

Learning motion discrimination with suppressed MT

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Abstract

We studied perceptual learning in motion discrimination when the brain's middle temporal area (MT/V5) was functionally suppressed. This was achieved by using the "paired-dots" motion stimulus where the two dots in a pair always move in counter-phase over a short distance [J. Neurosci. 14 (1994) 7357]. The motion directional signal of the stimulus is therefore always 0 on average. As a result, this stimulus activates MT in Rhesus monkeys no more than flicker noise does [J. Neurosci. 14 (1994) 7367]. We added a new manipulation to eliminate the Glass pattern in the original stimulus that would have otherwise provided a static orientation cue. Two such new motion stimuli were presented sequentially, in a 2AFC task. Subjects decided if the global motion-axis of the stimuli changed clockwise or counter-clockwise. When the task difficulty was set at 60% correct, none of the subjects could learn with feedback, even though their performance was well above chance. However, when the task difficulty was set instead at 70% correct, a new group of subjects was able to learn. Hence, learning motion discrimination was possible when MT was presumably eliminated.

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1. Introduction

Perceptual learning refers to performance improvement in a perceptual task after repeated practice (Gibson, 1967). For instance, in a motion discrimination task, a subject judges whether two random-dots stimuli move in the same or different directions (0° and 3°). After days of practice, the subject's performance improves from 75% to 90% correct (Ball & Sekuler, 1982).

Which brain area underlies this learning? The predominant hypothesis is that the neuronal changes in the brain take place at an early level of visual information processing (Gilbert, Sigman, & Crist, 2001). This hypothesis is primarily based on the trademark finding in almost all perceptual learning studies: stimulus and location specificity. For example, after a subject has learned to discriminate between 0° and 3° in motion directions, this learning does not transfer to directions 90° away and beyond, e.g., between 90° and 93° or between 180° and 183°. Nor does it transfer to a location

that does not overlap with the trained location. Such location specificity, together with evidence that learning transfers between the two eyes, has led to the speculation that learning takes place in the middle temporal area MT (Ball & Sekuler, 1987). In addition to motion direction, perceptual learning has also been found to be specific to stimulus orientation and spatial frequency (Fahle & Edelman, 1993; Fiorentini & Berardi, 1982; Gilbert, 1994; Karni & Sagi, 1991; McKee & Westheimer, 1978; O'Toole & Kersten, 1992; Ramachandran & Braddick, 1973).

Stimulus specific learning, however, has been challenged recently. In motion discrimination, for example, Liu (1995, 1999) found that learning transferred when the task difficulty was relaxed (Ahissar & Hochstein, 1997; Doane, Alderton, Sohn, & Pellegrino, 1996; Rubin, Nakayama, & Shapley, 1997). Even when the task difficulty remained unchanged, Liu and Weinshall (2000) found that learning was accelerated in a new pair of directions 90° away from the trained pair (Liu & Vaina, 1998; Sowden, Davies, Rose, & Kaye, 1996). These results indicate that motion discrimination learning may not be at a level as early as previously thought.

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In this paper, we address the question of specificity from a different perspective. We ask whether learning motion discrimination is possible without MT. We used a novel stimulus, modified from Qian, Andersen, and Adelson (1994), that functionally suppresses MT responses; MT is no more responsive to this stimulus than to flicker noise. Our hypothesis is that if learning takes place at MT or if MT is in the critical path of learning, then such a stimulus should not yield any learning. Otherwise, either learning does not take place exclusively at MT or MT is not in the critical path of such learning. In what follows, we will present evidence from the literature that supports the important role of MT in motion discrimination learning. We will then describe the original stimulus by Qian et al. (1994) and the evidence that supports its effectiveness in suppressing MT.

Using random-dots motion stimuli (Newsome & Pare, 1988), several studies have provided evidence that MT “is a prime candidate for representing global motion and changes in its discrimination with practice” (Vaina, Belliveau, des Roziers, & Zeffiro, 1998, p. 12658). Electrophysiological studies have shown that neurons in MT are particularly sensitive to motion directions (Felleman & van Essen, 1991; Merigan & Maunsell, 1993). It has also been shown that direction specificity of MT neurons increases with a monkey’s behavioral improvement during training (Salzman, Britten, & Newsome, 1990). For example, Zohary, Celebrini, Britten, and Newsome (1994) found that a 13% increase in sensitivity of motion-sensitive cells in MT is associated with a 19% improvement in the monkey’s ability to discriminate directions. In addition, lesions of MT, both in macaque monkeys and in human patients, impair the ability to discriminate motion directions (Bisley & Pasternak, 2000; Newsome, Britten, & Movshon, 1989; Newsome & Pare, 1988; Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990).

