Time course influences transfer of visual perceptual learning across spatial location

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ABSTRACT

Visual perceptual learning describes the improvement of visual perception with repeated practice. Previous research has established that the learning effects of perceptual training may be transferable to untrained stimulus attributes such as spatial location under certain circumstances. However, the mechanisms involved in transfer have not yet been fully elucidated. Here, we investigated the effect of altering training time course on the transferability of learning effects. Participants were trained on a motion direction discrimination task or a sinusoidal grating orientation discrimination task in a single visual hemifield. The 4000 training trials were either condensed into one day, or spread evenly across five training days. When participants were trained over a five-day period, there was transfer of learning to both the untrained visual hemifield and the untrained task. In contrast, when the same amount of training was condensed into a single day, participants did not show any transfer of learning. Thus, learning time course may influence the transferability of perceptual learning effects.

KEYWORDS

visual perceptual learning; learning specificity; psychophysics; vision; motion perception; perception

SECTION 1 - INTRODUCTION

Visual perceptual learning (VPL) describes the improvement in performance of a psychophysical task with repeated practice (Fahle & Poggio, 2002). Over recent years, the use of VPL to augment visual function, both in healthy individuals and in those with specific visual disorders, has increased considerably. In the healthy visual system, positive benefits of VPL have been documented for motion perception (Zhang & Yang, 2014), speed of visual processing (Lev et al., 2014), reading speed (Chung et al., 2004), visual acuity and contrast sensitivity (Deveau et al., 2014). In amblyopia a number of studies have shown an enhancement in stereoscopic vision (Astle et al., 2011; Ding & Levi, 2011), contrast sensitivity (Polat et al., 2004), spatial and stereo acuity (Xi et al., 2014) following extensive training. In patients with visual cortical damage, VPL may be used to boost residual visual function, either by recruiting neighbouring cortical tissue or by increasing visual activity in partially damaged pathways. Indeed, there have been initial reports of some visual recovery following extended VPL of around 3 months in such patients (Das et al., 2014; Henriksson et al., 2007; Huxlin et al., 2009; Sahraie et al., 2006; Sahraie et al., 2010). However, an effective short-term protocol would make such treatments more attractive as long-term training requires significant commitment and effort on behalf of the patient.

The transferability of visual improvements following VPL remains the subject of considerable debate. Initially, VPL was considered specific to the trained task, and not transferable to untrained retinal locations (Karni & Sagi, 1991), stimulus orientations (Poggio et al., 1992) or other parameters (Ahissar & Hochstein, 1993; Fahle & Morgan, 1996; Fiorentini & Berardi, 1980). However, more recent work suggests that learning can be transferred spatially (Xiao et al., 2008) and across stimulus parameters (Liu, 1999) and tasks (McGovern et al., 2012).

Under a 'double training' paradigm, when separate areas of the visual field are trained on different tasks in an interleaved manner, it has been shown that there can be transfer of learning to an untrained location, indicating a lack of spatial specificity (Mastropasqua et al., 2015; Xiao et al., 2008). Furthermore, simultaneous or subsequent passive exposure to untrained stimulus attributes (such as an untrained motion direction) may induce transfer of learning across such parameters in the trained part of the visual field (Zhang et al., 2010; Zhang & Yang, 2014). Easier tasks are more likely to show transfer of learning across stimulus parameters, such as motion direction (Liu, 1999) and orientation (Wang et al., 2013); this transfer effect has been shown to disappear if the training task is very difficult (Hung & Seitz, 2014). When the basic stimulus elements are comparable across tasks, perceptual learning can transfer even to unrelated tasks (McGovern et al., 2012). The type of learning demanded by a task is influential in determining the extent of transfer. For instance, if a task encourages learning of stimulus-specific rules then learning is likely to be less transferable compared to a task that encourages learning of rules that are generalisable to different stimuli (Green et al., 2015). Increasing the amount of training has been shown to increase the specificity of perceptual learning effects across visual location and stimulus parameters (Jeter et al., 2010; Mastropasqua & Turatto, 2015), likely due to sensory adaptation (Harris et al., 2012).

Other factors, such as time course of learning, have not yet been fully investigated for their impact on the transferability of perceptual learning effects. A study looking at the effect of a foveal hyperacuity task found that when training of was delivered across two days, there was no transfer of learning to a similar untrained stimulus presented in the same retinal location. However, when an equivalent amount of training was delivered spread across four weeks, participants showed improvement of the untrained stimulus. This result indicated that increasing the time course across which training was delivered may increase the transfer of perceptual learning effects to similar, untrained stimuli (Aberg et al., 2009). Here, we aimed to quantify the extent to which the effects of a simple five-day training protocol are transferred across spatial location (hemifield) and different stimulus elements (moving dots compared to sinusoidal gratings), when compared to a one-day training protocol.

SECTION 2 - METHODS

2.1 Participants

Forty-four subjects (21 female and 23 male; M=23.2 years; SD=3.89 years) with normal or corrected-to-normal vision were included in the study. All were naïve to visual psychophysical experiments. The study was approved by the local InterDivisional Research Ethics Committee (IDREC) at the University of Oxford and all subjects gave written, informed consent. Research was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). 22 participants were assigned to a motion coherence training protocol ("motion training group") and the remaining 22 to a sinusoidal grating orientation training protocol ("orientation training group"). In each of the two groups, 12 subjects participated in a training protocol lasting for one day ("one-day group") and the remaining 10 participated in a training protocol lasting for five days ("five-day group").

2.2 Experimental setup

Visual stimuli were programmed using Processing Java v2.0b6 (MIT) and Matlab (vR2012a) with Psychtoolbox, and were presented on a CRT monitor (ViewSonic E70fSB, 1280x1024 pixel resolution, 75Hz refresh rate, 17-inch display) in a darkened room. Participants were positioned 57cm from the screen and used a chin-rest to minimise head movements.

2.3 Visual Stimuli and Tasks

Two tasks were used in this project: a motion direction discrimination task and a sinusoidal grating orientation discrimination task, abbreviated as "motion task" and "orientation task" respectively. For the motion task (Figure 1), participants identified whether a group of white coherently-moving dots (luminance 96.8cd/m^2) had leftwards or rightwards motion, when displayed amongst randomly-moving distractor dots ("noise") on a black background (luminance=0.92cd/m^2). Moving dots (n=200) were presented within a circular area 13° in diameter centred 9° to the left or right of fixation (the edge of the stimulus aperture was 2.5° from fixation). The dot diameter was 0.15°, and they moved with a speed of 6°/s for a limited lifetime of 200ms (12 frames), at a density of 1.5 dots/$degree^2$. Dots were born or reborn at random, non-overlapping locations within the stimulus aperture. Coherent motion direction was variable but restricted to within a 90° angle centred around the horizontal meridian. A high contrast stimulus was applied so it was more salient and easily detectable by the visual system.

