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Learning motion discrimination with suppressed and un-suppressed MT

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Abstract

Perceptual learning of motion direction discrimination is generally thought to rely on the middle temporal area of the brain (MT/V5). A recent study investigating learning of motion discrimination when MT was psychophysically suppressed found that learning was possible with suppressed MT, but only when the task was sufficiently easy [Lu, H., Qian, N., Liu, Z. (2004). Learning motion discrimination with suppressed MT. *Vision Research 44*, 1817–1825]. We investigated whether this effect was indeed due to MT suppression or whether it could be explained by task difficulty alone. By comparing learning of motion discrimination when MT was suppressed vs. un-suppressed, at different task difficulties, we found that task difficulty alone could not explain the effects. At the highest difficulty, learning was not possible with suppressed MT, confirming [Lu, H., Qian, N., Liu, Z. (2004). Learning motion discrimination with suppressed MT. *Vision Research 44*, 1817–1825]. In comparison, learning was possible with un-suppressed MT at the same difficulty level. At the intermediate task difficulty, there was a clear learning disadvantage when MT was suppressed. Only for the easiest level of difficulty, did learning become equally possible for both suppressed and un-suppressed conditions. These findings suggest that MT plays an important role in learning to discriminate relatively fine differences in motion direction.
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Keywords: Perceptual learning; MT/V5; Motion discrimination; Paired-dots; Suppression

1. Introduction

Practice can often improve performance on a visual perceptual task. This improvement is termed perceptual learning (Epstein, 1967; Gibson, 1967). Understanding the mechanisms of perceptual learning is important because the characteristics of learning can reveal the nature of underlying perceptual representations. Learning mechanisms can also provide insight into the neural plasticity and functional mechanisms within the visual system. So far, learning has been found in almost all visual perceptual tasks (Ball & Sekuler, 1982; Dosher & Lu, 1998; Fiorentini & Berardi, 1980; Gilbert, 1994; Karni & Sagi, 1991; McKee & Westheimer, 1978; Ramachandran, 1976; Vaina, Belliveau, Des Roziers, & Zeffiro, 1998; Watanabe, Nanez, & Sasaki, 2001) (see Fine & Jacobs (2002) & Fahle & Poggio (2002), for reviews). In this context, a recent finding reported by Lu, Qian, and Liu (2004) is an exception in that, although task performance was well above chance, no learning was possible even after prolonged training at a motion discrimination task. This finding was significant because it provided an important new constraint on the role of the brain's middle temporal area (MT/V5) in motion perceptual learning.

MT was first implicated as a potential locus of motion perceptual learning by Ball and Sekuler (1982, 1987). In this classic study, participants were shown two sequential random-dot motion stimuli whose directions were either the same or differed by 3°. Over training, participants learnt to better discriminate between trials of the same vs. different directions. This improvement was direction specific, i.e., learning could not transfer to non-trained directions that were more than 90° away from the trained directions. Learning did, however, show a large amount of binocular transfer. Based on this pattern of specificity and transfer, Ball and Sekuler (1982, 1987) proposed that the learning may have taken place in MT, where neurons

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are binocular and tuned to motion direction (Maunsell & Van Essen, 1983). Further evidence that motion discrimination learning was due, at least in part, to changes in MT, rather than other potential candidate areas such as V1 was provided by Zohary, Celebrini, Britten, and Newsome (1994), who showed that behavioral improvement in motion direction discrimination was accompanied by an increase in neuronal sensitivity at MT. Additional support for the role of MT in motion direction discrimination and learning was provided by Rudolph and Pasternak (1999), who found that after lesion of MT and MST, fine motion discrimination was impaired even after intensive behavioral training.

The approach of impairing MT to investigate its role in learning to discriminate motion directions was also used by Lu et al. (2004). However, rather than using a physical lesion, Lu et al. (2004) used a specially constructed stimulus to psychophysically suppress MT. Using this approach, Lu et al. (2004) found that a difficult, fine motion discrimination task could not be learnt when MT was functionally suppressed, a result complementary to Rudolph and Pasternak's findings (1999).

The stimulus adapted by Lu et al. (2004) to suppress MT was originally designed by Qian, Andersen, and Adelson (1994) to take advantage of the direction selectivity and motion opponency of MT neurons (Levinson & Sekuler, 1975; Mather & Moulden, 1983). MT neurons are excited by a preferred motion direction and inhibited by the opposite direction. To exploit this property of MT neurons, Qian et al. (1994) used a field of moving dots within which the dots were arranged into pairs. Within a pair, the two dots oscillated back and forth toward and away from each other (counter-phase motion) within a limited range. The motion trajectory will be referred to as motion axis orientation. By pairing the dots, a dot field can be created that maintains a locally balanced motion directional signal (zero on average). Fig. 1 depicts a group of counter-phase dot pairs.

To allow for psychophysical assessment of task performance, Lu et al. (2004) presented two of these dot fields sequentially with a certain change in motion axis orientation from the first stimulus to the second. Participants reported whether this change was clockwise or counterclockwise. Task difficulty was manipulated by controlling the size of the orientational change (angular difference).

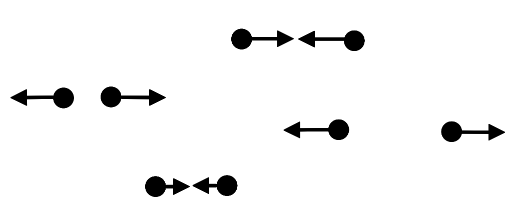

Fig. 1. A schematic and exaggerated example of the motion of a group of counter-phase paired-dots. The (horizontal) orientation along which the dots oscillate is called the motion axis orientation.

Lu et al. (2004) found that no learning was possible when participants were trained to discriminate small angular differences, even though performance was well above chance (≈75% correct). Learning was enabled only when the angular difference became sufficiently large, i.e., when the task was easier.

Lu et al. (2004) attributed the lack of learning found for smaller angular differences to the fact that MT responses were impaired by the local balancing of motion signals in the stimulus. This conclusion was based on previous neurophysiological findings from Qian and Andersen (1994) who demonstrated that counter-phase paired-dots elicited, on average, no more activation in MT neurons than did flicker noise. This suggests that MT as a whole was "suppressed" by the paired-dots stimulus and could not carry a useful motion directional signal. No such suppression was observed when dots were unpaired. The ability of paired-dots to suppress MT relative to unpaired-dots was further confirmed by Heeger, Boynton, Demb, Seidemann, and Newsome (1999) using human functional magnetic resonance imaging (fMRI).