While Newsome and Pare (1988) developed the ingenious random-dots motion stimulus to parametrically activate MT, Qian et al. (1994) developed a paired-dots motion stimulus to suppress MT. The paired-dots generated suppression because of motion opponency in MT neurons. Specifically, although an MT neuron is strongly selective for motion direction (Albright, 1993; Dubner & Zeki, 1971; Zeki, 1974), when a stimulus moving in one direction is superimposed with a stimulus moving in the opposite direction within the same MT neuron’s receptive field, the neuron’s response is substantially suppressed. In other words, the response of MT neurons can be suppressed by maintaining motion directional balance locally. Such a stimulus consists of many randomly located pairs of dots. In each pair, two dots move across each other in opposite directions with a constant speed over a small distance. Therefore, in any local region, the net motion directional signal is 0. With monkey electrophysiology, Qian and Andersen (1994) demonstrated that the paired-dots stimulus suppressed

MT neuronal activity, as compared with an unpaired control stimulus. Very importantly, they also found that the MT response to the paired-dots stimulus is not significantly different from that to flicker noise. They concluded that “the average MT activity does not carry motion information for the paired-dot patterns” (Qian & Andersen, 1994, p. 7479).

Heeger, Boynton, Demb, Seidemann, and Newsome (1999) replicated the above study with monkey electrophysiology. They then used functional magnetic resonance imaging (fMRI) to study the human homologue MT+, which corresponds to monkey MT and its adjacent motion-sensitive areas, such as MST and FST (Tootell & Taylor, 1995; Zeki et al., 1991). They found that fMRI responses in human MT+ were indeed reduced for paired versus unpaired dots, confirming the motion opponency in human MT+.

In the following, we will first specify in detail how we modified the original paired-dots stimulus of Qian et al. (1994) to ensure that only motion information is available for the motion discrimination task. We will then present experimental results that learning in motion discrimination is possible without MT. In Experiment 1, we will demonstrate that without MT and when the task was difficult (i.e., low signal-to-noise ratio), learning was impossible even though the discrimination was well above chance. In Experiment 2, we relaxed the task difficulty while keeping MT suppressed, and found that learning became possible.

2. Experiment 1: A hard task without MT

2.1. Stimuli

We made a major modification of the original paired-dots stimulus by Qian et al. (1994). This was to ensure that the motion-axis information, defined as the orientation along which the dots moved, was provided only by motion cues. In other words, no static frames of the stimulus should provide any information about the motion-axis. This requirement was not critical in the original study in Qian et al. (1994), since the purpose there was to study motion transparency. Here, since our question was whether learning would be at all possible without MT, it was crucial that the motion-axis information was provided by motion alone.

We created “paired-pairs” by positioning a copy of a pair next to this pair itself. The two pairs had the identical motion and therefore formed at all times a parallelogram (Fig. 1). The two pairs were so close to each other (from 0.06° to 0.15° , while the maximal within-pair distance was 0.30°) that the shorter side of the parallelogram was often between dots of different pairs. This shorter side defines, according to proximity, the salient orientation of the four dots. Since this salient

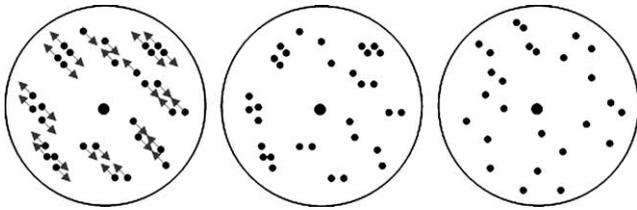


Fig. 1. Schematic of one frame of the stimulus. Left: paired-dots moving across each other in counter-phase. Middle: same as left without the arrows. One dot pair was placed next to another pair to form a parallelogram. Right: one dot pair was positioned independently of others as in Qian et al. (1994) forming a noisy Glass pattern, which was not used in our experiments.

orientation was manipulated independently from one parallelogram to the next, a single frame of the stimulus as a whole had no global orientation. This was verified by our pilot study.¹ Since a single frame of the original paired-dots stimulus is a Glass pattern (1969) in Fig. 1(right), our creation of “paired-pairs” destroyed this Glass pattern (Fig. 1(middle)).