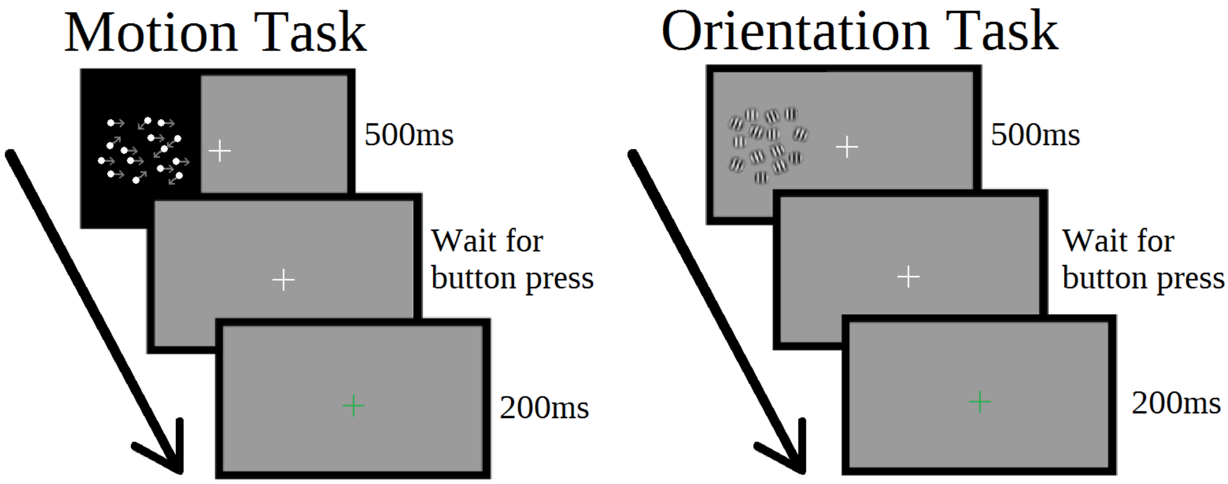

Figure 1: *The motion task (left) and the orientation task (right). Participants were shown the stimulus on one side of the screen for 500ms. The stimulus then disappeared and the program paused until the subject gave their response. The fixation cross then flashed green or red for 200ms to indicate a correct or incorrect response for the trial. The next trial then began immediately.*

For the orientation task (Figure 1), participants identified whether the net orientation of sinusoidal gratings was vertically- or horizontally-oriented, when a proportion of the patches were oriented randomly ("noise"). Sinusoidal gratings (n=50) were presented within a circular area 13° in diameter centred 9° to the left or right of fixation (the edge was 2.5° from fixation). Sinusoidal grating diameter was 1° and spatial frequency was 5 cycles/°. Gratings were 90% contrast, calculated using Michelson contrast with maximum luminance of 96.8cd/m^2 and minimum luminance of 5.1cd/m^2.

Feedback for both tasks was provided visually on a trial-by-trial basis. Tasks were self-paced, where after the 500ms stimulus presentation, the program paused until user input was detected. It was emphasised that accuracy was more important than speed. The difficulty of both tasks was varied adaptively following a two-up one down staircase procedure using the implementation of García-Pérez (1998). Two consecutive correct responses resulted in coherence being decreased by a factor of 0.8, while an incorrect response resulted in an increase of 1.46. For the motion stimulus, the ratio of coherently-moving dots to randomly-moving dots was varied. For the orientation stimulus, the ratio of vertical or horizontal (coherent) to randomly-oriented patches was varied. Participants in both tasks started with a coherence level of 80% to ensure correct performance of the task. A new staircase was initiated each training session, and each assessment session. For the assessments, two independent staircases were interleaved for the two visual hemifields.

Coherence thresholds in each session were calculated by taking the mean of the coherence on each trial in which a reversal occurred (stimulation changed from increasing in difficulty to decreasing, or vice versa). The first 10 reversal values were always discarded. This provided a discrimination threshold at which the participant is predicted statistically to be correct 80% of the time.

2.4 Assessment and Training Paradigms

Initial performance on each task was assessed prior to any training to determine baseline ability on the tasks. Once all training sessions of the appropriate task had been completed, the performance assessment was repeated. The motion training group were assessed on the motion task only. The orientation training group were assessed on the motion and the orientation tasks. Motion assessment was included for the orientation training group so that any transfer of learning effects across tasks could be determined.

During the ten training sessions (400 trials in each), participants were shown stimuli in a single visual hemifield, counterbalanced across subjects. Therefore, there was always a “trained” and an “untrained” visual hemifield. Each training session lasted around 10 minutes. In all pre-training and post-training visual assessments, stimuli were presented separately to the left and the right visual hemifields (200 trials per hemifield) in an pseudorandomly interleaved manner. This allowed separate assessment of each hemifield and permitted the effects of transfer of learning across the visual field to be determined. Each assessment lasted around 15 minutes. During training and assessments, participants were offered an optional break from the screen every 20 trials to reduce fatigue and boredom.

Participants in the five-day group completed the ten training sessions distributed across five days, with two sessions per day (Figure 2). There was a brief 3-minute pause between sessions. The pre-training assessment was performed on day 1 and post-training assessment on day 5. Participants in the one-day group completed all tasks in a single day, and were permitted three 15-minute breaks (Figure 2). Both groups completed the same number of training trials (4000).

