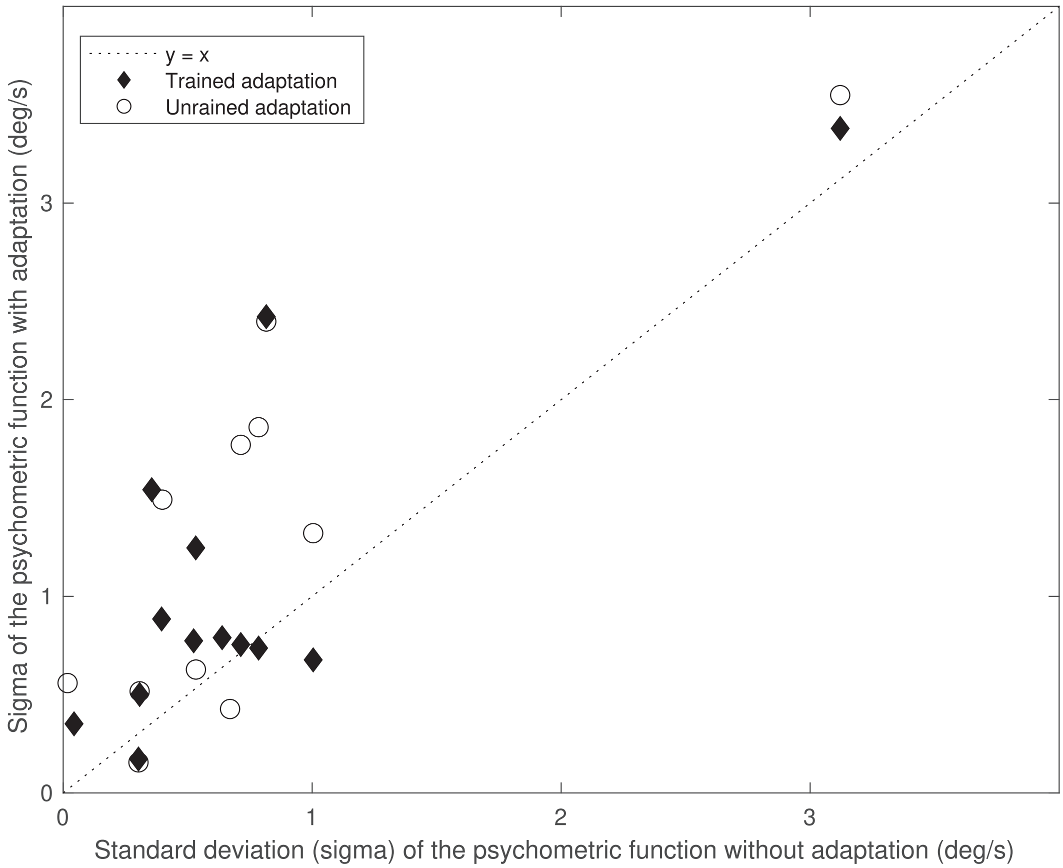

Fig. 7. Exp. 3. Scatter plot of the 11 trained participants, with their no-adaptation final session's σ as the x-value, the trained adaption final session's σ as the y-value in filled diamonds, and the untrained adaption final session's σ as the y-value in open circles. Each of the 11 pairs therefore was vertically aligned. Two additional data points are also plotted, from authors GE and ZL. But they contributed only two filled diamond points because they had no untrained adaptation directions. Any data point above the 45° line indicates that the adaptation σ was greater than its no-adaptation counterpart. In both trained and untrained adaptation conditions, the majority of participants showed, with statistical significance, lower discrimination sensitivity ($=1/\sigma$) with adaptation than without adaptation.