The result from Lu et al. (2004) showing that learning of counter-phase paired-dots could take place only for an easy task opens up a number of possible explanations. The first is that MT was fully suppressed by the counter-phase paired-dots and was therefore uninvolved in the perceptual learning that took place. In this scenario, the learning that occurred when the orientational change of the motion axis was sufficiently large has to be attributed to other brain areas such as V1. The second possibility is that when the orientational change of the motion axis was sufficiently large, MT was able to overcome its initial suppression through repeated training and as a result, learning was enabled. Whilst these two possibilities both assume suppression of MT by the counter-phase paired-dots, a third possibility is that task difficulty alone dictated whether learning was possible. In other words, the lack of learning demonstrated by Lu et al. (2004) could have been entirely due to the difficulty of the task and therefore unrelated to whether the dots were counter-phase or not. This third possible explanation is addressed in this paper.

To address this possibility, we designed an experiment to directly compare learning of counter-phase paired-dots (when MT was presumably suppressed) with learning when MT was un-suppressed. To test learning when MT was un-suppressed, we changed the phase of within-pair dot motion from 180° (counter-phase) to 0° (in-phase) whilst keeping all other parameters the same. Therefore, within each pair the dots now oscillated along the same trajectory as before, but moved in the same direction a certain distance apart. This manipulation resulted in a stimulus which would not suppress MT and which, we believe, allowed for a closer comparison with the counter-phase paired-dots than the unpaired-dots used by Qian and Andersen (1994) and Heeger et al. (1999). Learning for counter-phase and in-phase dots was then directly compared at different task difficulties in a parametric manner. We found that, for the hardest task, learning was not possible with counter-phase paired-dots, confirming previous results from Lu et al. (2004). In contrast, learning was possible for in-phase paired-dots at the same task difficulty, though the learning was not pronounced. When the task difficulty was intermediate, the advantage of learning for in-phase over counter-phase paired-dots became apparent. Finally, only when the task became easier still, did the difference in amount of learning between the two conditions diminish. We concluded that task difficulty was not the only determining factor in whether learning motion axis orientation discrimination was possible. Counter-phase paired-dots were indeed more difficult to learn, a finding that can be explained by MT being suppressed. To further characterize the learning that took place we tested different potential decision criteria. We found that participants learnt to make motion axis orientation discriminations relative to an orientation that bisected the two orientations they had been trained to discriminate.

2. Methods

2.1. Stimuli

The same stimuli used by Lu et al. (2004) to suppress MT and modified from the original by Qian et al. (1994), were used in this study. Each stimulus display was made up of 50 'twin pairs' of counter-phase (180°) dots that moved along a common motion axis (Fig. 2A). Each twin pair consisted of two identical pairs of dots positioned 0.06°–0.15° apart from each other to form a parallelogram. This manipulation masked the Glass pattern (1969) otherwise present in the display, since dots could no longer be consistently grouped over time along the global motion axis orientation. As in the original stimuli of Qian et al. (1994) the two dots making up each pair moved across each other at a speed of 2°/sec. The minimum distance between the two dots in a pair was 0.06° and the maximum was 0.30°. Each dot subtended 0.06°. Dots never overlapped so that the dot density remained constant. The dots were dark (0.01 cd/m^2) and presented on a light background (8.01 cd/m^2) within a 7.8° circular aperture. Each twin pair had a lifetime of 120 ms. When one twin pair disappeared, a new twin pair appeared at a random location within the display aperture. The lifetime and phase of twin pairs were randomly asynchronized using a flat distribution of ±10% around the half lifetime and ±10% of half maximum distance between two dots in a pair, respectively. To ensure that participants viewed the whole display rather then just small subsets of dots, a certain percentage of the twin pairs presented were noise pairs and accordingly each had a randomly oriented motion axis from trial to trial.

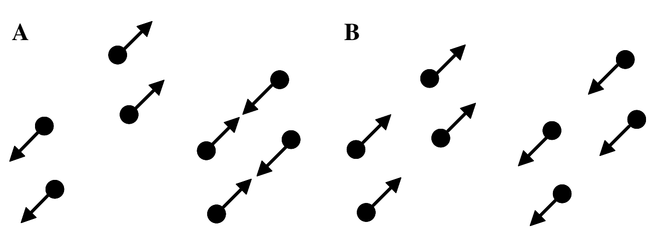

Fig. 2. A schematic representation of the twin pairs making up the stimuli used in this experiment. (A) The two movement patterns that defined counter-phase (180°) dots. (B) The two movement patterns that defined in-phase (0°) dots. In both (A) and (B) twin pairs have a 45° motion axis orientation. The full stimuli consisted of 50 twin pairs of dots (200 dots in total).

For the un-suppressed MT condition, the stimuli were identical except that the dots no longer moved counter-phase to one another, but moved in-phase (0°) (all dots in a twin pair moved in the same direction at time *t*, Fig. 2B). In-phase dots provided a motion signal able to activate MT without changing the overall motion statistics of the stimulus. We assumed that task difficulty was unchanged when the dot phase was changed from 180° to 0°. The motion directions presented remained globally balanced since at any time half of the signal twin pairs on average moved in one direction along the global motion axis and the other half moved in the opposite direction. The local balancing, however, was removed.

We employed a 2AFC (two alternative forced choice) design whereby each trial was made up of two sequential presentations of the stimulus. From the first presentation to the second the motion axis orientation would rotate either clockwise or counter-clockwise by a certain angle. The task was to discriminate whether the motion axis rotation was clockwise or counter-clockwise. The size of the angular difference of this rotation was manipulated to make the discrimination easy or hard. During training, feedback was provided per trial with a beep indicating an incorrect response. Fig. 3 shows the sequence of a single trial. A fixation cross was presented for 500 ms. The first stimulus was then presented for 200 ms, a duration short enough to prevent eye movements. After a 500 ms inter-stimulus-interval (ISI), included to prevent any apparent motion cues to the motion axis rotation, the second stimulus was presented for 200 ms and was then replaced by a fixation cross until the participant responded. When the stimuli were presented and during the ISI, the fixation cross became a red disk to avoid any extraneous orientation cues.

3. Experiment 1 (pilot study)

Lu et al. (2004) found that when trained on a counter-phase stimulus with high difficulty (the angular difference gave rise to 60% correct performance pre-training), none of the three participants were able to improve at the task, even after 15 daily training sessions of 400 trials per session with trial-wise feedback. This lack of learning was not due to an inability to perform the task, since all participants performed well above chance ($d' \approx 1$). Presumably this effect was due to MT being suppressed by the counter-phase paired-dots.