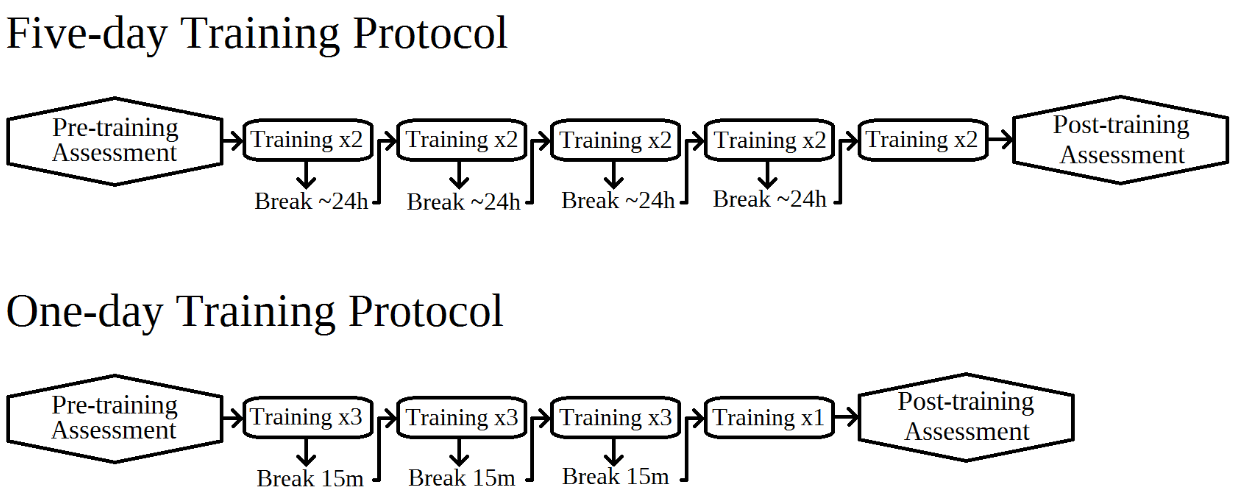

Figure 2: *Participants were assigned to the five-day training protocol (top) or the one-day training protocol (bottom). Subjects in the five-day group were assessed on the first day (pre-training assessment), and then completed 2 training sessions of 400 trials each. The participant then completed a further 2 training sessions per day for four consecutive days, followed by a post-training assessment on the final day. Subjects in the one-day group completed all 4000 training trials, plus the pre-training and post-training assessments, on a*

single day. Each block of three 400-trial training sessions was followed by a 15-minute break.

2.5 Fixation monitoring

An eye tracker (Eyelink1000, SR Research) was used to monitor fixation for three of the four groups during training and testing. For the motion training group who completed the 5-day protocol, however, eye movements were not monitored. Although there is no objective measurement for this group, which weakens the study slightly, there is little reason to believe that this group would perform significantly differently from the others. Indeed a previous study used a separate group of observers to determine the effects of eye movements on learning and concluded that eye movements did not differ before and after training and therefore were unlikely to bias the learning effects shown in the study (Zhang et al. 2010). Furthermore, we have no reason to expect that one group would be any more likely to have fixation losses compared to the others.

Loss of fixation was defined as a deviation of eye position larger than 2° in the horizontal meridian, lasting longer than 100ms, during stimulus presentation. During training, fixation losses occurred during 6.9% of trials (median average across all subjects). During assessment sessions, fixation losses occurred during 2.1% of trials at pre-training assessments and 2.9% of trials at post-training assessments (median averages across all subjects). There was no significant difference between groups, or between pre-training and post-training assessments (univariate analysis with factors 'group' and 'timing'; Group: $F(3,2) = 0.435$, $p = 0.652$; Timing: $F(3,1) = 0.180$, $df = 1$, $p = 0.674$).

SECTION 3 - RESULTS

3.1 All groups showed effective learning of the task during training

During the training phase, both the one-day and five-day training groups showed learning of the trained task, either motion (Figure 3A and C) or orientation (Figure 3B and D). This was confirmed by comparing the discrimination threshold at the initial training session with the threshold at subsequent training sessions. A three-way ANOVA confirmed that the discrimination threshold decreased from the initial training session across subsequent training sessions, regardless of training protocol or task (three-way ANOVA using data normalised to Session 1, with factors 'session', 'training protocol' and 'task'; Session: $F=5.301$, $df=8$, $p=3x10^{-6}$; Session*Protocol: $F=0.071$, $df=8$, $p=0.081$; Session*Task; $F=0.015$, $df=8$, $p=0.939$). There was therefore a similar amount of learning across all four groups.

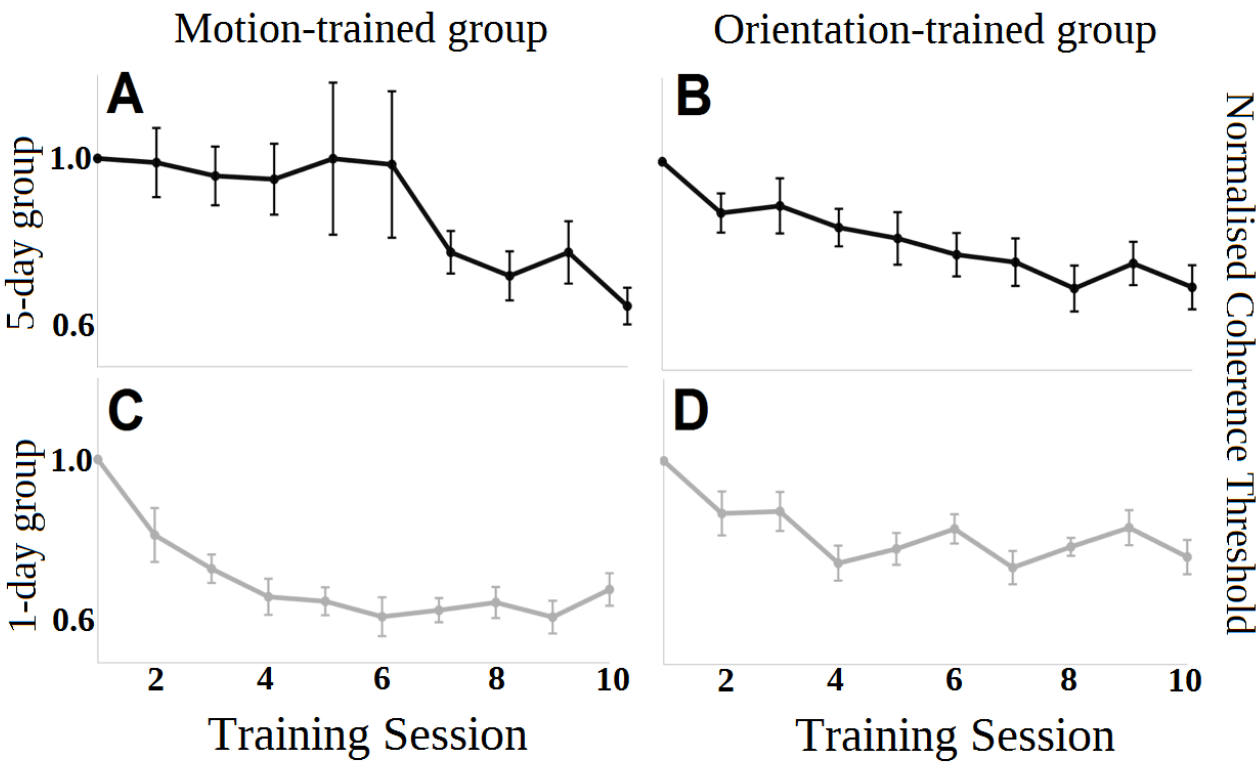

Figure 3: *Direction discrimination thresholds across all ten training sessions were normalised to performance at the initial session. Each graph shows that the normalised discrimination threshold decreased across the sessions, in both the motion and orientation tasks and the 1- and 5-day training schedules. (A) Motion-trained, 5-day group. (B) Orientation-trained, 5-day group. (C) Motion-trained, 1-day group. (D) Orientation-trained, 1-day group. Error bars are +/-SEM.*

