# Direction selective habituation of motion adaptation

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Both adaptation and perceptual learning can change how we perceive the visual environment, reflecting the plasticity of the visual system. Our previous work has investigated the interaction between the two aspects of visual plasticity. One of the main findings is that multiple days of repeated motion adaptation attenuates motion aftereffect, which is explained by habituation of motion adaptation. Interestingly, there was almost no transfer of the effect to the untrained adapter, which differed from the trained adapter in the features including retinotopic location, spatiotopic location, and motion direction. Given that the reference frame of motion aftereffect is proposed to be retinotopic, it remains unclear whether the effect we refer to as habituation effect of motion adaptation is more like a special type of motion adaptation or not. Therefore, in three experiments, we examined the role of retinotopic location, spatiotopic location, and motion direction on the transfer of habituation, respectively. In each experiment, only one of the features was kept the same for the trained and untrained conditions. We found that the habituation effect transferred across both the retinotopic and spatiotopic locations as long as the adapting direction remained the same. The findings indicate that the effect we refer to as habituation of motion adaptation is anchored neither in eye-centered (retinotopic) nor world-centered (spatiotopic) coordinates. Rather, it is specific to the direction of the adapter. Therefore, the habituation effect of motion adaptation cannot be ascribed to a variant of motion adaptation.

## Introduction

Our visual system is plastic; it can be shaped by both relatively short-term (i.e., adaptation) and long-term experiences (i.e., perceptual learning). Adaptation is a phenomenon that prolonged viewing of a stimulus briefly alters the sensitivity or perception when exposed to a new stimulus (for reviews, see Kohn, 2007; Webster, 2011, 2015). A common example of motion adaptation (Anstis, Verstraten, & Mather, 1998) is known as the waterfall illusion (Addams, 1834). Perceptual learning is traditionally known as the long-term plasticity of visual system that practice of a visual task can result in improved performance or visual function (Polat, 2009; Polat, Ma-Naim, Belkin, & Sagi, 2004; Sagi, 2011; Sasaki, Nanez, & Watanabe, 2010). Meanwhile, quite a few studies have suggested that perceptual learning can also refer to the change of visual capability after repeatedly exposure to a stimulus rather than a task-based practice (Gutnisky, Hansen, Iliescu, & Dragoi, 2009; Nishina, Seitz, Kawato, & Watanabe, 2007; Paffen, Verstraten, & Vidnyánszky, 2008; Seitz, Nanez, Holloway, Koyama, & Watanabe, 2005; Watanabe, Náñez, & Sasaki, 2001).

Though most past work has focused on either adaptation or perceptual learning, some recent studies indicate that adaptation and perceptual learning are not completely independent of one another. Adaptation to the stimuli or visual environment during

perceptual learning could affect the transfer of learning effect to other retinal locations (Harris, Gliksberg, & Sagi, 2012; Harris & Sagi, 2015; Harris & Sagi, 2018; Tanaka, Miyauchi, Misaki, & Tashiro, 2007). On the other hand, learning can also influence adaptation. For example, adaptation to contrast reduction or distortion strengthens after viewing the altered visual environment for a few days (Haak, Fast, Bao, Lee, & Engel, 2014; Yehezkel, Sagi, Sterkin, Belkin, & Polat, 2010). Furthermore, the persistence of tilt aftereffect induced by texture discrimination task increases with training (Pinchuk-Yacobi, Harris, & Sagi, 2016). However, there are also exceptions. For instance, passively viewing the motion adapter while performing a direction discrimination task for several days reconfigures the discrimination performance but does not change the motion aftereffect (MAE) duration (McGovern, Roach, & Webb, 2012).

One possible factor causing the mixed finding is whether the adapter is passively viewed during repeated adaptation. To answer this question, our previous work systematically investigates how the effect of adaptation changes as a function of daily sessions when the adapter needs to be attended or not (Dong, Gao, Lv, & Bao, 2016). The procedure of repeated adaptation across days was referred to as training of adaptation, since it is frequently reported that perceptual learning can occur independent of a perceptual task (Gutnisky et al., 2009; Nishina et al., 2007; Paffen et al., 2008; Seitz et al., 2005; Watanabe et al., 2001) and the term "learning to adapt" was introduced to the field years ago (Yehezkel et al., 2010).

Different groups of participants were trained to adapt to either a coherently moving dots pattern or a medium contrast grating for several days, respectively (Dong et al., 2016). Their effects of adaptation were continuously tracked across daily sessions. The results showed that the adaptation effects attenuated over training if the adapter was passively viewed. However, if the adapter was attended using another task, the adaptation effect was found to decrease for an easy task but showed a trend of increase followed by a decrease when the task was hard (Dong et al., 2016). Our results of the MAE measured with a nulling task (Castet, Keeble, & Verstraten, 2002; Hiris & Blake, 1992) disagreed with McGovern et al. (2012)'s conclusion, though similar negative results were observed on MAE duration. Thus, to estimate the MAE, the nulling task appears to be more sensitive than testing the MAE duration. More importantly, the decrease of adaptation effect over training suggests that attention is not the only factor determining the effect of training on adaptation since attention is thought to enhance adaptation (Boynton, Ciaramitaro, & Arman, 2006; Rezec, Krekelberg, & Dobkins, 2004).