We brought back two of the three participants (one of whom, ZL, was co-author of this paper), switched the phase difference from 180° to 0°, and kept all other parameters the same. Fig. 4 shows the two participants' performance over seven and nine daily sessions, respectively. For comparison, Fig. 4 also shows the same participants' performance with the counter-phase stimulus from Lu et al. (2004). Apparently, when the stimulus was switched to 0°, not only was learning enabled, but performance was also immediately elevated. This indicated that the 0° stimulus was indeed easier to learn than its 180° counterpart.

Caution should be taken, however, when drawing conclusions from this result since both participants had already been trained for 15 daily sessions before the 180° dots were changed to 0°. Although learning was not manifested over these 15 days, it is not possible to rule out that this training influenced subsequent performance for the in-phase stimulus. A fully controlled experiment using a between-participants design was therefore conducted.

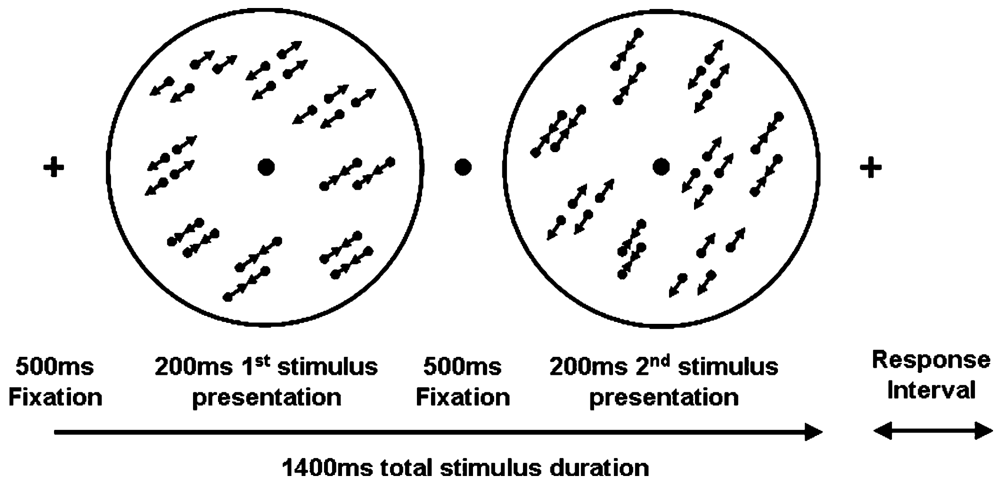

Fig. 3. A schematic of a single trial. The participant reported whether the motion axis orientation changed clockwise or counter-clockwise from the first stimulus presentation to the second. This figure depicts a counter-clockwise trial about a bisecting orientation of 45°.

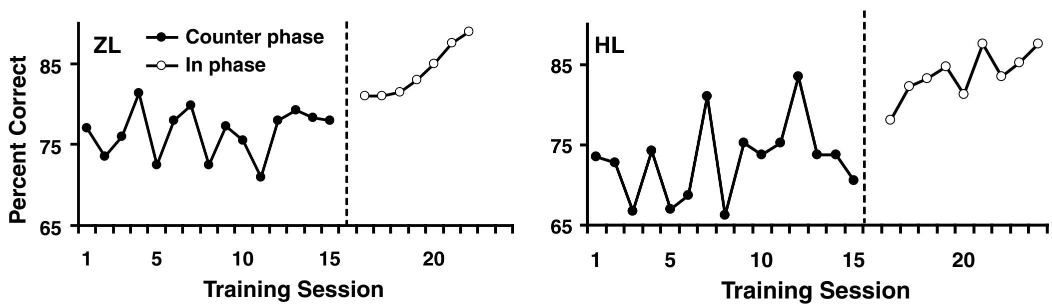

Fig. 4. Learning performance for participants ZL and HL in motion axis orientation discrimination of 5° angular difference. The participants were first trained with counter-phase (180°) dots for 15 sessions [data from Lu et al. (2004)], with no learning. They were then trained with in-phase (0°) dots (seven and nine training sessions, respectively), with all other parameters kept the same. Learning became possible.

4. Experiment 2

4.1. Procedure

This experiment was made up of four components: practice, psychometric curve measurements, training, and a final series of psychometric curve measurements.

4.1.1. Practice and pre-training psychometric curve measurement

Participants were introduced to the stimulus and the task. For the practice and psychometric curve measurement sessions, only 180° dots were used. This ensured that, if the 180° condition were to give rise to worse performance than the 0° condition, this could not be due to less familiarity and practice with the 180° dots. Participants practiced the task with an angular difference of 30°, with trial-wise feedback, until 95% correct performance was achieved. Practice sessions were conducted at an bisecting motion axis orientation of either 45° or 135°. As an example, 45° was the bisecting orientation between the two possible motion axis orientations in a practice trial: 30° and 60°. For each individual participant the motion axis orientation used for practice was also used for all subsequent pre-training psychometric curve measurements and then rotated by 90° for training. Therefore, a participant with a practice orientation of 45° would complete the psychometric curve measurements with this 45° orientation, and then complete the training at 135°.

After practice, psychometric curves were measured for each participant. Performance was assessed at five angular differences: 4°, 8°, 14°, 20°, and 30°. These angular differences were presented in a blocked design without feedback. There were 40 trials per block and each block was presented twice. Block order was randomized for the first presentation and counter balanced for the second in an ABCDE EDCBA manner. Measurements were made with 20% of the twin pairs presented as noise.[1] Each participant completed at least two psychometric curve measurements. Angular difference thresholds for 65%, 70%, and 75%

[1] For two participants in the hard condition, 65% correct performance could not be achieved by only manipulating angular difference, due to monitor resolution and viewing distance restrictions. The noise density of the stimulus was thus increased from 20% to 40%. Psychometric functions were then re-measured to ascertain the correct angular difference to elicit 65% correct performance. This procedure assured that task difficulty remained constant within this group.

correct were acquired by fitting a Weibul function to the final curve measurement.

4.1.2. Training

Participants were paired based on their psychometric curve performance. One member of each pair was randomly chosen to be trained on 180° dots whilst the other was trained on 0° dots. Training consisted of 15 daily sessions of 400 trials with trial-wise feedback. The method of constant stimuli was used. Two pairs of participants were assigned to hard, medium, and easy difficulty conditions, respectively. Task difficulty was equated within a difficulty group by using for training the angular difference that gave rise to 65% correct (hard), 70% (medium), or 75% (easy)[2] for each individual participant.