3.2 Significant effect of training in the five-day training group and in the one-day training group

To quantify the change in discrimination threshold between the pre-training and post-training assessments, a learning index was calculated from the motion coherence thresholds before and after training, using the following formula:

$$LearningIndex = \frac{(T_{preTrain} - T_{postTrain})}{(T_{preTrain} + T_{postTrain})}$$

where $T_{preTrain}$ and $T_{postTrain}$ are the thresholds for the pre- and post-training assessments respectively.

For both groups completing the training across five days (Figure 4A), the learning index was significantly greater than zero in the trained visual hemifield, confirming that there was learning in both tasks (one-sample t-test with test value=0, $p<0.0125$ inclusive of Bonferroni correction for multiple comparisons; Motion task, trained hemifield: t=24.271, df=9, p=2.0x10^{-4}; Orientation task, trained hemifield: t=4.179, df=9, p=0.002). For the motion-training task, the learning index was also found to be greater than zero in the untrained visual hemifield (t=32.673, df=9, p=5.3x10^{-5}). For the orientation task, learning index was not greater than zero in the untrained hemifield (t=2.598, df=9, p=0.029).

Across both tasks completed with the one-day protocol (Figure 4B), the learning index was significantly greater than zero in the trained hemifield, but the learning indices for the untrained hemifield were not above zero (one-sample t-test with test value=0, p<0.0125 inclusive of Bonferroni correction for multiple comparisons; Motion task, trained hemifield: t=9.298, df=11, p=5x10^{-6}; Orientation task, trained hemifield: t=5.414, df=11, p=2.1x10^{-4}; Motion task, untrained hemifield: t=0.471, df=11, p=0.647; Orientation task, untrained hemifield: t=0.375, df=11, p=0.715).

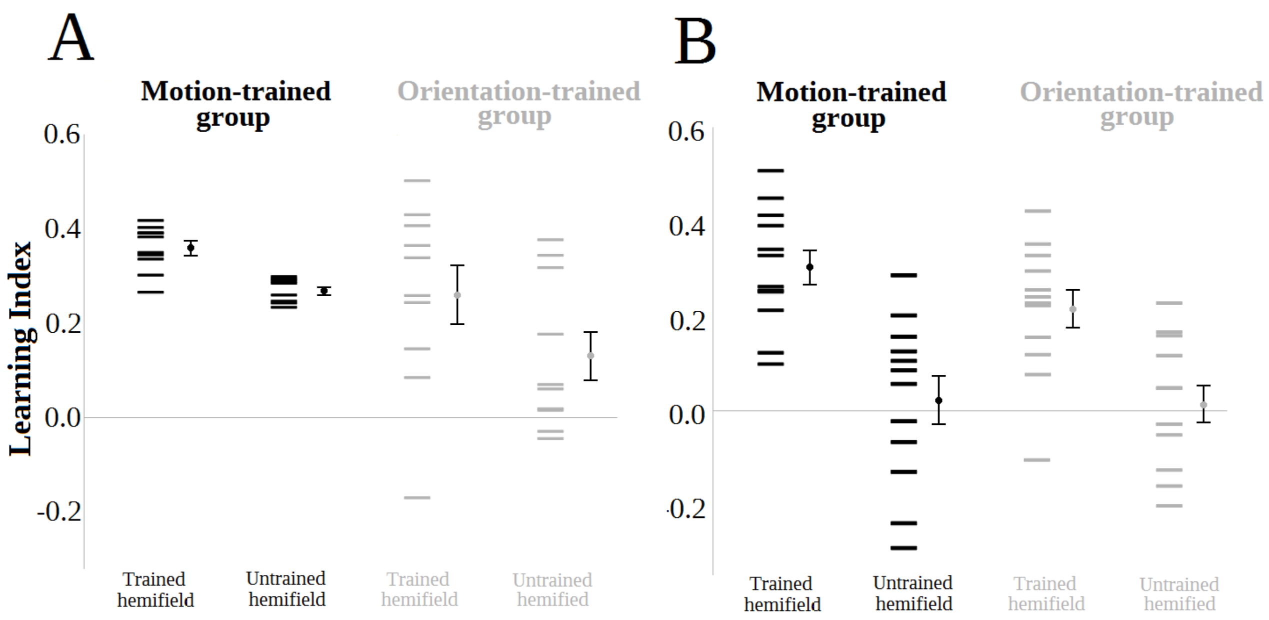

Figure 4: *Learning index for participants across both training protocols and training tasks, (A) Five-day protocol. (B) One-day protocol. Each horizontal bar represents an individual subject. Circles represent the mean of the group and error bars are +/-SEM. Participants trained and tested on the motion task are illustrated in black and participants trained and tested on the orientation task are illustrated in grey.*

A two-way ANOVA with factors 'training protocol' and 'task' was carried out to determine differences in learning index in the trained visual hemifield across all four groups (Protocol: F=0.243, df=1, p=0.243; Task: F=4.848, df=1, p=0.034; Protocol*Task: F=0.017, df=1, p=0.896). The results indicated that the training protocol had no effect on the amount of learning. However, subjects completing the motion task showed more learning than those completing the orientation task.

3.3 Training time course impacts amount of learning in untrained visual hemifield

In order to determine the effect of training a single visual hemifield on performance, a three-way ANOVA was carried out using learning indices for both the trained and untrained visual hemifields, across all four groups (Protocol: F=14.896, df=1, p=2.1x10-4; Task: F=7.534, df=1, p=0.007; Hemifield: F=34.362, df=1, p=9.79x10-8; Protocol*Task: F=1.368, df=1, p=0.246; Protocol*Hemifield: F=4.760, df=1, p=0.032; Task*Hemifield: F=0.090, df=1, p=0.765; Protocol*Task*Hemifield: F=0.939, df=1, p=0.336). This analysis showed there was a significant overall difference in learning dependent on training group, task, and hemifield. There was a significant interaction between training protocol and hemifield, indicating that the effect of hemifield was dependent on the training protocol.