Our stimulus, except for two additional minor modifications that will be specified below, was otherwise identical to the original in Qian et al. (1994). Within a circular aperture of 7.8° in visual angle, 100 pairs of dark dots (0.01 cd/m^2) against a light background (8.01 cd/m^2) were presented. Each dot was 0.06° in diameter with a constant speed of $2^\circ/\text{s}$. Within each pair, the maximal distance between two dots was 0.30° , and the minimal distance 0.06° . The non-zero minimal distance, which was our first minor modification, was used so that the two dots would never overlap to become one dot. Therefore, the dot density remained constant. Each “paired-pair” had a life-time of 120 ms. When one “paired-pair” disappeared, another appeared at a new random location inside the aperture. These “paired-pairs” were randomly asynchronized, following a flat distribution within $\pm 10\%$ of the half life-time and $\pm 10\%$ around the half maximum distance within a pair. In order to encourage subjects to look at the entire stimulus, we modified the original stimulus by adding a certain proportion of noisy “paired-pairs,” each of which had a random motion-axis. This was our second minor modification.

Within one experimental trial, two stimuli were presented sequentially (Fig. 2). A subject determined whether the angular change of the motion-axis from the first

stimulus to the second was clockwise or counter-clockwise, and feedback was provided by a computer beep. As shown in Fig. 2, a trial started with a fixation cross for 500 ms. This was followed by the first stimulus for 200 ms, which was brief enough to prevent eye movements. After an inter-stimulus-interval of 500 ms in order to prevent apparent motion cues from the first stimulus to the second, the second stimulus was presented for 200 ms. This was replaced by a fixation cross, and the next trial started automatically after the subject’s response. During the stimulus presentation, the cross fixation became a red disk, to prevent any orientation cues that were otherwise available due to using a cross as fixation.

2.2. Apparatus

From a chin-rest, subjects viewed the stimuli binocularly through a dark tube that abutted the computer monitor to prevent any external reference of orientation. The viewing distance was 115 cm. Two computer monitors were used for the experiment. One was a 17” Apple Studio Display, the other a 17” Viewsonic G75F. The vertical refresh rate of the monitors was 60 Hz. Both monitors were calibrated with a Minolta CS-100 photometer.

2.3. Procedure

Each subject went through six steps to finish the entire experiment, as follows.

2.3.1. Practice

To reduce any effect of task familiarization, subjects practiced at least 50 trials with a large (30°) angular change of the motion-axis. This practice with feedback would continue until a subject reached 95% accuracy with at least 50 trials. These motion-axis orientations were different from those to be used in training. For example, a subject could use 100° and 130° for practice, and 40° and 45° for training.

2.3.2. Measuring the psychometric function

The next step was to choose the right size of the angular change for each subject, so that every subject’s initial performance before training would be 60% correct. We measured each subject’s psychometric curve as a function of the size of the angular change. Six angular sizes were used that were tailored for each subject from a pilot run (see Fig. 5 for details). The proportion of the noisy “paired-pairs” was also determined in the pilot run. Each of the six angles was tested 100 times in a randomly interleaved manner without feedback. The average of the two motion-axis orientations was 90° away from that to be used in training. The two average orientations were counter-balanced across subjects. This step of 600 trials lasted for around 30 min. After training,

¹ In this control experiment (see Fig. 2 for details), each motion stimulus was replaced by a static frame randomly chosen from the motion sequence. Subjects determined whether the stimulus’s axis of orientation changed clockwise or counter-clockwise. The angular size of this orientational change was 15° for all subjects. This control experiment was otherwise identical to Experiment 1. Author HL and four naïve subjects participated, and their performance was at chance. The mean accuracy was 51.2% correct, with a standard error of 2.5% ($t(4) = 0.48$; $p = 0.66$).

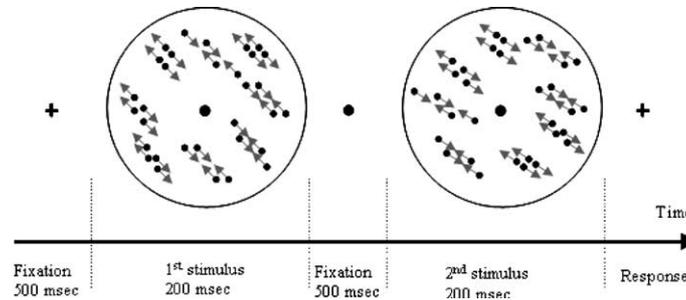


Fig. 2. Schematic of one experimental trial. The subject determined whether the change of motion-axis from the first to the second stimulus was clockwise or counter-clockwise.

a linear least-square fit was used to fit the psychometric curve, and the angular size corresponding to 60% was chosen for that particular subject. The linear fit for each subject was statistically significant ($p < 0.05$).