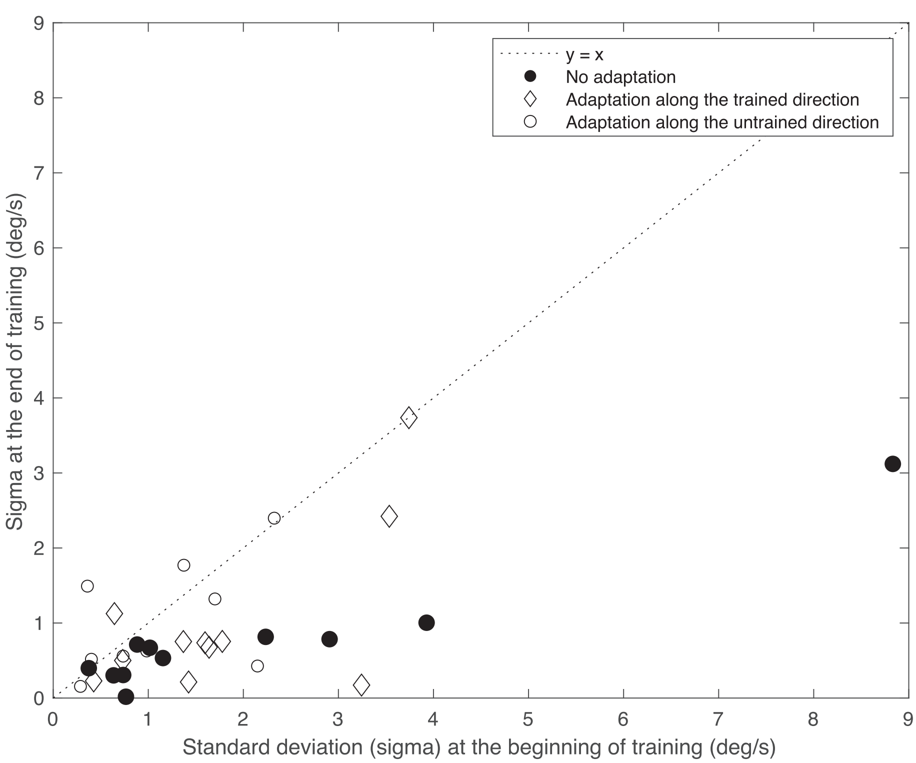

Fig. 8. Exp. 3. Scatter plot of the 11 trained participants of their initial session's σ (x-axis), and the final session's σ (y-axis), for the no adaptation condition (filled circles), the trained adaptation condition (diamonds), and the untrained adaptation condition (open circles). Only one of the 11 participants did not improve in the first two conditions. But four out of the nine available participants did not improve their discrimination sensitivities in the untrained condition. For the four participants who trained through two school quarters at UCLA, these y-values were those at the end of the entire training.

relative sensitivity reduction may be due to improved consistency in psychophysical measurements as a result of the perceptual training.

4.2.2. Perceptual learning of motion discrimination with and without adaptation

Next, we looked at the learning of the 11 participants in the no-adaptation and trained adaptation conditions. We compared the σ's between the initial and final sessions for these two conditions, respectively. Fig. 8 shows the scatter plot of these participants' data. There was only one participant whose σ increased in the course of training for the no-adaptation condition (i.e., no learning) and the same participant did not learn in the trained adaptation condition either. The rest of the 10 participants showed reduction of σ in both these conditions: $T = 1 < 3_{critical-value}, \alpha = 0.005; T = 3 < 5_{critical-value}, \alpha = 0.01$ for the no adaptation and trained adaptation conditions, respectively.

Fig. 8 also shows the σ scatter plot of the untrained condition for nine of the 11 participants. For the 10th participant, the initial psychometric function was practically flat, such that the corresponding $\sigma \rightarrow \infty$. The 11th participant by mistake forgot to collect data for this condition at pre-training. Therefore, these two participants' data could not be plotted. Among the nine participants whose data were available, four increased their σ's from the initial to the final sessions. Taken together, there was no statistically significant reduction of σ in this condition, meaning that there was no statistically reliable transfer from the two trained conditions to this untrained condition ($T = 18 > 8_{critical-value}$, $\alpha = 0.05$).

To better visualize the behavioral performance of the 11 participants at the end of the eight week training, Fig. 9 shows the no adaptation and trained adaptation psychometric functions at their respective final sessions, for each of the 11 participants. Eight out of the 11 participants showed a reduced discrimination sensitivity for the adaption as compared to no adaption conditions.

To provide further concrete illustrations of the behavioral performance, Fig. 10 shows the four participants' data who trained in two eight-week school quarters, which spanned about six months including the winter break in between the two quarters. The figure shows σ, the reciprocal of discrimination sensitivity in the top row; and μ, the discrimination bias in the bottom row; in the no adaptation, trained adaptation, and untrained adaptation conditions. The first three participants showed learning in training, and transferred to the untrained condition. Two of these three participants, at the end of the 16-week training, showed comparable σ's among all three conditions. This indicates that perceptual learning could eventually overcome the adaptation effect. The same three participants also showed reduced biases in the adaptation conditions. The fourth participant did not learn in the first school quarter, nor in the second quarter. In fact, both discrimination sensitivity and bias became worse for the two adaptation conditions as a function of time, while the no adaption performance remained flat for both sensitivity and bias.