In our motion adaptation experiments, the decrease of adaptation effect did not transfer to the untrained adapter, which differed from the trained one in the retinotopic location, spatiotopic location, and moving direction. It has been shown that the reference frame of motion adaptation is retinotopic (Knapen, Rolfs, & Cavanagh, 2009). One may surmise that the decrease of adaptation effect over training could be a variant of adaptation. However, this adaptation account cannot explain why the training effect transferred completely to an untrained condition for contrast adaptation (Dong et al., 2016). This intriguing difference of result pattern spurs the present work to further explore what determines the transfer in the training of motion adaptation. The answer to this question can further elucidate whether the effect is a special form of adaptation or not.

A number of studies on visual perceptual learning have revealed that the transfer of learning effect depends on multiple factors, such as the retinal location (Yu, Klein, & Levi, 2004), spatiotopic location (Zhang & Li, 2010; Zhang, Zhang, & Li, 2013), motion direction (Ball & Sekuler, 1982, 1987), orientation (Dosher, Jeter, Liu, & Lu, 2013; Fiorentini & Berardi, 1980), etc. In our previous study, adapters in the trained and untrained conditions differed in three kinds of features, i.e. the retinotopic locations, spatiotopic locations, and motion directions (Dong et al., 2016). Thus, in the present experiments, we aimed to investigate whether these differences limited the transfer of attenuation of motion adaptation, and more importantly, which one was the determinant factor for the transfer. On this purpose, in each experiment only one of the three factors (i.e., retinotopic location, spatiotopic location, or motion direction) was kept identical for the trained and untrained conditions in the pre- and posttests. If a significant transfer can be observed when one feature is rendered the same for the trained and untrained conditions, but not when that feature differs across the conditions, then that feature would be the key factor determining the transfer.

## Methods

### Participants

Forty-five naïve participants finished the experiments, 15 in each experiment (Experiment 1: seven males, mean age = 21.67 years; Experiment 2: eight males, mean age = 21.20 years; Experiment 3: eight males, mean age = 21.33 years). All had normal or corrected-to-normal vision and provided the informed consent. It should be noted that the nulling task we used to measure the MAE is found to be hard and not

effective for all participants. Another 25 participants who failed to show significant MAE in the nulling task were not allowed to continue the training sessions. The experimental procedures were approved by the Institutional Review Board of the Institute of Psychology, Chinese Academy of Sciences. The study was carried out in accordance with the Code of Ethics of the World Medical Association.

## Apparatus

The stimuli were presented on a Sony GDM-F520 CRT monitor (1600 × 1200-pixel resolution at the refresh rate of 85 Hz; Tijuana, Mexico). Stimuli were programmed using MATLAB (MathWorks, Natick, MA) and Psychtoolbox (Brainard, 1997; Pelli, 1997). Participants viewed the display at a distance of 100 cm in a dark room. A chinrest was used to help maintain head position.

## Stimuli

All the stimuli were presented on a gray background (95.14 cd/m$^2$) with a circle fixation (0.23° in diameter). Previous literature (Castet et al., 2002) suggests that the nulling method may underestimate the MAE when testing at low dot densities (e.g. 39 dots/deg$^2$). Since signal dots are not sufficiently integrated or paired with the noise dots at low dot densities, the measured MAE may be in close correlation with the coherence threshold (Castet et al., 2002; Qian & Andersen, 1994). Therefore, a relatively high dot density (239 dots/deg$^2$) was adopted for both the adapter and test stimuli in this study. The adapter consisted of 3,000 dots (dot size: 0.056°), half of which were light gray (117.40 cd/m$^2$, Weber contrast = 23.40%) and the other half were dark gray (20.22 cd/m$^2$, Weber contrast = −78.75%). The dots were initially randomly positioned and then moved coherently upward or downward in an imaginary circular window (4° in diameter). If the dots fell outside, they would be wrapped to the opposite side of the circular window. The test stimuli were 1,688 dark gray and light gray dots that moved in a circular (3° in diameter) window and were presented at the same locations as the adapters. We made the adapters larger than the test stimuli to ensure that the tests were located in the adapting area even if small eye movements occurred. In the test stimuli, part of the dots moved randomly while the others moved coherently either upward or downward. The coherence ratio, which was positive for upward motion and negative for downward motion, was adjusted according to participants' judgments. Dots in both the adapters and the tests moved at a constant speed of 5°/s without any limited lifetime.

We examined the effect of retinotopic location, spatiotopic location, and motion direction on the transfer of effects of training on motion adaptation in three individual experiments. In Experiment 1, to test the effect of retinotopic location alone, the stimuli in the trained and untrained conditions were placed at the same retinal location but different spatial locations, and the motion directions were opposite. Specifically, in these two conditions, we put the fixation on either the center or the right (left) of the screen, while we kept the relative position between the fixation and adapters consistent (Figure 1a shows the conditions where the adapters are always presented to the left of the fixation). In Experiment 2, we tested the effect of spatiotopic location. The stimuli were always presented on the center of the screen, while participants fixated on the left and right of the screen in the trained and untrained conditions. The motion directions of two conditions were opposite (see Figure 1b). In Experiment 3, the effect of motion direction was examined. Motion directions of adapters in the trained and untrained conditions were consistent. Participants always stared at the central fixation, and the stimuli were presented on either the left or the right of the screen. Thus, both the retinal location and spatial location in two conditions were still different (see Figure 1c).