4.1.3. Post-training psychometric curve measurements

After training, a series of psychometric measurements were made to better characterize the learning, if any, that had taken place. The following three measurements were taken for each participant (in this order):

(1) A Psychometric function was again measured along the orientation 90° away from the trained orientation to test for transfer of leaning. This measurement was the same as the pre-training measurements. For this measurement motion axis orientation was kept constant and angular difference was varied.
(2) Psychometric functions were measured along the trained bisecting motion axis orientation. Motion axis orientation was kept constant and angular difference was varied. Two types of psychometric function were measured, one using a blocked presentation of angular differences and the other using a randomly interleaved presentation. All measurements were made using the participant's trained dot phase.

The five angular differences used for these measurements were customized for each participant so as to include their trained angular difference. The two measurements, blocked (B) and interleaved (I), were repeated over two daily sessions. In each session, two sets of blocked measurements and two sets of interleaved measurements were taken in either the order BIIB or IBBI. If the order BIIB was taken first, for instance, the order for the next day's session would be counter balanced as IBBI. The order of the sequence was also counter balanced between participants. Each set of blocked measurements consisted of 10 blocks with 10 trials each. The order of the first five blocks was randomized and was counter balanced by the last five blocks. Interleaved measurements used the same trials as in the blocked measurements except that the order of the trials was randomized.

(3) A psychometric function was measured by keeping angular difference constant at the same value used during training and varying bisecting motion axis orientation. All measurements were made using the participant's trained dot phase.

Six bisecting motion axis orientations were used for this measurement, including the 45° and 135° orientations, one of which was the trained orientation. The other four bisecting orientations were chosen under the condition that the motion axis of an actual stimulus must be at least 15° away from any cardinal orientations (0°, 90°, and 180°). For example, a participant trained with an angular difference of 10° would have stimuli of (15°, 25°), (40°, 50°), (65°, 75°), (105°, 115°), (130°, 140°), and (155°, 165°). This technique provided six bisecting motion axis orientations as dispersed as possible whilst avoiding close proximity to any cardinal axis. Trials were presented in a randomly interleaved manner, with 80 trials for each of the six bisecting orientations.

4.2. Apparatus

Participants binocularly viewed the stimuli from a distance of 120 cm (maintained by a chin rest) in a dark room. A viewing tube running from the chin rest to the monitor was used to exclude any extraneous orientation reference cues. Stimuli were presented on an NEC MultiSync FE771SB monitor with a vertical refresh rate of 60 Hz and a resolution of 800 × 600 pixels. Stimuli were generated and presented using MatLab (MathWorks, Inc.) with the psychophysics toolbox (Brainard, 1997; Pelli, 1997).

4.3. Participants

Twelve University of California Los Angeles (UCLA) undergraduate students, unaware of the purpose of the experiment, participated. Table 1 in Appendix A shows the details of the parameters used for each participant.

4.4. Results and discussion

4.4.1. Learning with MT suppressed vs. un-suppressed

The presence or absence of learning was contingent on both task difficulty and the dot phase. Fig. 5 shows the learning curves for each pair of participants. A linear regression was performed on each participant's data. Table 1 in the Appendix A shows the linear regression results. For the four participants trained on the hardest task, only the learning curves of the two in-phase (0°) participants showed slopes significantly greater than zero. Learning slopes for the medium and easiest tasks were all significantly above zero (except for participant VR who was trained on counter-phase paired-dots in the easiest condition).

The influence of 0° vs. 180° phase difference can be clearly seen in Fig. 5. For the hardest task (starting threshold at

[2] One pair of participants was initially assigned to a threshold of 60% correct. However, after six training sessions, they were not able to learn. This pair was then assigned to the threshold of 75% correct (see Fig. 5).

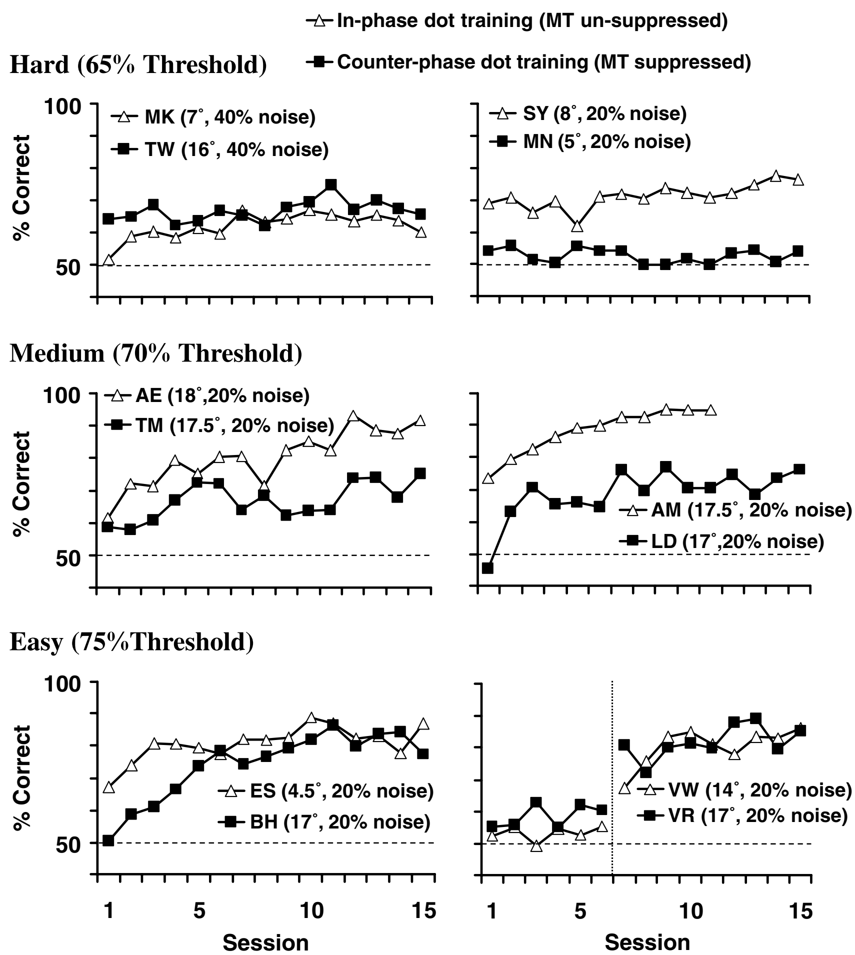

Fig. 5. Percent correct as a function of training session for each pair of participants. The horizontal dashed lines at 50% correct show chance performance. In the *hard condition* (top row),[1] only the "in-phase" participants could learn, but learning was modest; the "counter-phase" participants could not learn, confirming Lu et al. (2004). In the *medium condition* (middle row), "in-phase" participants showed a clear advantage in learning over "counter-phase" participants. Only in the *easy condition* (bottom row), did the difference between "in-phase" and "counter-phase" diminish. [VW and VR (bottom right) were trained at an angular difference corresponding to 60% for the first six sessions (shown left of the vertical dotted line). After the participants were discouraged due to low accuracy (53.21% and 58.54% correct, respectively) and little learning, they were then trained at 75% for the remaining sessions (shown right of the vertical dotted line)].