2.3.3. Measuring baseline performance for control stimuli

In order to assess the specificity of learning, we used three other stimuli to gauge the extent to which learning could transfer. This step measured the baseline performance for these stimuli. They were: (1) Unpaired-dots—no two dots were paired but the stimulus was otherwise unchanged. Here, motion transparency was perceived (Qian et al., 1994). (2) In-phase paired-dots—the motion of the four dots in each “paired-pair” was identical. (3) Static low-contrast lines—a single frame from the experimental stimulus was used, where the paired-dots were connected with low-contrast lines (1/30 of the experimental stimulus contrast). We used three angular sizes for this condition: 5° that was the angle to be used in training, 3° , and 7° . Fig. 3 illustrates these stimuli. The motion axes or orientations of these stimuli were identical to those of the training stimuli. One hundred trials each were tested for (1), (2), and each of three angles for (3) in a blocked design without feedback. The order of testing was counter-balanced across subjects.

2.3.4. Training

Each subject was trained with the experimental stimulus for 15 daily sessions with trial-wise feedback. Each session had 400 trials that lasted for about 20 min.

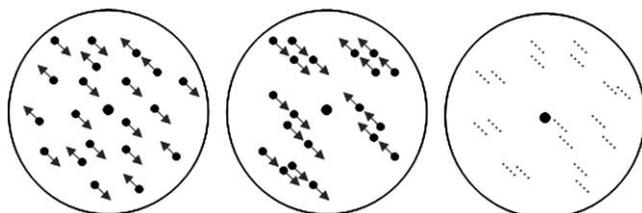


Fig. 3. Schematic illustration of three baseline stimuli. Left: unpaired-dots. Moving dots were unpaired, resulting in a percept of motion transparency. Middle: in-phase paired-dots. The four dots in each paired-pair moved identically, so that local directional signals were unbalanced; Right: static oriented lines.

2.3.5. Testing transfer

After training, the three baseline experiments were repeated in the same order as before.

2.3.6. Re-measuring the psychometric function

Finally, each subject’s psychometric function was measured again along the same orientations as before (90° away from the training orientations). This was used to determine how much learning transferred 90° away.

2.4. Subjects

Two of the authors HL and ZL, and a naïve subject KF participated. Subject HL used 145° and 150° as motion-axes for training, and 20% noise. ZL used 45° and 50° , and 20% noise. KF used 30° and 33° , and 50% noise.²

2.5. Results

A polynomial trend analysis was performed to parameterize the learning curve. No subject’s learning curve showed any significant linear, quadratic, or cubic trend. Linear regression was then used to fit the learning slope for each subject. No subject showed a learning slope significantly different from 0: subject HL, $F(1, 13) = 1.26$, $p = 0.28$; subject KF, $F(1, 13) = 4.15$, $p = 0.063$; subject ZL, $F(1, 13) = 0.205$, $p = 0.66$. Apparently, the subjects showed little learning. Fig. 4 shows the three subjects’ performance. We note that this was under the condition of extensive training (15 sessions, 400 trials each), with feedback after every trial. We further note that although no learning was evident, the subjects’ performance was all well above chance

² The reason that 50% noise was used for KF was as follows. It was decided before the experiment that 20% noise would be used for all subjects, while the angular change would be adjusted for each subject. However, KF’s performance was still too good when the angular size was reduced to 3° —the minimal angle that could be reached given the monitor resolutions. The noise proportion was therefore increased for KF while the angular size was kept at 3° . In addition, the angles used for the control stimuli of low-contrast static lines became 3° , 4° , and 7° rather than 3° , 5° , and 7° .