## Procedures

The experiments lasted for 10 days. In the first and last day, the pre- and posttraining MAEs in two different adapting conditions were measured. After the pretest, one of the adapting conditions was randomly selected for the trained condition. During the other 8 days, participants only performed the motion adaptation task of the trained condition (Figure 2). The magnitude of MAE was reflected by the percentage of the coherent dots in the test that could null the MAE perception (nulling percentage, Hiris & Blake, 1992), i.e., the ratio of coherent dots required to perceptually eliminate any global upward or downward motion.

### Coherence threshold measurements

Since nulling percentage is likely to be affected by coherence threshold (Castet et al., 2002), the coherence threshold without prior adaptation to any given direction was measured in pre- and posttraining days to examine this possibility. The measurements were completed before the adaptation sessions for two locations corresponding to the trained and untrained conditions. To ensure that participants had a stable performance before the formal experiments, they practiced the coherence detection task with stimuli at the two locations sufficiently in advance [Experiment 1:
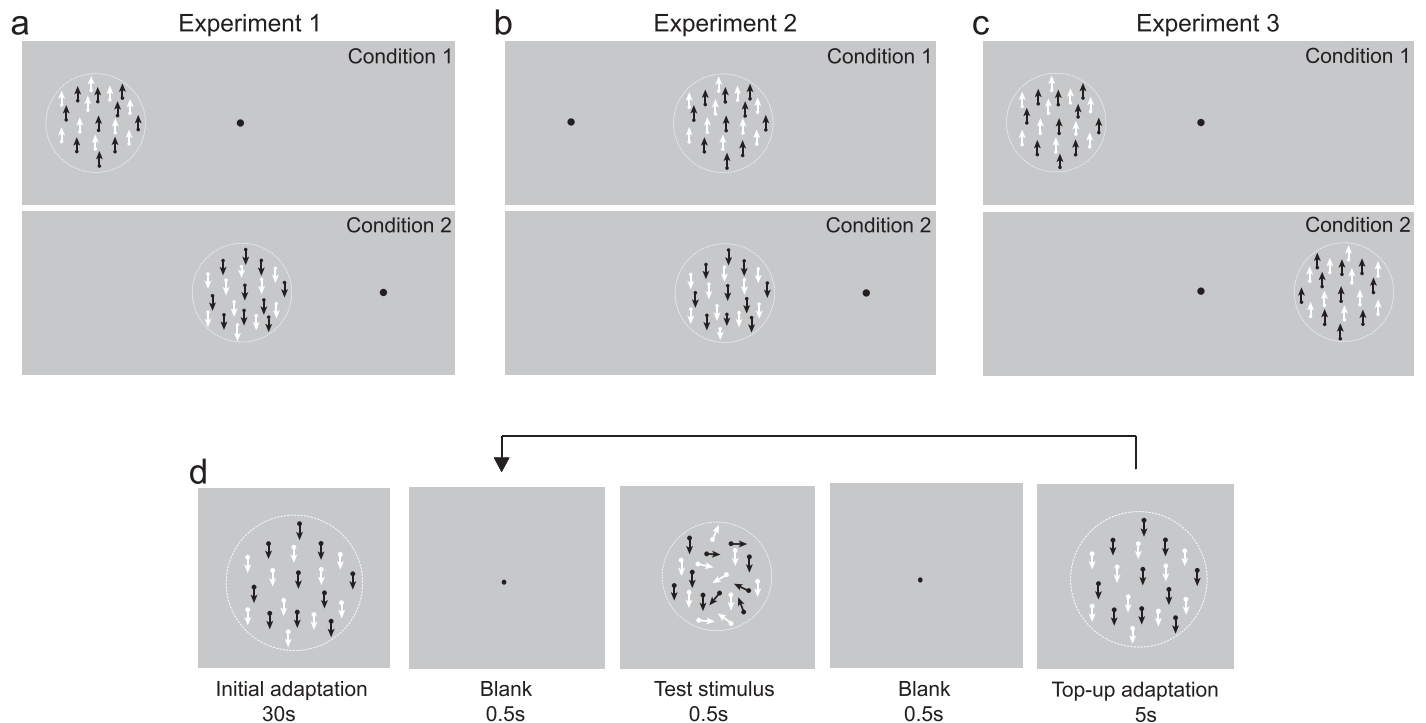
Figure 1. The design and procedure. (a) In Experiment 1, the motion stimuli were presented on the center or left (right) of the screen, while fixation was always located to the right (left) of the stimuli. Adapters in two conditions moved in the opposite direction. (b) In Experiment 2, the stimuli were presented on the center of the screen, and participants fixed on the left or right of the screen. Adapters in two conditions moved in the opposite direction. (c) In Experiment 3, the stimuli were presented on the right or left of the screen, while participants fixed on the center. Adapters in two conditions moved in the same direction. (d) The procedure of an adaptation session. Each session started with a 30-s initial adaptation, after a 0.5-s blank, a test stimulus was presented for 0.5 s. Then the 5-s top-up adapter was presented after a 0.5-s ISI. "Condition 1" and "Condition 2" represent two different adapting conditions. One of them was selected for the trained condition, and the other for the untrained condition, depending on the counterbalancing across the participants. Arrows indicate the motion directions. The white circular boundaries show the areas of moving dots and were not presented during the experiments.

Location1 (left or right of the screen): 4.33 ± 0.72 sessions (mean ± *SD*), Location2 (center of the screen): 4.47 ± 0.74 sessions; Experiment 2: Location1 (right to the fixation): 4.67 ± 0.90 sessions, Location2 (left to the fixation): 4.60 ± 0.99 sessions; Experiment 3: Location1 (left of the screen): 4.67 ± 0.82 sessions, Location2 (right of the screen): 4.47 ± 0.99 sessions].