65% correct), only participants trained with in-phase dots showed statistically significant positive slopes. Learning with counter-phase dots was not possible at this difficulty level, confirming results in Lu et al. (2004). Specifically, for Pair 1 (top left in Fig. 5),[2] only the in-phase participant (MK) showed a positive slope that was statistically significant, and slightly greater than the counter-phase slope. A closer inspection showed that the in-phase participant MK dropped performance on the first training session, possibly biasing the slope of the learning curve. We therefore, removed the first datum point of MK and recalculated the slope. The learning slope was still significantly greater than zero ($F(1,12) = 4.27$, $p = 0.03$, one tailed). For Pair 2 (top right in Fig. 5), the in-phase participant SY showed learning, whereas the counter-phase participant MN showed flat performance. MN dropped to 54% correct performance on the first session of training even though MN's psychometric measurements showed that this angular difference elicited 65% correct performance at the orientation 90° away. MN's performance did not improve above 55.5% correct for the entire training period.[3]

For the medium difficulty task (Pairs 3 and 4, starting threshold at 70% correct, middle row, Fig. 5), the in-phase participants showed a clear advantage in both the learning rate and amount of learning.

[3] Due to MN's low accuracy (52.55%), it is reasonable to be cautious and regard the performance as being at chance. In this regard, MN's performance did not confirm results in Lu et al. (2004) where performance was well above chance (≈75% correct) even without learning. The exact cause of this discrepancy is unclear, we list the following possibilities. (1) In Lu et al. (2004), the threshold was at 60% correct; here the threshold was at 65% correct. (2) In Lu et al. (2004), the psychometric function was measured in a randomly interleaved manner to obtain the threshold; here it was blocked and counter balanced. (3) In Lu et al. (2004), the participants were experienced; here they were inexperienced. (4) In Lu et al. (2004), after the psychometric measurement and before training, orientation discrimination with lines was measured along the training orientation; here no such measurement was made.

Finally, for the easy task (Pairs 5 and 6, starting threshold at 75% correct, bottom row Fig. 5), it can be seen that whilst performance improved, there was little difference in the rate and amount of learning between in-phase and counter-phase conditions.

We conducted a further analysis designed to provide a more stringent comparison between 180° and 0° learning so that the initial drop in performance during training would not in itself disadvantage the 180° condition (given that more 180° participants dropped in initial performance relative to 0° participants). Performance on the final session of training was used to assess the difference in the amount of learning between participants trained on 0° phase and those trained on 180° phase. A Wilcoxon test showed that participants trained on the 0° stimuli had higher final accuracies than those trained on 180° stimuli ($Z(6) = -1.782$, $p = 0.038$, one tailed).

4.4.2. Characterization of the learning

A series of post-training measurements were made so that the learning, when it occurred, could be better understood. These measurements addressed the following issues: (1) transfer of learning to an untrained orientation, (2) changes in response bias associated with learning, and (3) characterization of the decision criterion underlying any improved performance.

4.4.2.1. Orientation specificity. To investigate the issue of transfer,[4] we directly tested whether learning transferred back to the old orientation that was 90° away from the trained orientation. We compared psychometric functions for the untrained orientation pre and post-training (Fig. 6). A two-way, repeated measures ANOVA yielded the expected significant main effect of angular difference ($F(4,44) = 33.21$, $p < 0.001$), but showed no significant main effect of training (pre vs. post) ($F(1,11) = 0.19 < 1$) and no significant interaction ($F(4,44) = 0.51 < 1$). Therefore no transfer occurred.

4.4.2.2. Response bias β. It has been argued that perceptual learning can be accounted for by changes in response bias rather than in perceptual sensitivity (Rasche & Wenger, 2004). To address this question, the response bias β was calculated for each participant for each training session. A one-way repeated measure ANOVA showed no significant main effect of training session ($F(14,112) = 1.18$, $p = 0.34$). This analysis was further repeated with data only from participants who learnt. Once again there was no significant main effect of training session, ($F(14,84) = 0.99 < 1$), showing that there were no systematic changes in response bias that could account for participants' learning.

4.4.2.3. Testing for a decision criterion. Given that response bias could not account for the learning, it is reasonable to assume that the participants who did learn were making increasingly accurate orientation discriminations relative to a fixed decision criterion. For this task one reliable criterion was the orientation (45° or 135°) that bisected the two possible motion axis orientations presented during a trial. A previous study has shown that in a contrast discrimination task, if trials with different decision criteria (different pedestal contrasts) were randomly interleaved, then performance was worse than when trials were presented in blocks with a fixed criterion (single pedestal) (Adini, Wilkonsky, Haspel, Tsodyks, & Sagi, 2004). In other words, varying the decision criterion of a task in an unpredictable manner by interleaving trials impairs trained performance. We extrapolated this use of stimulus uncertainty (random interleaving) as a probe to identify the decision criterion in our task. If the decision criterion was indeed the bisecting orientation, then creating uncertainty by varying angular difference alone should not influence task performance since the bisecting orientation remained unchanged from trial to trial. Conversely, if uncertainty of bisecting orientation were to be introduced whilst angular difference was kept at the same values as used during training, performance should diminish. Furthermore, if a different criterion, such as template matching was the underlying mechanism of the learning then a different pattern of results would be anticipated. If training had allowed for the development of two specific templates (one per stimulus) then both angular and motion axis uncertainty should impair task performance since changes in either of these variables away from the precise trained parameters would invalidate the templates.