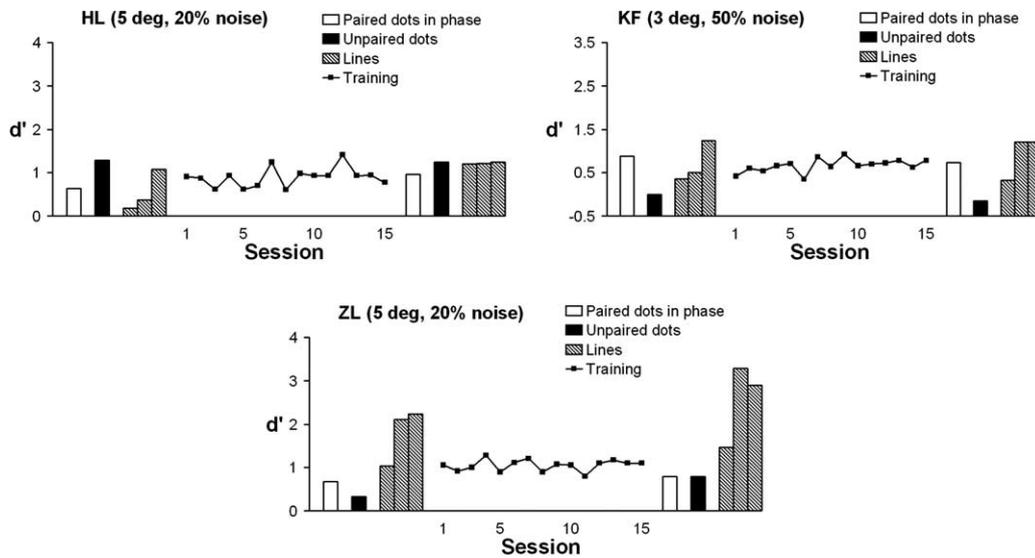


Fig. 4. Discrimination sensitivity d' in Experiment 1 as a function of training session and performance of the three control conditions before and after training. No subject showed any significant learning. There was no consistent transfer to any of the control stimuli as a result of the training either.

(d' around 1).³ In addition, the training did not have any effect on the control stimuli or on the orientations 90° away from the two trained orientations (Fig. 4). Fig. 5 shows the psychometric curves measured before and after learning. Subjects HL and KF showed no significant changes after learning (HL: $Z(6, 6) = 0.94$, $p = 0.34$; KF: $Z(6, 6) = 1.57$, $p = 0.12$). Only subject ZL showed improvement with $Z(6, 6) = 2.21$, $p = 0.027$.

The results in this experiment suggest that subjects could not learn the task either because there was minimal MT involvement or because the task was too difficult. To tease these two possibilities apart, the next experiment relaxed the task difficulty.

3. Experiment 2: An easier task without MT

There were three differences between Experiment 2 and Experiment 1. First, Experiment 2 was easier in that the angular change of the discrimination in training was chosen for each individual subject so that it corresponded to 70% correct in measuring the psychometric function prior to training, as opposed to 60% in Experiment 1. Second, the angles used for the control stimuli of low-contrast lines were chosen as follows. If

the training angle was 5°, then 3°, 5°, and 7° were used. If the training angle was 8°, then 6°, 8°, and 10° were used. If the training angle was 15°, then 5°, 10°, and 15° were used. The third and final difference was that additional subjects participated in this experiment.

In total, six subjects participated in Experiment 2. Subjects HL and KF had participated in Experiment 1. Subject BR was aware of the experimental purpose. The remaining three subjects had no prior psychophysical experience and were unaware of the experimental purpose. Table 1 shows the orientation of the motion axes that were used by each subject. Except for KF who used 35% noise, all subjects used 20% noise. Training for a subject would stop if the subject reached above 90% accuracy (for two subjects: JKR and JR) or leveled three times in a row.

Fig. 6 shows each of the six subjects' performance. A linear regression was performed for each subject's data. Every subject's learning slope was significantly greater than 0 ($p < 0.05$ for all subjects)—as shown in Table 1. We then used the Wilcoxon signed rank test for the group data, and found that the six subjects showed significant improvement indeed: $Z(6, 6) = 2.20$, $p = 0.028$.

After testing transfer to the three control stimuli, we found the following. For the in-phase paired-dots, the performance of five out of the six subjects increased after learning. The outlier was subject and author HL, who programmed all the experiments. HL's performance decreased. As a group, using the Wilcoxon signed rank test, the subjects marginally improved their performance ($Z(6, 6) = 1.78$, $p = 0.075$), and the trend suggested that learning on the counter-phase paired-dots stimulus transferred to the in-phase counterpart.

³ The discrepancy between the 60% correct performance in the psychometric curve measurement versus the $d' = 1$ (approximately 75% correct) in training is that the former task was harder, since trials with different angular sizes were randomly interleaved. In contrast, during training, constant stimuli were used. In addition, in step 3, baseline performance for control stimuli was measured before training and along the training orientations. This may have helped subjects' performance in training.