4.2.3. Discrimination bias μ as a result of perceptual learning

In the last section, we showed the bias as a function of time for the

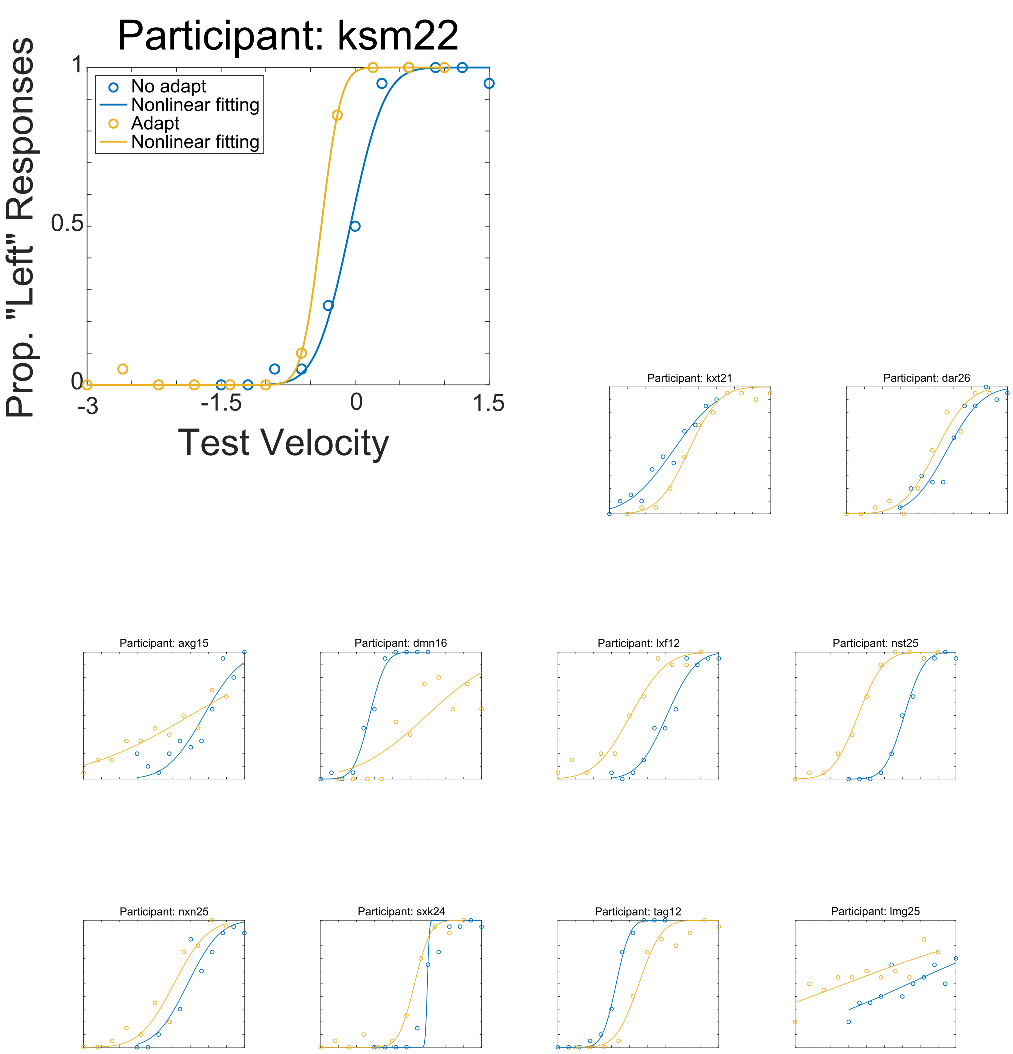

Fig. 9. Exp. 3. Psychometric functions at the end of the eight-week perceptual learning, with (yellow or lighter curves) and without (blue or darker curves) adaptation, for each of the 11 participants. The three participants in the top row had a steeper psychometric function with adaptation than without adaptation. The eight participants in the two lower rows had the opposite difference. The last participant was the same last participant in Exp. 2 who had difficulty obtaining a reasonable psychometric function.