4.4.2.4. Angular difference uncertainty with constant bisecting orientation. Psychometric curves were measured using both randomly interleaved (stimulus uncertainty) and blocked (baseline) designs along each participant's trained orientation using their trained dot phase (0° or 180°) (see Table 2, Appendix A). A $2 \times 5 \times 3 \times 2$ ANOVA with measurement type (interleaved vs. blocked), angular difference, training difficulty (hard vs. medium vs. easy), and phase (180° vs. 0°) was performed on the accuracy data. This analysis yielded a significant main effect of measurement type ($F(1,6) = 17.96$, $p = 0.005$, blocked 78.15% vs. interleaved 80.04% correct), a significant main effect of angular difference ($F(4,24) = 97.58$, $p < 0.001$), and a significant interaction between measurement and angular difference ($F(4,24) = 48.19$, $p = 0.039$). No other main effects or

[4] In the first sessions of training, several participants showed a drop in performance (Wilcoxon test, $Z(12) = -2.353$, $p = 0.019$) relative to their respective thresholds (65%, 70%, and 75% correct) that were established during the pre-training psychometric curve measurements along the orientation 90° away from the training orientation. This statistically significant drop indicated that the practice and two psychometric measurements induced learning that was orientation specific. No reliable difference was found between the two groups of participants (0° and 180° phase-difference) however. This drop in performance was no longer evident after the second training session (Wilcoxon test $Z(12) = -1.38$, $p = 0.19$). Performance on the first training session therefore demonstrated that practice and pre-training psychometric measurements were orientation specific and did not transfer to the training orientation.

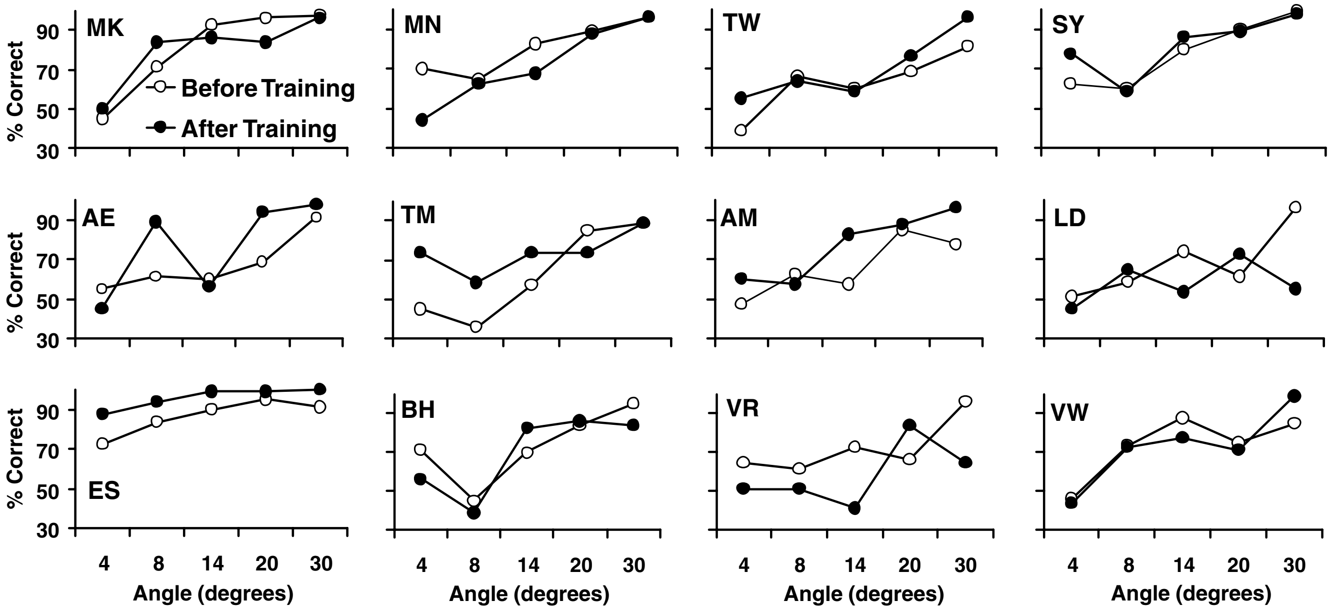

Fig. 6. Psychometric measurements of motion axis orientation discrimination for counter-phase dots before (empty symbols) and after (filled symbols) training. Orientations used for psychometric curve measurements were 90° away from training orientations.

interactions reached significance ($p > 0.05$). Therefore, performance was not impaired by generating stimulus uncertainty in the angular difference variable. In fact performance was slightly better for the interleaved, more uncertain condition.

Fig. 7 shows that the main effect of measurement type and the measurement type × angular difference interaction was characterized by an increasing advantage for interleaved measurements with decreasing angular size. These results suggested that interleaved presentation facilitated task performance, particularly for the smallest angle tested (Ahissar & Hochstein, 1997; Liu, 1995; Rubin, Nakayama, & Shapley, 1997). A series of post hoc pair-wise comparisons between blocked and interleaved performance at each angular size further confirmed this effect. For the smallest angle there was a significant difference between the interleaved (64.79% correct) and blocked (59.79%) conditions ($t(11) = 3.43$, $p = 0.006$, two tailed, corrected for multiple comparisons). No other comparisons showed significant differences.

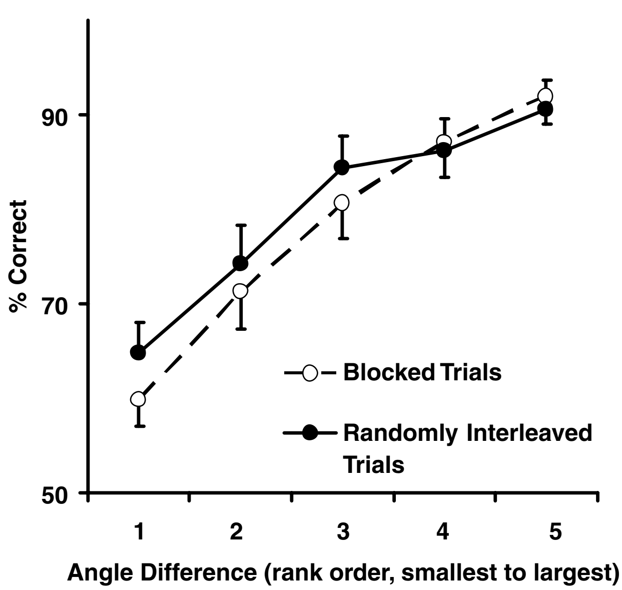

Fig. 7. Accuracy scores across participants for the blocked and randomly interleaved psychometric curve measurements as a function of angular difference. Motion axis orientation was kept constant. Angular differences are shown in rank order from the smallest to the largest since the actual values used for each participant were tailored to include their trained angles (see Appendix A). Error bars show standard error of the mean.