To control potential factors irrelevant to motion adaptation (e.g., stimulus timing and contrast adaptation), the procedure of coherence detection task almost replicated that in the adaptation sessions, except that the adapters were incoherently moving dots. As the adapters were random dots patterns, no MAE would be observed. The coherence threshold was measured using a top-up
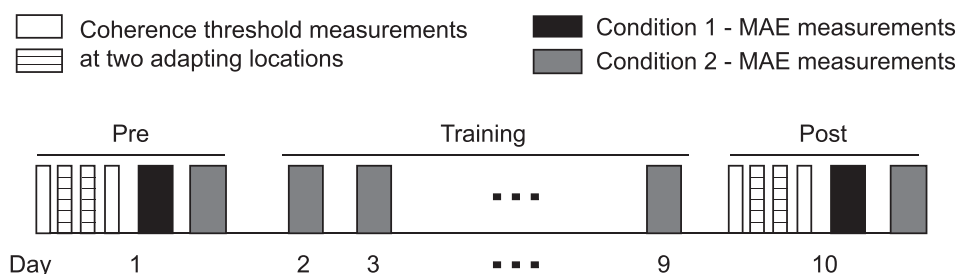


Figure 2. Flowchart of the experiments. The experiments lasted for 10 days. On the first and the 10th day, the coherence thresholds were first measured at the locations corresponding to the two adapting conditions. Then, the MAEs of two adapting conditions were measured. One of the adapting conditions was then selected to be trained (e.g. Condition 2 in the flowchart). During the training period (day 2–9), participants performed the motion adaptation task of the trained condition repeatedly for 8 days.

paradigm and a staircase procedure. Each session began with a 30-s initial adaptation period, after a 0.5-s blank interval, the test was presented for 0.5 s, and then a 5-s top-up adaptation followed a 0.5-s interstimulus interval (see Figure 1d). Forty-three coherence levels were predetermined, which increased logarithmically from 0.47% to 84.77% (the decimal portion was rounded if the coherence levels did not correspond to a whole number of dots). The initial coherence ratio of test was 46.03% either upward or downward. Participants judged the direction of coherence motion by pressing the Up Arrow or Down Arrow on the keyboard. The response could be made at any time by the end of the immediately subsequent top-up adaptation period. The coherence ratio of next test was adjusted using two interleaved 2-down-1-up staircases for upward motion and downward motion, respectively. The step size was initially three levels, and decreased to one level after four reversals. A staircase ended after reaching eight reversals or the number of trials reached 150. For each staircase, the mean of the last six reversal points was taken as the 71% correct threshold. The coherence threshold was calculated as half the difference between the upward and downward thresholds (Castet et al., 2002) and was measured twice for each location. To counteract any response bias in the task, the mean threshold across the two sessions was taken as the starting level of coherence percentage in the MAE measurements.

### MAE measurements

The procedure and task in adaptation sessions were similar to those for measuring coherence threshold, except that dots in the adapters moved coherently upward or downward. Each condition was measured for one session, including five blocks. A 1-min break was given between every two blocks. In each block, the nulling percentage was measured using two interleaved 1-down-1-up staircases. A 1-down-1-up staircase was adopted since it would converge to the coherence ratio at which the participants reported perceiving either upward or downward motion at a chance level, i.e., 50%. The step size for each staircase was initially 16%. It decreased to 8% after the first reversal, and then to 4% after the second reversal. Thirty-four trials were tested in each staircase. The mean of the last six reversals of each staircase was calculated as nulling percentage. Ten nulling percentages were acquired for averaging in each testing session.

## Results

### Experiment 1: Effect of retinotopic location

To examine the role of retinotopic location on the transfer of attenuation of motion adaptation, we presented the adapters in both the trained and untrained conditions at the same retinal location. The MAEs across days were shown in Figure 3a. Nulling percentages in the trained condition attenuated significantly over training [linear trend analysis: $t(14) = 5.09$, $p < 0.001$, Cohen's $d = 1.86$]. A 2 (Session: pretest vs. posttest) $\times$ 2 (Condition: trained vs. untrained) repeated-measures analysis of variance (ANOVA) was then performed on the nulling percentage. The results did not show a significant main effect of Session, $F(1, 14) = 3.09$, $p = 0.10$, $\eta_p^2 = 0.18$, but showed a significant main effect of Condition, $F(1, 14) = 9.27$, $p < 0.01$, $\eta_p^2 = 0.40$, and a significant interaction between Session and Condition, $F(1, 14) = 18.57$, $p < 0.001$, $\eta_p^2 = 0.57$. Paired $t$-test revealed that the nulling percentages reduced significantly after training in the trained condition, $t(14) = 5.48$, $p < 0.001$, Cohen's $d = 1.50$, but not in the untrained condition, $t(14) = 1.25$, $p = 0.23$, Cohen's $d = 0.28$. We calculated the change of nulling percentage by subtracting pretest effect from the posttest effect. The mean changes were $-22.16\%$ ($SD = 15.64\%$) and $5.47\%$ ($SD = 16.94\%$) in the trained and untrained conditions, respectively. The proportion of transfer, which was reflected by the ratio of the change of nulling percentage in the untrained condition to that in the trained condition, was $-24.73\%$.