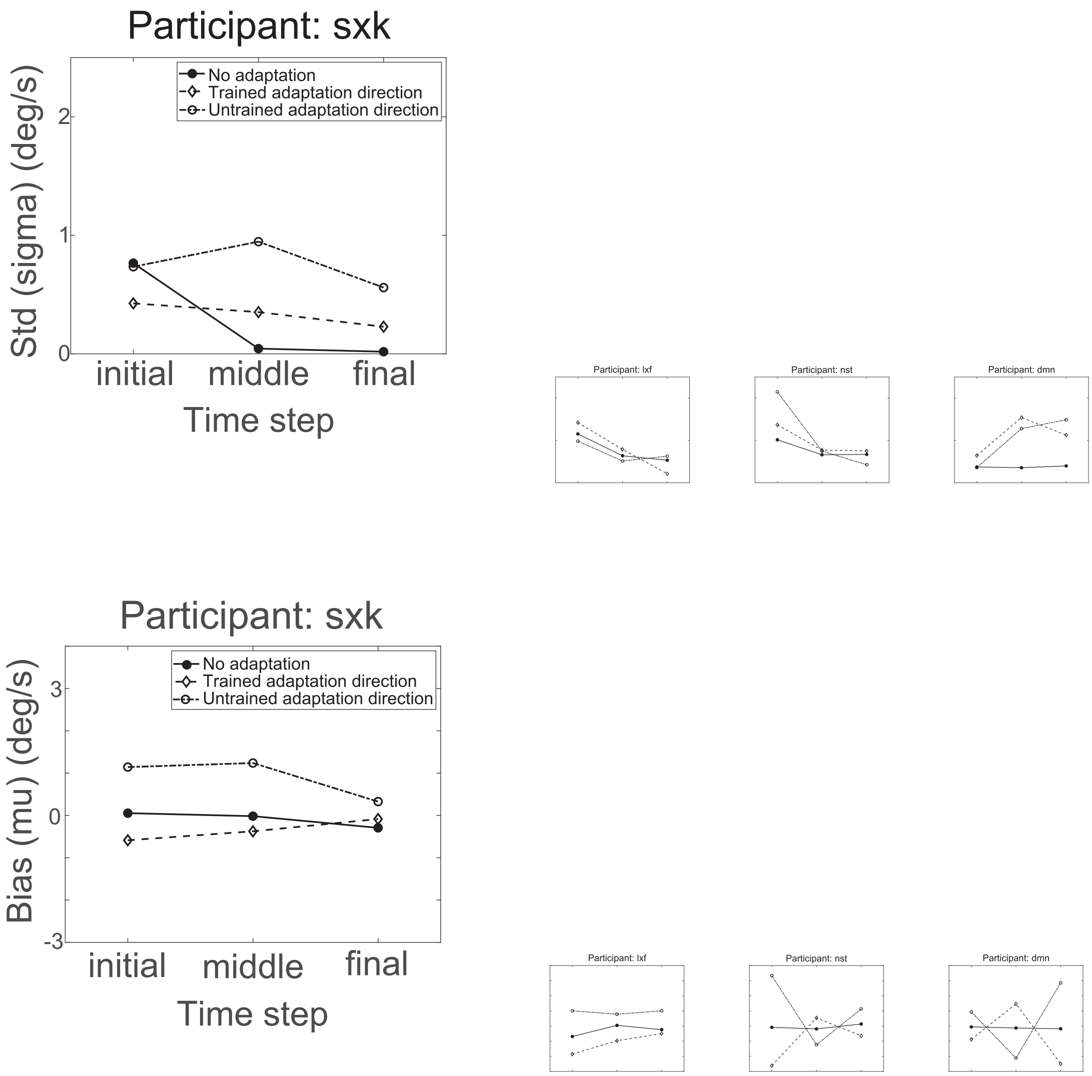

Fig. 10. Exp. 3. **Top**: Standard deviation (σ) of the Gaussian used to fit a psychometric function as a function of time. This row shows the change of σ from the initial measurement, to the end of the first school quarter, and to the end of the second quarter, for each of the four participants. **Bottom**: Similar as the top row except that bias (μ) is plotted.

four participants who trained for 16 weeks. It should be informative to look at the change of discrimination bias μ for all participants. To visualize the data, we first normalized the data as if all participants adapted to rightward motion during perceptual training, whereas adaptation to leftward motion was treated as the transfer condition. This normalization was achieved by simply flipping the left-right indexes so that all participants' trained adaptation direction was aligned. Fig. 11 shows the scatter plot of a participant's initial (x) and final (y) biases (μ's) in each of the following three conditions: no-adaptation (filled circles), adaptation to the trained direction (diamonds), and adaptation to the transfer direction (open circles). Consequently, each participant contributed three data points to the scatter plot.