One possible explanation for the facilitation effect observed within the interleaved condition is as follows. As the bisecting orientation was constant from trial to trial, a trial with a large angular size that preceded a trial of the smallest angle may have provided a clearer signal of the bisecting orientation that could then aid performance for the subsequent smallest angle trial. It is unclear, however, why only the smallest angle was benefited and not other angles. It is also unclear which preceding trials were most facilitatory. We analyzed the trial sequence to identify the angular sizes that immediately preceded the smallest angle trials, but did not find a reliable difference in facilitation when the preceding trial had a larger angle as compared to a smaller angle. Nor did we find a reliable advantage for when the immediately preceding trial was correct rather than incorrect.

4.4.2.5. Motion axis orientation uncertainty, constant angular difference. Discrimination performance was measured along six bisecting orientations in a randomly interleaved manner whilst angular difference and dot phase were kept constant at the values used during training (see Section 4.1.3 for details). Fig. 8 shows the results. To establish a

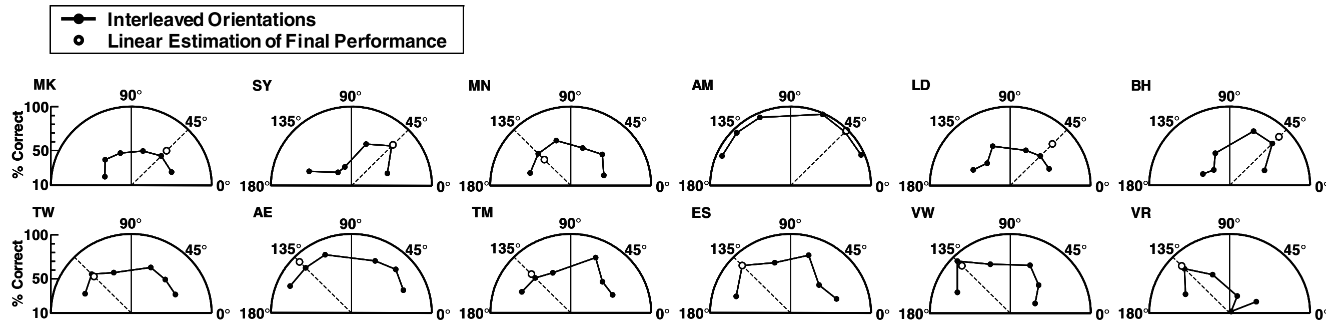

Fig. 8. Performance along each of the six interleaved motion axis orientations tested for each participant. The top row shows participants trained at the 45° orientation ordered from hard to easy. The bottom row shows 135° trained participants. Filled circles show performance for each motion axis orientation tested. Unfilled circles show the last training session performance approximated by linear fitting.

baseline with which to assess the effect of motion orientation uncertainty on trained performance, we compared performance along the trained orientation in the uncertainty condition with performance at the end of training. To achieve this we used linear fitting of each participant's performance throughout training (Table 1, Appendix A) to approximate their performance in the last training session.[5] We found that, along the trained orientation, performance in the interleaved measurement was reliably lower than that approximated by the linear fitting at the end of training (Wilcoxon test, $Z(11) = 1.96$, $p = 0.05$, two tailed).

The reduction in performance for the trained orientation when measured using the interleaved orientation technique did not, however, show a drop all the way back to pre-training levels. We measured the size of the drop by comparing the interleaved measurement performance along the trained orientation with its mirror counterpart that was 90° away (45° vs. 135°). There was a significant difference between the two (Wilcoxon test $Z(11) = 2.94$, $p = 0.003$, two tailed), showing that superior performance was maintained along the trained orientation (74.42% vs. 53.85% correct). We note that a psychometric function was measured along the mirror orientation both before and after training and that the mirror orientation was therefore relatively well practiced. In this sense, our measure of performance retention along the trained orientation was conservative. We also note that performance along the mirror orientation was well below chance for some participants (e.g., 12% correct for VR). Nevertheless, after we removed the cases (three in total) of below-chance performance along the mirror orientation, the difference between the trained orientation and its mirror counterpart was still reliable ($Z(8) = 2.32$, $p = 0.02$, two tailed). This means that the partial retention along the trained orientation, even with the randomly interleaved measurement, was robust.

An alternative measure of learning retention along the trained orientation, independent of performance along the mirror orientation, was to compute the following retention index r:

$$r = \frac{p_I - p_L^0}{p_L - p_L^0},$$

where p_I is interleaved performance along the trained orientation, p_L^0 is the first training session performance approximated by linear fitting, and p_L is the last training session performance approximated by linear fitting,. To illustrate, if interleaving fully retained the training, retention = 100%. At the other extreme, if interleaving made it impossible to retain any learning, retention = 0%. We computed this measure across the 11 participants (excluding MN[5]), and obtained a mean of 61.92% ± 16.84%, the latter being the standard error. This again indicated how robust the retention of learning was for the interleaved measurement.

5. General discussion

Our experimental results demonstrate that at an equivalent task difficulty, motion direction discrimination was more difficult to learn for counter-phase (180°) paired-dots than for their in-phase (0°) counterparts. Furthermore, at the hardest difficulty, learning was not possible for 180° phase dots whereas 0° phase dots allowed for a modest improvement in performance. As task difficulty was carefully controlled, dot phase was isolated as the factor influencing learning. Given the previous evidence that 180° phase dots suppressed average MT activity whereas unpaired-dots did not, combined with the nature of our task that forced the observer to rely solely on motion signals to provide the motion axis orientation from trial to trial, we conclude that psychophysically impairing MT function impacted directly on the ability to learn fine motion axis orientation discrimination. It is important to note that our assertion of equal task difficulty for both 180° and 0° phase conditions was based on the assumption that the "signal" in each stimulus was the estimated angular difference derived from

[5] Data from participant MN, who was trained with the hardest counter-phase condition and exhibited no learning, were excluded because the linear slope of learning was negative, and because the average performance was at chance (52.55% correct). The other two participants who did not show reliable learning were included because, even though they did not learn, their performance was above chance, making it possible for their performance to drop in the interleaved measurement. Removing one or both of them only increased the significance of the statistical Wilcoxon test.

the trajectories of the dots; and that the 'noise' was the uncertainty associated with this estimation, plus the contribution from the noise dot pairs whose motion axes were randomized. Therefore, we assumed that the orientation estimation of a dot's trajectory determined the signal-noise nature of the stimulus and hence the task difficulty, regardless of the phase difference of the dot pairs.