Nulling the MAE relies on the integration of noise and signal dots. If the integration is insufficient, the signal dots will appear to be moving transparently over the noise dots as long as the ratio of signal dots exceeds the coherence threshold. Consequently, the magnitude of nulling percentage will depend on coherence threshold under low dot densities (Castet et al., 2002). To avoid transparent motion, signal dots and noise dots need to be paired (Qian & Andersen, 1994). Castet et al. (2002) have suggested that the nulling method is more effective with high dot density since high dot density may increase the probability of signal dots being paired with noise dots. The present study adopted high dot density for both the adapter and the test stimuli, thus the nulling percentage should not be influenced by coherence threshold (Castet et al., 2002).

Nevertheless, we still performed a 2 (Session: pretest vs. posttest) $\times$ 2 (Condition: trained vs. untrained) repeated-measures ANOVA on the coherence threshold for a stringent examination. The results showed a main effect of Session, $F(1, 14) = 4.66$, $p = 0.049$, $\eta_p^2 = 0.25$, but no significant main effect of Condition, $F(1, 14) = 0.15$, $p = 0.70$, $\eta_p^2 = 0.01$, or interaction, $F(1, 14) = 0.07$, $p = 0.80$, $\eta_p^2 = 0.01$. The significant main effect of Session revealed that the coherence thresholds in both conditions actually increased after training rather than decreased (Figure 3d). If the coherence threshold had dominated the measured nulling percentage, we would have observed increased nulling percentage in the
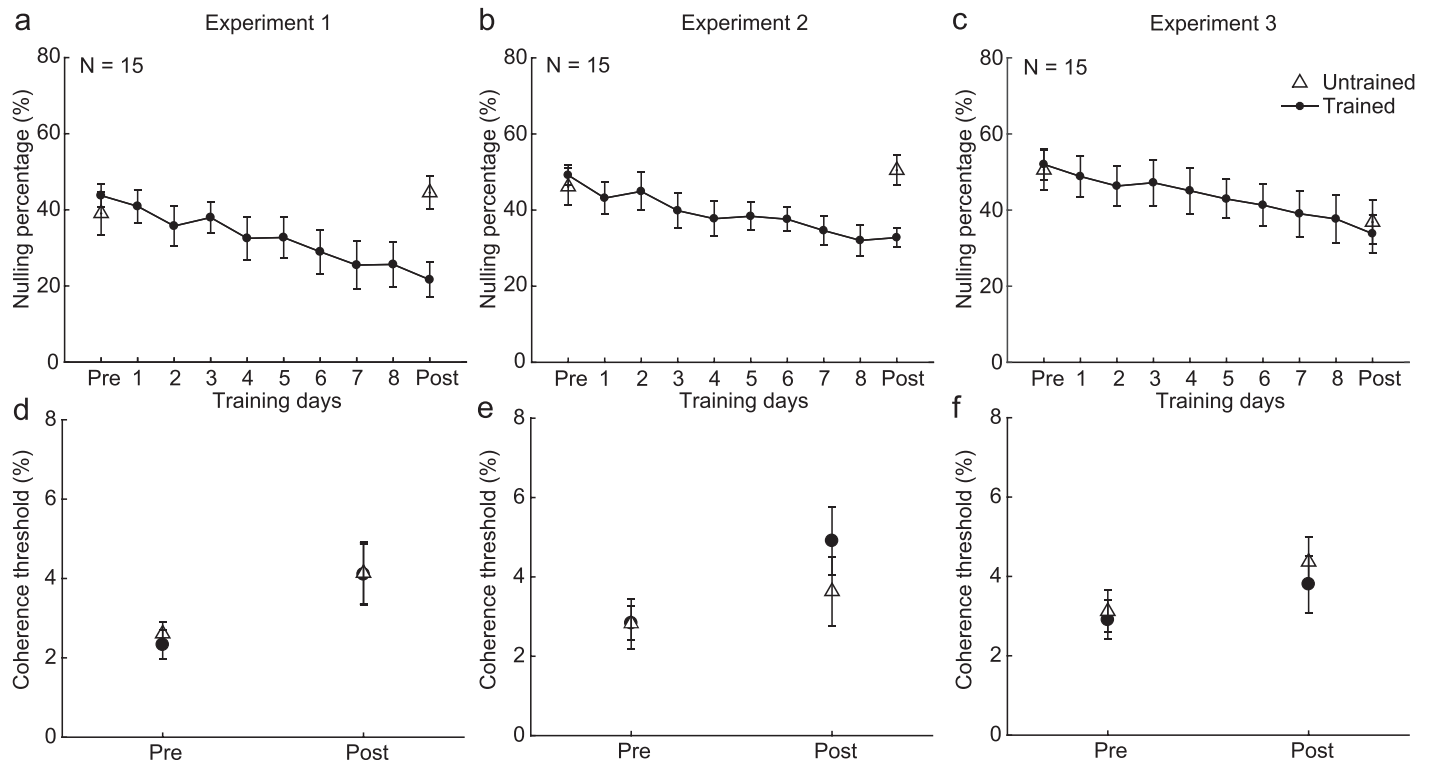
Figure 3. The upper panels display the nulling percentages measured in the trained and untrained conditions of (a) Experiment 1, (b) Experiment 2, and (c) Experiment 3. The lower panels show the coherence thresholds in each experiment. Black dots represent the trained condition and white triangles represent the untrained condition. Error bars denote the standard errors of means.

posttest. Evidently, this contradicted with the results of attenuation of the motion adaptation.