For the no adaptation condition, there was no systematic bias toward left or right, not surprisingly. We calculated bias changes in terms of the magnitude change $|\mu_{last}| - |\mu_{1st}|$. The five largest absolute value changes were all reductions, which can be seen since the 11 filled circles form into a horizontally elongated cluster in Fig. 11. However, for the remaining five of the six participants, their biases slightly increased, likely due to random fluctuations since these biases were already small. The Wilcoxon two-tailed test did not give rise to a statistically significant reduction of bias ($T = 18_{critical-value} > 10, \alpha = 0.05$).

For the trained adaptation condition, 10 out of the 11 participants reduced their biases as a function of time. Specifically, nine data points were above the 45° line in the 3rd quadrant. The 10th participant had an opposite (or "wrong") bias in the initial session, but subsequently the bias moved to the direction consistent with MAE (diamond point in the 4th quadrant). The 11th participant showed no reduction in bias (diamond in the 3rd quadrant, below the 45° line). The overall reduction in bias (in time) was statistically significant ($T = 9 < 10_{critical-value}, \alpha = 0.05$).

For the transfer condition, there was no systematic reduction of bias μ. Out of the nine participants who had their pre-training measurements, half increased their biases. No statistical effect could be significant for this condition. This result was consistent with the companion analysis, in discrimination sensitivity, which showed little improvement on average. Therefore, there was little transfer of perceptual learning from the two trained conditions to this untrained condition, as measured by the bias μ.

5. Exp. 4: An easier experiment with trained participants

In all experiments in this study so far, the test stimulus duration of 75 ms appeared to be a major challenge to the participants. This duration was originally used for the two psychophysically experienced

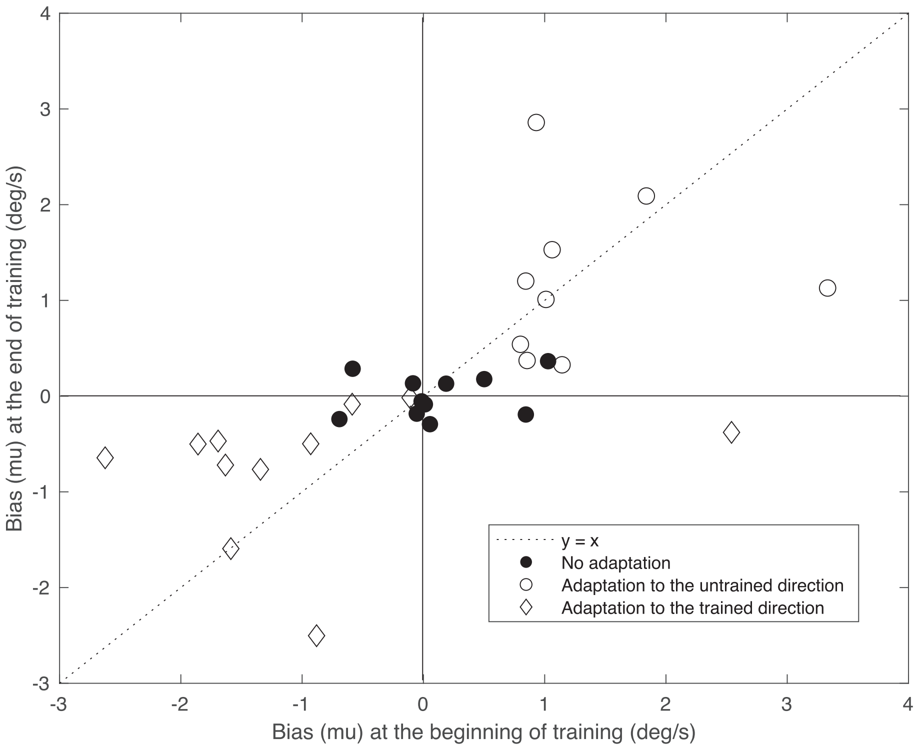

Fig. 11. Exp. 3. Scatter plot of the 11 participants' biases (μ's) in the no-adaption (filled circle), adaptation to the trained direction (diamonds), and adaptation to the transfer direction (open circles). The x-coordinate is the initial bias, and the y-coordinate is the final bias after perceptual training. One participant's initial μ estimation in the transfer condition was not available due to the poor fitting of the psychometric function, where the μ was completely uncertain. Another participant did not run the initial transfer condition, by mistake. As a result, there are only nine data points (nine open circles) in the condition of adaptation to the untrained direction.

participants in Sachtler and Zaidi (1993). However, if the effect we had found so far was robust, we would expect that the same effect could be replicated from trained participants without the need of extensive perceptual learning, so long as the task was easier with a longer test stimulus duration. The current experiment tested this prediction.