Although our results demonstrate that suppressing MT function has a detrimental effect on the perceptual learning of motion discrimination, we cannot ascertain whether, when 180° phase paired-dots were viewed, MT was completely suppressed to the extent that it could not provide a useful motion directional signal or whether a subset of MT neurons still functioned to allow discrimination when the angular size was small, and to enable learning when the angular size was relatively large.

Evidence for the above possibilities can be found in the original recordings of MT neurons made by Qian and Andersen (1994). Although on average the response of MT neurons to 180° paired-dots was less than the response to unpaired-dots and about the same as the response to flicker noise, there were neurons that did respond to the 180° phase paired-dots, in some cases more than to unpaired-dots. Therefore, it is possible that it was this population of MT neurons that allowed perceptual learning to take place for the easier condition here and in Lu et al. (2004). Indeed, the idea that motion discrimination (though not necessarily learning) is carried out by a subset of MT neurons, but not by the whole population, is suggested by a recent study by Purushothaman and Bradley (2005). These authors investigated how the responses of MT neurons were related to behavioral performance in a motion direction discrimination task. They found that monkeys' behavioral decisions were significantly correlated with the activity of those neurons showing the highest-precision for direction discrimination. Furthermore, the neural performance of the highest-precision MT neurons matched the monkeys' behavioral performance, whereas the correlation between behavior and the entire active population of neurons was poor (see also Salzman, Britten, & Newsome (1990)). Consequently, if a subset of the highest-precision neurons preferentially respond to 180° phase paired-dots, then these neurons could potentially allow for learning to take place. The fact that learning was enabled with larger angular differences here and in Lu et al. (2004) is consistent with this hypothesis, as an enlarged angular difference may have allowed more MT neurons to contribute to the discrimination.

However, even if a subset of MT neurons were responding to the 180° phase dots, this active population did not allow for the same amount of learning as the pool of MT neurons that presumably responded to the 0° phase dots. Consequently, we can assume that this subset provided impoverished information. Therefore, even if 180° phase motion did not completely suppress the response of MT neurons to our stimulus we can say that, at the very least, using the 180° phase paired-dots either reduced the effective number of the neurons responding to the stimulus or made the neurons less effective.

Assuming MT was suppressed by 180° phase paired-dots, we acknowledge the following. When task difficulty was sufficiently easy, our behavioral results of learning cannot distinguish whether MT remained suppressed in the course of learning, or became un-suppressed as a result of as the reason for the learning. We are exploring brain imaging techniques to tease apart these two possibilities.

In addition to the effect of MT suppression on learning, we were also interested in characterizing the nature of the learning that took place during training. One possibility was that participants had learnt to discriminate about a fixed criterion, namely the bisecting orientation (45° or 135°) between the two motion axis orientations within a trial. Another alternative was that learning had taken a different form such as the development of templates for the two presented orientations. Adini et al. (2004) found that in a contrast discrimination task, if performance of the trained task was measured when trials of different decision criteria were randomly interleaved, performance on the trained task was reduced. Using this same approach, we measured trained task performance under conditions when the angular difference was uncertain from trial to trial whilst the bisecting orientation remained constant, and also when the bisecting orientation was uncertain from trial to trial whilst angular difference remained constant. Relative to baseline trained performance, angular difference uncertainty did not decrease trained task performance whereas bisecting motion axis uncertainty did. This suggests that bisecting motion axis orientation was the decision criterion used by the participants. These results also rule out a template matching explanation for the task performance as both bisecting motion axis uncertainty and angular difference uncertainty would perturb the stimuli sufficiently away from the exact trained parameters to render any learnt templates invalid.

An additional finding was that interleaving trials of the same bisecting motion axis orientation but varying angular difference actually improved performance for the hardest trials (smallest angular difference between motion axis orientations) relative to blocked measurements. Our analysis revealed that this effect was due to easier trials aiding performance on harder trials, an effect supported by previous studies (Ahissar & Hochstein, 1997; Liu, 1995; Rubin et al., 1997). It would appear therefore, that when trials with the same decision criterion but with varying difficulties were interleaved, easier trials may facilitate performance on harder trials.

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We thank Hongjing Lu for her technical advice and her computer codes that this research was based on.

Appendix A

See Tables 1 and 2.

Table 1
Parameters under which each participant was trained[a] and the linear regression for the resulting learning curve

Participant	Pair 1		Pair 2		Pair 3		Pair 4		Pair 5		Pair 6	
	MK	TW	SY	MN	AE	TM	AM	LD	ES	BH	VW	VR
Phase difference (°)	0	180	0	180	0	180	0	180	0	180	0	180
Threshold (%)	65	65	65	65	70	70	70	70	75	75	75	75
Angle (°)	7	16	8	5	18	17.5	17.5	17	4.5	17	14	17
Noise (%)	40[1]	40[1]	20	20	20	20	20	20	20	20	20	20
R^2	0.40	0.20	0.53	0.062	0.78	0.39	0.88	0.45	0.45	0.73	0.49	0.34
Slope	0.57	0.33	0.64	−0.12	1.71	0.81	2.01	1.18	0.80	1.99	1.50	1.08
F	8.7	3.2	14.4	0.9	45.0	8.3	68.3	10.8	10.5	35.0	6.7	3.6
Degrees of freedom	1	1	1	1	1	1	1	1	1	1	1	1
	13	13	13	13	13	13	9	13	13	13	7	7
p (two tailed)	.011	.095	.002	.371	.000	.013	.000	.006	.006	.000	.037	.102

[a] Training for participant AM was stopped after 11 sessions since 95% correct accuracy had been achieved for three consecutive sessions. Participants VR and VW completed six training sessions at 60% correct threshold, corresponding to 6° angular size for VR and 4° for VW. However, this level of task difficulty turned out to be extremely difficult for the participants to learn. These two participants were then trained with nine sessions at 75% correct threshold. Linear regression was conducted on these nine training sessions only. Participant pairs AM, LD and AE, TM had 70% correct thresholds differing by 0.5° within pairs. Although these values were used in the software, our monitor could not resolve the differences of 0.5°.

Table 2
The five angle differences used for the blocked and interleaved psychometric curve measurements for each participant

Angle rank	Angular difference (°)											
	AE	AM	BH	ES	LD	MK	MN	SY	TM	TW	VR	VW
1	4	4	4	4.5	4	4	5	4	4	4	4	4
2	8	8	8	8	8	7	8	8	8	8	8	8
3	14	17.5	17	14	14	12	12	14	17.5	16	17	14
4	18	20	20	17	17	20	20	20	20	20	20	20
5	30	30	30	30	30	30	30	30	30	30	30	30

The five values were tailored for each participant to include their trained angle.

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