The impact of training protocol on transfer of learning from the trained to the untrained visual hemifield was clarified using t-tests. There was significantly more learning in the trained hemifield compared to the untrained hemifield for the motion task (paired t-test: t=10.891, df=9, p=$2x10^{-6}$), although there was still a large amount of learning in the untrained hemifield. For the orientation-trained group, there was no significant difference between hemifields (paired t-test: t=1.918, df=9, p=0.087). For the one-day training group, there was significantly more learning in the trained hemifield compared to the untrained hemifield for the motion task (paired t-test: t=4.096, df=11, p=0.002) and for the orientation task (paired t-test: t=3.806, df=11, p=0.003).

3.4 Extent of transfer of learning from trained hemifield to untrained hemifield is affected by training time course

In order to quantify the effect of training protocol on transfer of learning effects from the trained to the untrained hemifield, a transfer index was calculated using learning indices for each visual hemifield, across all assessments (Figure 6). Transfer index was calculated using the following formula:

$$TransferIndex = \frac{LI_{untrained}}{LI_{trained}}$$

where $LI_{trained}$ and $LI_{untrained}$ are the learning indices for the trained and untrained assessments respectively.

A two-way ANOVA (factors: one-day or five-day training protocol and motion task or orientation task) demonstrated that training protocol, but not task type, had an effect on the amount of learning (Protocol: F=5.330, df=1, p=0.026; Task: F=0.118, df=1, p=0.733; Protocol*Task: F=1.081, df=1, p=0.305).

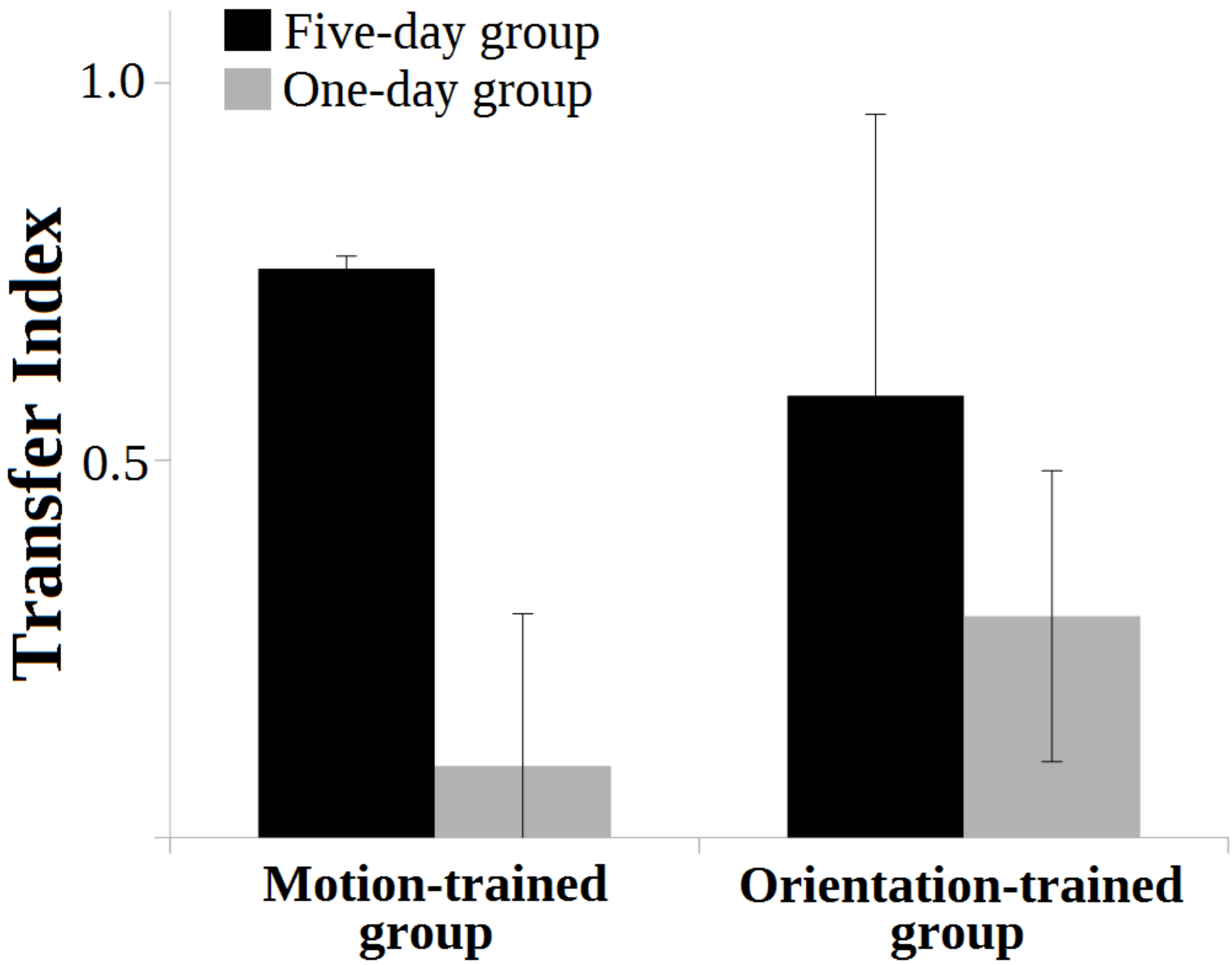

Figure 5: *A comparison of the difference in learning index in the trained hemifield compared to the untrained hemifield (transfer index) for motion-training group (left) and orientation-training group (right). Transfer index was calculated to determine the amount of transfer of learning from the trained to the untrained visual hemifield. There was more transfer of learning for the five-day protocol (black bars), compared to the one-day protocol (grey bars), for both training tasks (two-way ANOVA). This effect was most pronounced for the motion task. The findings indicated transfer of learning from the trained to the untrained hemifield in the five-day training group. Error bars are +/-SEM.*

To enable comparison with previous studies on transfer of learning effects, we also calculated metrics similar to another used in the literature to quantify transfer (Mastropasqua et al. 2015; Wang et al. 2012). The percent improvement was calculated for both the trained and untrained hemispheres, defined as PI = (Thresh_pre − Thres_post)/Thresh_pre. Values (mean ± standard error) for the trained hemisphere in each group were : 5-day motion training = ; 5-day orientation training = ; 1-day motion training = ; 1-day orientation training = . Values for the untrained hemisphere in each group were: 5-day motion training = ; 5-day orientation training = ; 1-day motion training = ; 1-day orientation training = . To quantify the amount of transfer, the transfer index of Wang et al (2012) was computed as the ratio of untrained PI/trained PI. Significant transfer of learning was defined as a TI greater than 0.5. The values (mean ± standard error) in the current study were: 5-day motion training = 0.78 ± 0.01; 5-day orientation training = 0.56 ± 0.33; 1-day motion training = 0.11 ± 0.26 ; 1-day orientation training = 0.25 ± 0.18. These results are consistent with the previous analysis, indicating that for both tasks there was greater transfer of learning in the 5-day compared to the 1-day protocols, with the greatest transfer effect in the 5-day motion training group.