5.1. Participants

Eleven UCLA undergraduate students participated. Five of these participants, including author SK, also participated in Exp. 3, because we thought it important to verify whether these participants could replicate the effect under a new stimulus test duration.

These participants, prior to Experiment 4 but in a different day, had run in a different, related experiment for another study. That experiment involved adapting to and discriminating between clockwise and counter-clockwise spiral motion stimuli. That experiment was unlikely to affect performance on a left-right discrimination task in any biased manner, because the first four of the five sessions for each participant had equal amount of clockwise and counter-clockwise rotations. Only the 5th session showed a single direction of rotation duration adaptation (clockwise or counter-clockwise), which was chosen independently from the left or right directional adaptation here in Exp. 4.

Nevertheless, such experience may well have facilitated familiarization and training for Exp. 4. Namely, except for the different stimuli (line drawing of a spiral on a uniform background, and its mirror image), a test stimulus duration of 100 ms, and different motion (rotational), the two experiments were otherwise the same. Each session of the rotational experiment was about 50 *min*.

5.2. Apparatus and procedure

The data were collected in May, 2020. Due to the pandemic, each participant ran the experiment at home using their own computers. All participants used their laptop displays, except one participant who used an HP LCD monitor. The refresh rate of all displays was set to 60 *Hz*, and the resolutions were set as close to that used in the prior experiments as possible, 1440 × 900. The viewing distance was the same as before 70 *cm*, although no chin rest was available.

The participants first ran a pilot experiment, which was identical to Exp. 3 except that the test stimulus duration was 200 ms. This duration of 200 ms was chosen such that it was still shorter than the time needed to initiate pursuit eye movement, but meanwhile as long as possible to allow stimulus familiarization. Each participant ran the following three conditions: no adaptation, adaptation to the left, and adaptation to the right.

The participants then ran the main experiment of Exp. 4, first with the no adaptation, and followed with an adaptation condition. For the five participants who had taken part in Exp. 3, this adaptation direction was the same as their trained direction in Exp. 3. For the rest of the six participants, this direction was randomized. The stimulus test duration was individually chosen within [100, 200] ms, based on their performance in the pilot run so that the experiment would not be too easy or too hard. Since this duration was the same for the no adaptation and adaptation conditions per participant, such within-subject comparison was ensured to be fair. This experiment was otherwise identical to Exp. 3.

5.3. Results

We fitted each of the two psychometric functions per participant in exactly the same way as before. All participants showed an MAE ($= \Delta\mu$) that was consistent with their respective adaptation direction. After this MAE's sign was properly adjusted according to the adaptation direction, every participant showed a horizontal shift of their psychometric function in the expected direction ($\alpha = 0.001$).

More importantly, 10 out of the 11 participants reproduced the same effect of a shallower psychometric function post-adaptation ($T = 7 < 8_{criticalvalue}(n = 11), \alpha = 0.025$). The outlier participant was one of the trained participant from Exp. 3, who did not show the effect in Exp. 3 either (top row, second column in Fig. 9; second row, third column in Fig. 12). However, another trained participant from Exp. 3, who did not show the effect then (top row, first column in Fig. 9), did show the effect here. This indicates that it was not guaranteed that a trained participant from Exp. 3 would necessarily give rise to the same effect as before.