One may argue that the coherence threshold reflects the direction discrimination sensitivity at an unadapted state; training may alter the direction discrimination sensitivity at the adapted state (McGovern et al., 2012). To answer this question, we fitted the staircase data from the adaptation sessions to a Logistic function $p = 1/(1 + e^{-\frac{l-b}{k}})$, where p is the percent of upwards response, $l$ is the coherence level, $b$ is the midpoint of the curve, $k$ is the slope of the curve. A 2 (Session: pretest vs. posttest) $\times$ 2 (Condition: trained vs. untrained) repeated-measures ANOVA was performed on the slopes ($k$) of the psychometric functions. The results indicated no significant main effects [Session: $F(1, 14) = 3.09$, $p = 0.10$, $\eta_p^2 = 0.18$; Condition: $F(1, 14) = 0.15$, $p = 0.71$, $\eta_p^2 = 0.01$] or interaction, $F(1, 14) = 0.29$, $p = 0.60$, $\eta_p^2 = 0.02$. Therefore, the decrease of nulling percentage we observed was unlikely to be caused by the variation of coherence discrimination at both the adapted and unadapted state.

Since the shared retinal location did not suffice the transfer to the untrained condition, the attenuation of motion adaptation should not occur at a retinotopic level. Considering the retinotopic reference frame of motion adaptation (Knapen et al., 2009), it is not appropriate to ascribe the attenuation of motion adaptation to a special form of adaptation.

## Experiment 2: Effect of spatiotopic location

In Experiment 2, we checked whether the transfer of attenuation of motion adaptation would be facilitated if the adapters were located at the same spatiotopic location. Similar to Experiment 1, training gradually reduced the nulling percentages in the trained condition [see Figure 3b, $t(14) = 4.02$, $p < 0.01$, Cohen's $d = 1.47$]. The $2 \times 2$ repeated-measures ANOVA on the nulling percentage revealed a significant interaction between Session and Condition, $F(1, 14) = 9.36$, $p < 0.01$, $\eta_p^2 = 0.40$. The main effects of Session, $F(1, 14) = 3.90$, $p = 0.07$, $\eta_p^2 = 0.22$, and Condition, $F(1, 14) = 3.44$, $p = 0.09$, $\eta_p^2 = 0.20$, were not significant. Paired $t$-test indicated that the MAE decreased significantly after training in the trained condition [$t(14) = 4.28$, $p < 0.001$, Cohen's $d = 1.67$, mean change $= -16.40\%$, $SD = 14.85\%$] but not in the untrained condition [$t(14) = 0.83$, $p = 0.42$, Cohen's $d = 0.25$, mean change $= 4.33\%$, $SD = 20.11\%$]. The transfer of training effect was $-26.40\%$.

Besides, after 8 days of repeated motion adaptation, we did not find any changes of coherence thresholds

without adaptation [Figure 3e, main effect: Session: $F(1, 14) = 3.56$, $p = 0.08$, $\eta_p^2 = 0.20$; Condition: $F(1, 14) = 1.23$, $p = 0.29$, $\eta_p^2 = 0.08$; interaction: $F(1, 14) = 1.33$, $p = 0.27$, $\eta_p^2 = 0.09$]. The coherence discrimination at the adapted state improved after training in both conditions [main effect: Session: $F(1, 14) = 9.58$, $p = 0.008$, $\eta_p^2 = 0.41$]. No significant main effect of Condition, $F(1, 14) = 1.29$, $p = 0.27$, $\eta_p^2 = 0.09$, or interaction, $F(1, 14) = 0.47$, $p = 0.50$, $\eta_p^2 = 0.03$, was found. Because the coherence discrimination sensitivity increased for both conditions but the reduction of MAE was only found in the trained condition, the attenuation of motion adaptation over training could not be simply explained by a result of improved coherence discrimination at the adapted state.

All these results indicated that the attenuation of motion adaptation did not transfer at the same spatiotopic location. In addition, the effect did not depend on coherence discrimination ability. Therefore, it should not be anchored at world-centered coordinates, either.

## Experiment 3: Effect of motion direction

In this experiment, participants adapted to the same motion direction at two different locations in pre- and posttest. The $2 \times 2$ repeated-measures ANOVA on the nulling percentage indicated a significant main effect of Session, $F(1, 14) = 19.80$, $p < 0.001$, $\eta_p^2 = 0.59$, but not the main effect of Condition, $F(1, 14) = 0.12$, $p = 0.73$, $\eta_p^2 = 0.009$, or interaction between these two factors [$F(1, 14) = 2.25$, $p = 0.16$, $\eta_p^2 = 0.14$, see Figure 3c]. Paired *t*-test revealed a significant decrease of MAE in posttest for both the trained [$t(14) = 5.29$, $p < 0.001$, Cohen's $d = 1.03$, mean change $= -18.20\%$, $SD = 13.32\%$] and untrained conditions [$t(14) = 3.20$, $p < 0.01$, Cohen's $d = 0.63$, mean change $= -13.71\%$, $SD = 16.61\%$]. The nulling percentages in the trained condition decreased significantly across days [$t(14) = 3.43$, $p < 0.01$, Cohen's $d = 1.25$] and this training effect transferred significantly to the untrained condition (transfer ratio $= 75.30\%$). This finding suggests that the attenuation of motion adaptation is direction selective.