3.5 Training time course affects performance of an untrained task

Half of the participants in this study were trained on an orientation task. These subjects were assessed on the untrained motion task before and after orientation training. Paired t-tests determining learning index for this motion task were performed for both the five-day and one-day training protocols (Figure 7). There was no significant difference in hemifield in the one-day training group (Trained hemifield mean=0.155, untrained hemifield mean=0.145, t=0.155, df=11, p=0.880). For the five-day training group, there was significantly more learning in the trained hemifield compared to the untrained hemifield (Trained hemifield mean=0.167, untrained hemifield mean=0.117, t=5.403, df=9, $p=4.31x10^{-4}$).

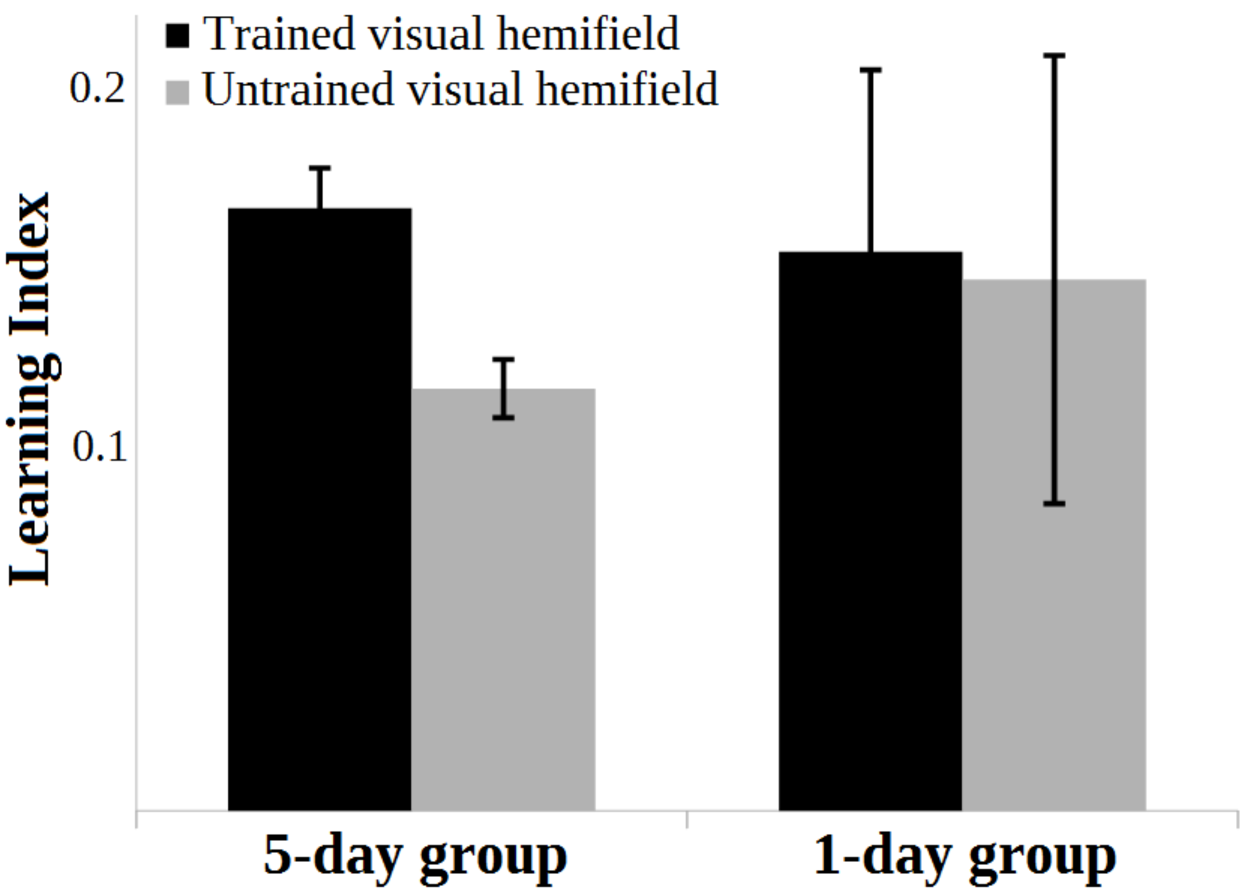

Figure 6: *Learning index for the untrained motion task, for participants in the orientation training group. There was a significant difference in performance according to hemifield in the group trained with the five-day protocol, but no significant difference in hemifields for the participants trained on the one-day protocol. Error bars are +/- SEM.*

SECTION 4 - DISCUSSION

In this study, participants were trained on either a motion direction discrimination task or a sinusoidal grating orientation discrimination task, in a single visual hemifield. All subjects were assessed on their performance in the trained task before and after training, in both the untrained and the trained visual hemifields. Training was completed across five days, or during a single day.

4.1 Learning intensity does not influence overall amount of learning of a motion direction discrimination or orientation discrimination task

Participants who completed the motion training task showed a decrease in the percentage of coherently-moving dots required to discriminate motion direction during the course of training. This improvement was present whether the training was delivered across five days or whether it was condensed into a single day. The same pattern was identified with the participants trained on the orientation task; the percentage of coherently-orientated gratings required to discriminate overall orientation decreased during training.

The time course was shown to have no impact on the overall amount of learning in either task, for the trained region of visual field. Previous studies have found robust perceptual learning effects using five-day protocols. For example, McGovern et al. (2016) trained participants on a visuo-spatial, visuo-temporal, auditory-spatial or auditory-temporal task every day for five consecutive days, with 300 trials per day. A similar level of learning was found for all four tasks compared to the learning identified here, with post-training threshold approximately 55-65% of pre-training thresholds.