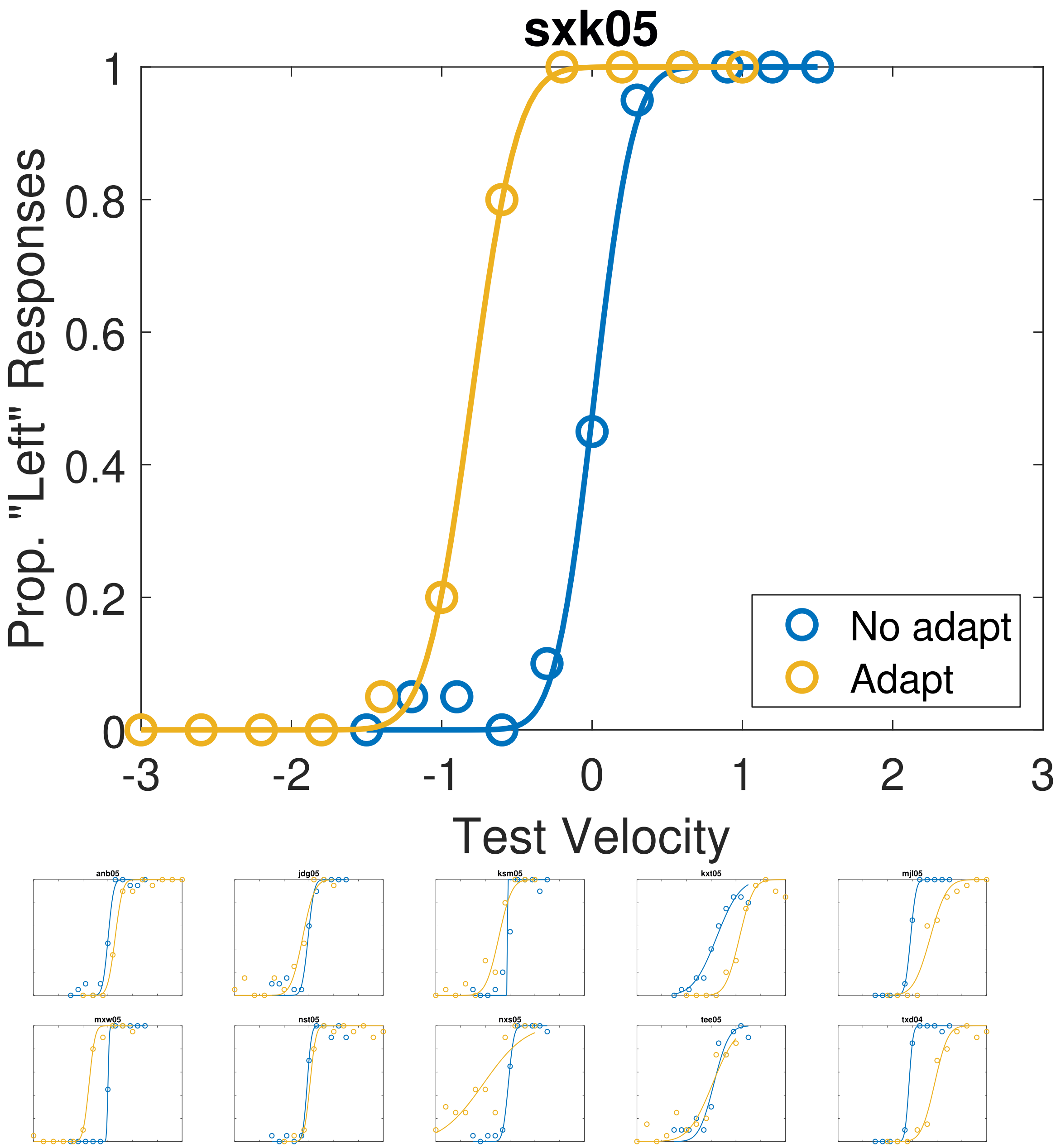

Fig. 12. Exp. 4. Psychometric functions of each of the 11 participants for the no adaptation (blue or darker curve) and adaptation (yellow or lighter curve) conditions. All psychometric functions shifted horizontally in the direction predicted by MAE. Except for the first participant (who happened to be author SK, the most trained participant), all participants showed a shallower psychometric function post-adaptation.

However, the fact that four out of the five trained participants from Exp. 3, and all six new participants in Exp. 4 showed the shallowing effect was reassuring that this effect was reasonably robust.

6. Discussion

In this study, we found that the left-right direction discrimination was impaired after velocity adaptation with leftward or rightward motion. However, this decreased discrimination sensitivity could be only observed from psychophysically experienced participants, and from inexperienced participants either after weeks of perceptual learning or when the task difficulty was reduced. Such psychophysical training was needed because, we believe, steady and precise discrimination were required in order to reveal the underlying difference in discrimination sensitivity between adaptation and no-adaptation conditions. This finding was also consistent with what had been found in a prior study where orientation discrimination was impaired post orientation adaptation (Erlikhman et al., 2019).