A $2 \times 2$ repeated-measures ANOVA on the coherence threshold showed no significant main effects [Figure 3f, Session: $F(1, 14) = 2.73$, $p = 0.12$, $\eta_p^2 = 0.16$, Condition: $F(1, 14) = 0.81$, $p = 0.38$, $\eta_p^2 = 0.06$] or interaction, $F(1, 14) = 0.18$, $p = 0.68$, $\eta_p^2 = 0.01$. An analysis of the coherence discrimination at the adapted state showed a significant main effect of Session, $F(1, 14) = 8.02$, $p = 0.013$, $\eta_p^2 = 0.36$, but not the main effect of Condition, $F(1, 14) = 0.005$, $p = 0.95$, $\eta_p^2 < 0.001$, or interaction, $F(1, 14) = 0.30$, $p = 0.59$, $\eta_p^2 = 0.21$.

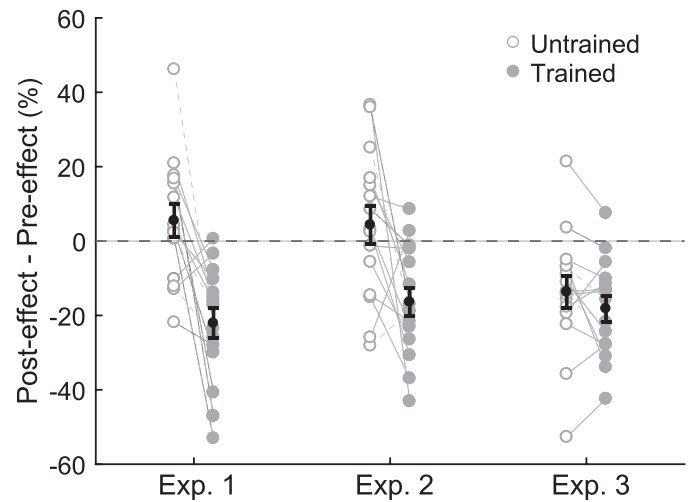To provide an overview of the extent of transfer in different experiments, Figure 4 plotted the individual



Figure 4. The differences between post- and pretraining MAE of three experiments. Filled circles represent the trained condition; open circles represent the untrained condition. Results from the same participant are connected by a dotted line. Black dots and bars represent the mean and standard error of mean of the differences in each condition.

changes of nulling percentages in all the three experiments. A negative value represents the decrease of nulling percentage after training; a positive value represents the increase. In both the Experiments 1 and 2, the nulling percentages decreased significantly in the trained condition but not in the untrained condition [Experiment 1: $t(14) = 4.31$, $p < 0.001$, Cohen's $d = 1.69$; Experiment 2: $t(14) = 3.06$, $p < 0.01$, Cohen's $d = 1.17$]. Interestingly, the decrease of nulling percentage was significant for both conditions in Experiment 3, $t(14) = 1.50$, $p = 0.16$, Cohen's $d = 0.30$.

## Discussion

Our study replicated the previous findings that motion adaptation attenuated after multiple days of training. More importantly, the results indicated that the attenuation of motion adaptation could largely transfer to other retinal and spatial locations as long as the adapters shared the same motion direction with the trained adapter. Because the attenuation of motion adaptation is neither anchored in eye-centered (retinotopic) nor world-centered (spatiotopic) coordinates, it is substantially different from motion adaptation, which has been demonstrated to be retinotopic (Knapen et al., 2009).

Besides the present findings, our previous work, which studied the changes of contrast adaptation and motion adaptation after multiple days of training, also disclosed three distinct characteristics of the training effect (Dong et al., 2016). First, the attenuation of

contrast adaptation largely transferred to the untrained condition. Second, the immediate effects of contrast adaptation decreased over training, whereas the time for the adaptation effects to return to baseline remained constant. Third, the attenuation of motion adaptation was very long-lasting, staying robust after 2–3 months. Combining all the previous and present findings, we believe that this phenomenon cannot be ascribed to a variant of visual adaptation, because a plethora of research have disclosed that adaption effect recovers soon after the adapter is withheld (Bai, Dong, He, & Bao, 2017; Greenlee, Georgeson, Magnussen, & Harris, 1991; Hershenson, 1989; Lunghi, Burr, & Morrone, 2013; Zhang, Bao, Kwon, He, & Engel, 2009) and it is usually specific to the adapter (Bex, Verstraten, & Mareschal, 1996; Blakemore & Campbell, 1969; Georgeson & Harris, 1984; Gilinsky, 1968). Instead, the phenomenon we observed should be a kind of relatively high-level learning.

A likely candidate of this learning is habituation, which is referred to as response decrement as a result of repeated stimulation (Rankin et al., 2009). According to the Stimulus-Model Comparator theory of habituation (Sokolov, 1960), the nervous system creates a model of the expected stimulus with repeated experience of a stimulus. Responses to the ensuing stimulus will be inhibited if the experienced stimulus matches the model. The model usually does not represent the experienced stimulus well initially; thus, the inhibition is weak due to mismatching. With more repetitions, the stimulus model will be improved and represent the stimulus more precisely, leading to increased inhibition on the response. Habituation can be retained for days or weeks and can transfer to other stimuli (Maschke et al., 2000; Rankin et al., 2009; Thompson, 2009). These characteristics of habituation accord well with the properties of the training effects we observed (Dong et al., 2016). More evidence supporting this notion is from the analysis of contrast adaptation experiments (Dong et al., 2016). We found that the immediate adaptation effect decreased as a function of training sessions, but the time required for the threshold to decay to baseline remained constant across different training sessions. Such a result pattern bears a striking resemblance to the manner in which adapting contrast modulates the time course of contrast adaptation (Greenlee et al., 1991). Based on these clues, we speculated that the attenuation of adaptation over training might be a result of habituation to the adapter. As training of adaptation proceeded, a stimulus model about the repeatedly presented adapter might gradually form in the brain, leading to increased inhibition to the neuronal activities in response to the adapter. As a result, the effective strength of the adapter reduced

after training, which in turn caused weaker adaptation effect.