Using both one- and five-day paradigms, Hauptmann & Karni (2002) trained subjects on a visual quantification task, where participants were asked to determine if the number of letters in the string was even or odd. The initial exposure to the task (repetition priming) needed to be saturated by sufficient repeated experience for consolidation of learning to occur. In both their one-day and five-day protocols participants showed learning, presumably due to sufficient repetition priming.

Using a face identification task, Hussain et al (2008) investigated the impact of time and sleep between task sessions on learning. Subjects completed two sessions of a face identification task, where sessions were separated by 3 hours without sleep, 12 hours without sleep, 12 hours with sleep or 24 hours with sleep.

Learning was found to be robust regardless of the duration of time or presence of sleep between sessions, although if sleep was present, there was marginally more improvement at the task. These findings are consistent with our findings that learning can occur within a single day, in the absence of sleep.

4.2 Extent of transfer of learning from trained hemifield to untrained hemifield is affected by training period

In the five-day learning protocol, perceptual learning was partially transferred to the untrained visual hemifield. In contrast, there was no transfer of learning effects in the one-day paradigm. Since the tasks and number of trials were otherwise identical, this suggests that the learning transfer depends on consolidation of the learning.

In the one-day group, the post-training assessment was carried out on the same day as the pre-training assessment, and in the five-day group, the post-training assessment was carried out five days after the pre-training assessment. If the differences between the five-day and one-day training groups was driven by time alone, rather than training, it would be predicted that there would be no difference between the trained and untrained visual hemifields. However, there was a clear difference between learning in the hemifields in the one-day group, indicating that time of post-assessment was not a confound in this experiment.

Previous work has shown that perceptual learning is initially fragile until consolidation of learning has occurred (Sasaki et al. 2010). Furthermore, perceptual learning is correlated with the amount of slow wave sleep (SWS) in the first quarter of the sleep period, and the amount of rapid eye movement (REM) sleep in the final quarter of the sleep session (Gais et al., 2000; Stickgold et al., 2000a). Baeck et al. (2014) demonstrated that perceptual learning of complex objects is greater if sleep is present between two sessions of task completion, compared with two sessions without sleep.

Perhaps in contrast to what is expected, one study identified a correlation between the power increase of sigma oscillations measured with EEG and improvement of task performance (Bang et al., 2014). However, the changes in oscillations were specific to the trained region of the early visual cortex, which would not explain transfer to another spatial location. Aberg et al. (2009) trained participants on a visual hyperacuity task where all subjects completed the same total number of trials, but over differing periods of time from 2 days to 10 weeks. Significant improvement occurred in both their 2-day and 2-week training protocols, but there was only transfer of improvement to an untrained stimulus in the 2-week protocol. This is consistent with the results presented here.

4.3 Type of task affected consistency of learning

In the motion task trained over five days there was improvement in task performance in both the trained and untrained visual hemifields, but there was significantly greater learning in the trained hemifield. In the orientation task, there was learning in both visual hemifields, but no difference between the trained and untrained hemifields.

In the one-day protocol, both the motion and the orientation tasks, there was significant task improvement that was specific to the trained visual hemifield. Neither task group showed learning in the untrained visual hemifield. Across both tasks for this training protocol, there were some participants who performed worse at the task in the untrained hemifield following training. This worsening of performance was not identified in any other task, condition or hemifield.

Thus, while there was a similar pattern of learning for the motion and orientation tasks in the one-day protocol, there was a divergence when training was delivered across five days. The difference is likely a result of the more variable learning shown in the orientation task. Indeed, the variability was considerable in both the one-day and five-day protocols. This raises questions about why there should be a difference in the transfer of VPL to the untrained hemisphere in the motion and orientation tasks. Neurophysiological studies have indicated that learning a visual discrimination task leads to changes in the LIP neurons that transform the motion into a saccadic response rather than in motion area MT itself (Law & Gold, 2008). At a more general level, there appears to be some consensus that perceptual learning occurs at different levels within the visual hierarchy, such that low-level changes in V1 neuronal tuning (Karni & Sagi, 1991) may result in some location and task specific learning. In addition, changes in position invariant, higher-level visual areas, are also necessary for transfer to other locations (Dosher et al., 2013).

While any general task related learning is likely to be comparable between the two stimulus types, the specific visual regions optimally activated are likely to differ. Moving dots preferentially activate motion area hMT+, an area that has relatively large receptive fields and some representation of the ipsilateral visual field, particularly in the MST section (Huk et al. 2002). In contrast, orientation tuning is characteristic of V1 (Hubel & Wiesel 1968), and to some extent V2, where receptive fields are small and less likely to compute global form. Thus, it may be that additional visual processing areas are required to perform the orientation task and, consequently, more levels of plasticity are required to make the response position invariant.

Stimulus relevance could also have affected the learning of the two tasks since it is useful to determine the global movement across a visual scene, whereas the oriented sinusoidal gratings did not lead to a global percept of form. Thus, the specific stimulus configuration used in the orientation task may be less likely to activate higher visual areas with larger receptive fields.

SECTION 5 - CONCLUSIONS

The lack of transfer of learning across the visual field seen in a one-day training protocol contrasts with the transfer of learning observed when the same amount of training is spread across a five-day protocol, suggesting the importance of consolidation in learning transfer. This should be taken into account when developing training regimes for rehabilitation.

SECTION 6 – ACKNOWLEDGEMENTS

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SECTION 7 - REFERENCES

Aberg KC, Tartaglia EM, Herzog MH. (2009). Perceptual learning with Chevrons requires a minimal number of trials, transfers to untrained directions, but does not require sleep. Vision Res 49(16):2087-94.

Aberg KC, Tartaglia EM, Herzog MH. (2009). Perceptual learning with Chevrons requires a minimal number of trials, transfers to untrained directions, but does not require sleep. Vision Res 49(16):2087-94.

Ahissar M, Hochstein S. (1993). Attentional control of early perceptual learning. Proc Natl Acad Sci U S A 90(12):5718-22.

Astle AT, McGraw PV, Webb BS. (2011). Recovery of stereo acuity in adults with amblyopia. BMJ Case Reports pii: bcr0720103143.

Baeck A, Rentmeesters N, Holtackers S, Op de Beeck HP. (2014). The effect of sleep in perceptual learning with complex objects. Vision Res 99:180-5.

Bang JW, Khalilzadeh O, Hämäläinen M, Watanabe T, Sasaki Y. (2014). Location specific sleep spindle activity in the early visual areas and perceptual learning. Vision Res 99:162-71.

Chung ST, Legge GE, Cheung SH. (2004). Letter-recognition and reading speed in peripheral vision benefit from perceptual learning. Vision Res 44(7):695-709.