We believe that psychophysical training was needed for all our student participants because the psychological experiments they had previously experienced were very different from the difficult task they encountered in the current study. Specifically, the test stimulus was 75 ms in duration with an abrupt onset and offset. This duration was chosen because, as argued in Sachtler and Zaidi (1993), it was shorter than time needed for pursuit eye movement. Although this 75 ms was adequate for authors GE and ZL and was adequate for the two experienced participants in Sachtler and Zaidi (1993), it was apparently too short for inexperienced participants. We suspect that the transients caused by the on- and offset of this brief test stimulus made it difficult to see its motion direction. The transients may also be why the task was so difficult for the undergraduate participants in Exp. 1, since they seldom encountered a dynamic test stimulus like this in experiments at the psychology department.

In our Exp. 2, participants ran three full sessions, each of which had a no-adaptation and an adaptation part. Six of the seven participants showed the effect that adaptation reduced discrimination sensitivity, even though it did not reach statistical significance due to the small number of participants.

In Exp. 3, the perceptual learning showed large individual differences, just like in most perceptual learning studies (Fahle & Poggio, 2002; Fahle, 2005; Sagi, 2011; Watanabe & Sasaki, 2015; Dosher & Lu, 2017). As a result, rather than choosing a parametric function to characterize the learning that would be hard to justify, we opted for what we considered the simplest method without introducing biases. Namely, we compared the first and last sessions' performance to quantify the learning. To characterize transfer, we similarly opted to measure the reduction of σ and the magnitude of μ from the first to the final session.

It is worth mentioning that the 11 participants as a whole did not transfer the motion discrimination from the trained adaptation direction to the untrained (and opposite) adaptation direction. This means that the participants could not deduce the abstract "rules" in direction discrimination under adaptation, and could not conceptually "flip" the left and right directions to completely transfer to the untrained condition.

One may argue that since the no-adaptation σ decreased via perceptual learning and the learning did not transfer, then the no-adaptation σ should be expectedly smaller than the transfer condition σ. This argument would have been true if the 11 participants had uniformly showed little transfer of learning. However, the reason there was no statistically significant transfer is that about half of the participants reduced their σ's while the remaining participants did not. In comparison, 10 of the 11 participants showed the effect of a greater σ (than no-adaptation) post adaptation in the transfer condition. In this sense, the effect of a greater σ in the transfer than no-adaptation condition is nontrivial, given the large data variation across conditions and participants. The transfer of this effect, that adaptation to the untrained direction increased σ as compared to no adaptation post-training, underscores the theoretically more important point that the perceptual learning primarily served to stabilize perceptual responses by the participants. This transfer of the effect was also consistent with the results that psychophysically experienced participants (i.e., authors GE and ZL), without training on this particular task, also showed a similar effect.

In Exp. 4, we lengthened the test stimulus duration, under the assumption that stable and expert-like performance could be achieved more quickly when task difficulty was reduced (Liu, 1995; Ahissar & Hochstein, 1997; Liu, 1999). Indeed, after training first on a similar task and then on the same task with a longer test duration, 10 out of the 11 participants replicated the shallowing effect, including all six new participants. For the five participants who had took part in Exp. 3, four gave rise to the same effect whereas the 5th retained the opposite effect as in Exp. 3. This result from the "old" participants is reassuring because the old results were either retained or flipped to the "expected" direction, whereas there was no flipping in the opposite direction. Taken together, the results from Exp. 4 indicate that the effect found is likely robust.

Why, then, was such an effect sensible to have taken place to begin with? From the signal-noise perspective, given that adaptation and its recovery are time dependent, it is plausible that estimation of motion direction under adaptation is more variable, i.e., more uncertain, than when the visual system is at a more stable state of no adaptation. Similar reasoning can also interpret the result of decreased orientation discrimination sensitivity post orientation adaptation in Erlikhman et al. (2019). However, this simple reasoning cannot explain why fine direction discrimination along an adapted motion direction became better, as in Phinney et al. (1997). We believe that the computational model proposed in Stocker and Simoncelli (2009) offers a promising direction to explain the full range of adaptation phenomena, because the model specifically emphasizes the analysis of discrimination sensitivity, in addition to adaptation induced bias. We are currently working on understanding our empirical results from the standpoint of this computational model.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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