Alternatively, the attenuation of adaptation could reflect a resistance to adaptation rather than the reduced neural responses to the adapter. Note that the effects we measured were aftereffects. Thus, the effects do not necessarily reflect changes in the adapted states. It is possible that they correspond to the transition of the visual system to an adapted state. In other words, the effects might occur on the adaptation process. Future neural evidence is still needed to ascertain whether the attenuation of adaptation represents the habituation of the neural response to the adapter, the habituation of the adaptation process on the adapter, or both.

Given the characteristics of the transfer, the attenuation of motion adaptation likely reflects the plasticity of direction-selective neurons with large receptive fields. Which brain areas do those neurons reside in? The middle temporal visual area (MT/V5) could be a candidate cortical region. MT/V5 is known to be important for the processing of motion information. Neurons in MT/V5 are direction selective and have considerably large receptive field (Albright, 2014; Desimone & Ungerleider, 1986; Lagae, Raiguel, & Orban, 1993; Van Essen, Maunsell, & Bixby, 1981). However, these neurons represent the contralateral visual field (Desimone & Ungerleider, 1986), and the retinotopic or spatiotopic property of MT/V5 remains controversial (Crespi et al., 2011; d'Avossa et al., 2007; Gardner, Merriam, Movshon, & Heeger, 2008). Therefore, the contribution of MT/V5 alone should not account for the transfer to the adapter located at different retinal and spatial locations. Neurons in the MST are also tuned to motion direction (Desimone & Ungerleider, 1986), and have been found to play a role in representing the MAE (Hogendoorn & Verstraten, 2013; Rühl, Bauermann, Dieterich, & zu Eulenburg, 2018). More importantly, their receptive fields are large enough to extend to ipsilateral hemifield (Desimone & Ungerleider, 1986; Huk, Dougherty, & Heeger, 2002). Similar properties have been found in the LIP (Hamed, Duhamel, Bremmer, & Graf, 2001; Fanini & Assad, 2009). Thus, these areas are more likely to be involved in the habituation of motion adaptation. Nevertheless, neuroimaging methods are needed to further explore the underlying mechanisms.

It should be noted that we cannot exclude the roles of other high-level functions in the present findings. For example, habituation effect may be based on memory. It is possible that participants remembered the features of the trained adapter during the training, especially the motion direction that is perhaps a predominant feature to form a model about the adapter in the brain. As long as a new adapter matched the

model in motion direction (Sokolov, 1960), the strength of the adapter would be weakened, leading to similar attenuation of the adaptation effects. As to the possible neural sites for this memory account, both physiological and psychophysical studies have revealed that MT/V5 and MST contribute to the encoding, storage, and retrieval of motion information in working memory (Bisley & Pasternak, 2000; Bisley, Zaksas, & Pasternak, 2001; Ong, Hooshvar, Zhang, & Bisley, 2009). Whether MT/V5 and MST affect longer-term memory about motion information remains to be explored. Besides, memory-related areas beyond the visual pathway, such as the medial temporal lobe memory system (Lech & Suchan, 2013), are also likely candidates. Future work may test whether habituation of visual adaptation can occur without memory or not.

Unlike other studies of perceptual learning affecting adaptation (Haak et al., 2014; McGovern et al., 2012; Pinchuk-Yacobi et al., 2016; Yehezkel et al., 2010), where increased or unchanged adaptation effects were observed after training, we found decreased adaptation effects over training. Note that the current experimental design differs from theirs in several aspects. First, we used laboratory stimuli (moving dots or gratings) rather than natural scenes as the adapters. The natural scenes for adaptation in those studies are in close relation with the observer's ongoing activity. By contrast, the adapters in our experiments were task irrelevant, and should be ignored in strategy. This makes the neural system more likely to habituate to them. Second, we used a nulling task to estimate the magnitude of MAE, whereas the negative finding from McGovern et al. (2012) is based on the recording of the MAE duration. Although the measurement of MAE duration is also a commonly used method, it may depend on low-speed units (Verstraten, van der Smagt, Fredericksen, & van de Grind, 1999; Verstraten, van der Smagt, & van de Grind, 1998). Instead, in the nulling method, random moving dots are used, which are more similar to the adapter in McGovern et al.'s work (McGovern et al., 2012). Thus, the nulling method may be more useful to examine such higher-level dynamic MAE. Empirically, the MAE duration might be a less sensitive index for measuring the MAE than the nulling percentage due to large variation across trials and individuals. In our previous work, we also recorded the MAE duration on each training day. However, neither we (Dong et al., 2016) nor McGovern et al. (2012) found any changes of the MAE duration as a function of training. Nevertheless, the MAE duration can be a more useful test when the effect size *per se* is sufficiently large (e.g. Bai, Bao, Zhang, & Jiang, 2018; Harris, Morgan, & Still, 1981).

*Keywords: motion adaptation, training, habituation, transfer*

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