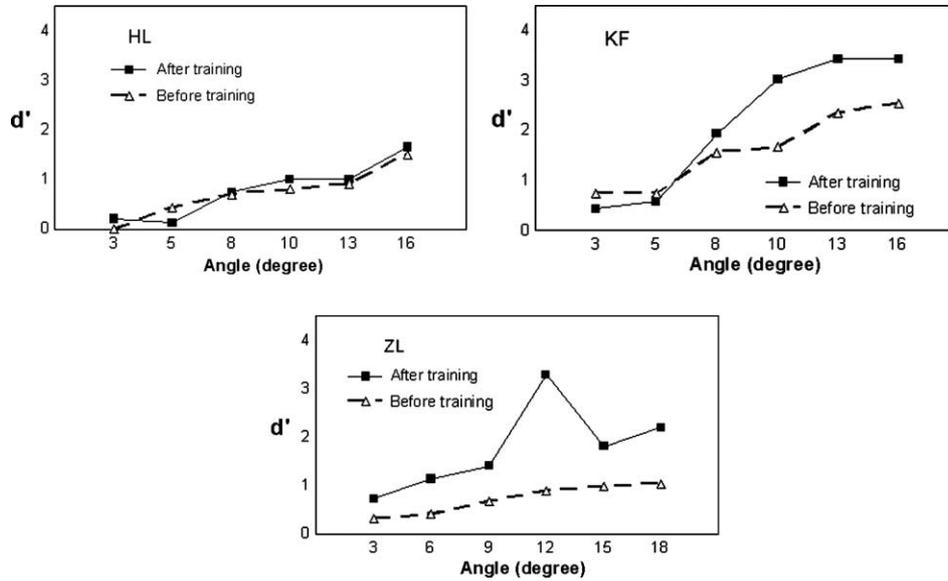


Fig. 5. Psychometric curves of each subject’s discrimination as a function of the size of the angular difference of the motion-axis. These orientations were 90° away from those of the training stimuli. Only subject (and author) ZL showed improvement after training.

Table 1
Training orientations and linear regression for each subject’s learning curve

	Subject					
	BR	HL	JKR	JR	KF	RO
Orientations	135°, 140°	142°, 150°	30°, 45°	130°, 145°	30°, 35°	40°, 48°
Slope	0.09	0.20	0.56	0.48	0.09	0.13
<i>F</i>	<i>F</i> (1, 7) = 8.1	<i>F</i> (1, 4) = 22.7	<i>F</i> (1, 4) = 101.7	<i>F</i> (1, 4) = 52.1	<i>F</i> (1, 9) = 39.6	<i>F</i> (1, 9) = 43.8
<i>p</i>	0.025	0.009	0.0005	0.002	0.0001	0.0001

Every subject showed learning.

In contrast, for unpaired-dots, we could not find such transfer ($Z(6, 6) = 0.94, p = 0.35$). For the static lines, learning transferred when considering all angles used in the control stimuli ($Z(18, 18) = 2.92, p = 0.004$). Upon a closer look, we found that this transfer was primarily due to those stimuli whose angular changes were smaller than those used in the training ($Z(10, 10) = 2.60, p = 0.009$), which was likely due to the ceiling effect for the stimuli with larger angles.

Finally, we tested the transfer from the trained orientations to orientations 90° away. As shown in Fig. 7, the psychometric curves for the six subjects changed little before versus after learning, indicating that there was little transfer. We used the Wilcoxon signed rank test to quantitatively make the comparison. Only subject and author HL showed significant improvement of the psychometric function with $Z(6, 6) = 2.2, p < 0.05$, whereas the other five subjects did not show any significant difference (BR: $Z(6, 6) = 0.52, p = 0.60$; KF: $Z(6, 6) = 0.73, p = 0.46$; JKR: $Z(6, 6) = 1.15, p = 0.25$; JR: $Z(6, 6) = 0.84, p = 0.40$; RO: $Z(6, 6) = 1.78, p = 0.075$).

4. Discussion

Our results indicate that when MT was suppressed and when the task was difficult, learning was not possible even though subjects’ performance was well above chance. However, when the task was less difficult while MT presumably remained suppressed, learning was enabled. This suggests that MT is neither absolutely needed nor in the critical path for motion discrimination learning. We acknowledge that our results are also consistent with partially suppressed MT, as opposed to fully suppressed MT. We nevertheless interpret our results as a consequence of fully suppressed MT, because it is completely consistent with the electrophysiology results in Qian and Andersen (1994). It is also consistent with the lesion studies by Bisley and Pasternak (2000) who found that the effect of monkey MT/MST lesions was most pronounced when small directional differences were discriminated using random-dots motion stimuli. We also acknowledge the possibility that, in Experiment 2, MT may have become less suppressed, either as a result of or as a cause of the learning.