Das A, Tadin D, Huxlin KR. (2014). Beyond blindsight: properties of visual relearning in cortically blind fields. J Neurosci 34(35):11652-64.

Deveau J, Lovcik G, Seitz AR. (2014). Broad-based visual benefits from training with an integrated perceptual-learning video game. Vision Res 99:134-40.

Ding J, Levi DM. (2011). Recovery of stereopsis through perceptual learning in human adults with abnormal binocular vision. Proc Natl Acad Sci U S A 108(37):E733-41.

Dosher BA, Jeter P, Liu J, Lu ZL. (2013). An integrated reweighting theory of perceptual learning. Proc Natl Acad Sci USA 110(33):13678-83.

Fahle M, Morgan M. (1996). No transfer of perceptual learning between similar stimuli in the same retinal position. Curr Biol 6(3), 292–297.

Fahle M, Poggio T. Perceptual Learning (MIT Press, 2002).

Fiorentini A, Berardi N. (1980). Perceptual learning specific for orientation and spatial frequency. Nature 287(5777):43-4.

Gais S, Plihal W, Wagner U, Born J. (2000). Early sleep triggers memory for early visual discrimination skills. Nat Neurosci 3(12):1335-9.

García-Pérez MA. (1998). Forced-choice staircases with fixed step sizes: asymptotic and small-sample properties. Vision Res 38(12):1861-81.

Green CS, Kattner F, Siegel MH, Kersten D, Schrater PR. (2015). Differences in perceptual learning transfer as a function of training task. J Vis 15(10):5.

Harris H, Gliksberg M, Sagi D. (2012). Generalized perceptual learning in the absence of sensory adaptation. Curr Biol 22(19):1813-7.

Hauptmann B, Karni A. (2002). From primed to learn: the saturation of repetition priming and the induction of long-term memory. Brain Res Cogn Brain Res 13(3):313-22.

Henriksson L, Raninen A, Näsänen R, Hyvärinen L, Vanni S. (2007). Training-induced cortical representation of a hemianopic hemifield. J Neurol Neurosurg Psychiatry 78(1):74-81.

Hubel DH, Wiesel TN. (1968). Receptive fields and functional architecture of monkey striate cortex. J Physiol 195(1):215-43.

Huk AC, Dougherty RF, Heeger DJ. (2002). Retinotopy and functional subdivision of human areas MT and MST. J Neurosci 22(16):7195-7205.

Hung SC, Seitz AR. (2014). Prolonged training at threshold promotes robust retinotopic specificity in perceptual learning. J Neurosci 34(25):8423-31.

Hussain Z, Sekuler AB, Bennett PJ. (2008). Robust perceptual learning of faces in the absence of sleep. Vision Res 48(28):2785-92.

Huxlin KR, Martin T, Kelly K, Riley M, Friedman DI, Burgin WS, Hayhoe M. (2009). Perceptual relearning of complex visual motion after V1 damage in humans. J Neurosci 29(13):3981-91.

Jeter PE, Dosher BA, Li SH, Lu ZL. (2010). Specificity of perceptual learning increases with increased training. Vision Research 50:1928-1940.

Karni A, Sagi D. (1991). Where practice makes perfect in texture discrimination: evidence for primary visual cortex plasticity. Proc Natl Acad Sci USA 88(11):4966-70.

Law CT, Gold JI. (2008). Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. Nat Neurosci11(4):505-13.

Lev M, Ludwig K, Gilaie-Dotan S, Voss S, Sterzer P, Hesselmann G, Polat U. (2014). Training improves visual processing speed and generalizes to untrained functions. Sci Rep 4:7251.

Liu Z. (1999). Perceptual learning in motion discrimination that generalizes across motion directions. Proc Natl Acad Sci U S A 96(24):14085-7.

Mastropasqua T, Galliussi J, Pascucci D, Turatto M. (2015). Location transfer of perceptual learning: Passive stimulation and double training. Vision Res 108:93-102.

Mastropasqua T, Turatto M. (2015). Reference-frame specificity of perceptual learning: the effect of practice. Vision Res 106:1-6.

McGovern DP, Astle AT, Clavin SL, Newell FN. (2016). Task-specific transfer of perceptual learning across sensory modalities. Curr Biol 26(1):R20-1.

McGovern DP, Webb BS, Peirce JW. (2012). Transfer of perceptual learning between different visual tasks. J Vis 12(11):4.

Poggio T, Fahle M, Edelman S. (1992) Fast perceptual learning in visual hyperacuity. Science 256(5059):1018-21.

Polat U, Ma-Naim T, Belkin M, Sagi D. (2004). Improving vision in adult amblyopia by perceptual learning. Proc Natl Acad Sci U S A 101(17):6692-7.

Sahraie A, Macleod MJ, Trevethan CT, Robson SE, Olson JA, Callaghan P, Yip B. (2010). Improved detection following Neuro-Eye Therapy in patients with post-geniculate brain damage. Exp Brain Res 206(1):25-34.

Sahraie A, Trevethan CT, MacLeod MJ, Murray AD, Olson JA, Weiskrantz L. (2006). Increased sensitivity after repeated stimulation of residual spatial channels in blindsight. Proc Natl Acad Sci U S A 103(40):14971-6.

Sasaki Y, Nanez JE, Watanabe T. (2010). Advances in visual perceptual learning and plasticity. Nat Rev Neurosci 11(1):53-60.

Stickgold R, Whidbee D, Schirmer B, Patel V, Hobson JA. (2000). Visual discrimination task improvement: A multi-step process occurring during sleep. J Cogn Neurosci 12(2):246-54.

Wang X, Zhou Y, Liu Z. (2013). Transfer in motion perceptual learning depends on the difficulty of the training task. J Vis 13(7):5.

Xi J, Jia WL, Feng LX, Lu ZL, Huang CB. (2014). Perceptual learning improves stereoacuity in amblyopia. Invest Ophthalmol Vis Sci 55(4):2384-91.

Xiao LQ, Zhang JY, Wang R, Klein SA, Levi DM, Yu C. (2008). Complete transfer of perceptual learning across retinal locations enabled by double training. Curr Biol 18(24):1922-6.

Zhang JY, Yang YX. (2014). Perceptual learning of motion direction discrimination transfers to an opposite direction with TPE training. Vision Res 99:93-8.

Zhang JY, Zhang GL, Xiao LQ, Klein SA, Levi DM, Yu C. (2010). Rule-based learning explains visual perceptual learning and its specificity and transfer. J Neurosci 30(37):12323-8.