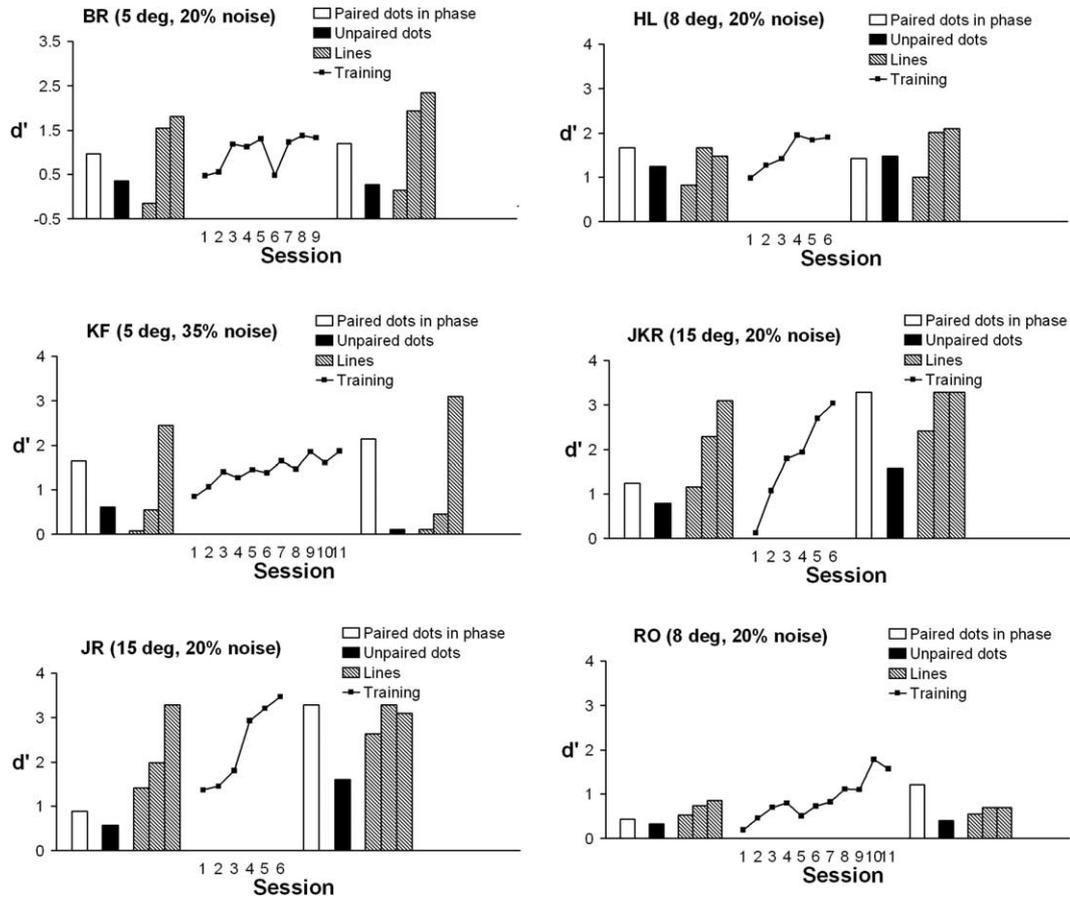


Fig. 6. Discrimination sensitivity d' in Experiment 2 as a function of training session and performance of the three control conditions before and after training.

We further acknowledge that our results can be accounted for by learning at V1, even though, to our knowledge, V1 has never been proposed as a candidate for motion discrimination learning. It is possible that, when MT is suppressed, V1 then assumes a more important role in learning. For instance, V1 cells might directly use the motion information of the dots or the orientation information from the motion trajectory (the “motion streak”) (Geisler, 1999; Geisler, Albrecht, & Stern, 2001; Jancke, 2000). This latter possibility is consistent with our findings in Experiment 2 that learning transferred to orientation discrimination learning using static lines. Caution, however, needs to be taken interpreting this transfer. First of all, if V1 were responsible for the learning, we would have expected transfer to all stimuli, not just the static lines. We would also have expected that, in Ball and Sekuler (1987), Newsome and Pare (1988), and Liu (1999), learning in motion direction discrimination transferred to the opposite directions. This was not the case. Here, we cannot claim that this transfer to static lines is necessarily specific to motion-axis discrimination learning as opposed to, for example, general practice with the psychophysical task or exposure to the stimulus. One pos-

sible control to verify such specificity is to use nearly identical stimuli, but instead of using a motion-axis discrimination task, using a contrast discrimination task (“which of the two stimuli is brighter?”) or a density discrimination task (“which of the two stimuli has more dots?”). We did not conduct this control experiment for the following two reasons. (1) All experiments in this paper were adjusted for each individual subject, so ensuring the same task difficulty with constant stimuli between the experimental and control subjects was impossible. (2) Even if the learning is proven to be specific to motion-axis discrimination, this will only be weak evidence for V1 learning. As the results stand now, we cannot distinguish whether learning took place in V1, or in areas above MT (e.g., MST), or both.

Another reason that we remain cautious about localizing the brain areas responsible for the learning is that learning is not necessarily local in the first place (Liu & Weinshall, 2000; Mollon & Danilova, 1996; Newsome, 1995). In fact, the apparent transfer from the training stimulus of counter-phase paired-dots to in-phase paired-dots, together with the result of little transfer to the unpaired-dots stimuli, indicated that transfer may have more to do with overall similarity of

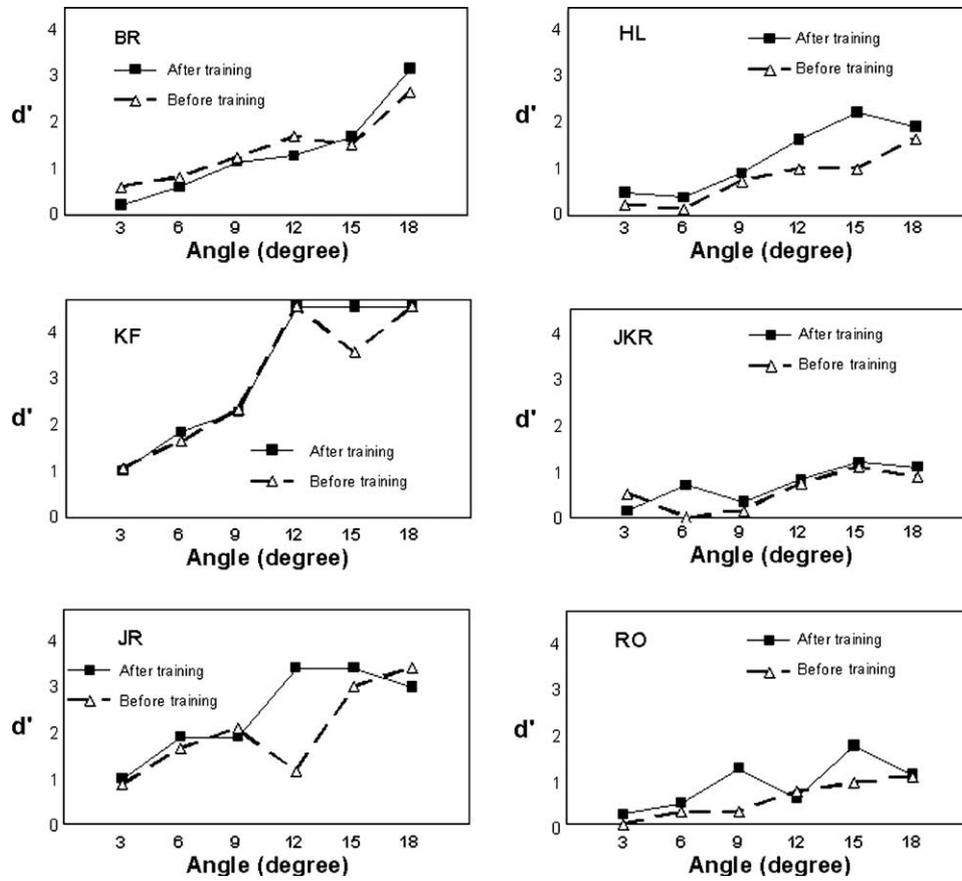


Fig. 7. Psychometric curves of each subject's discrimination as a function of the size of the angular difference of the motion-axis. These orientations were 90° away from the training orientations.

the stimuli rather than the activation of a certain brain area (the counter-phase paired-dots are presumed to be more similar to the in-phase paired-dots than to the unpaired-dots, while both in-phase paired-dots and unpaired-dots activate MT). In addition to the level of MT activation, a more important factor for learning appears to be task difficulty, which is consistent with Liu (1995, 1999) and Ahissar and Hochstein (1997).

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