Decoupling location specificity from perceptual learning of orientation discrimination

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ABSTRACT

Perceptual learning of orientation discrimination is reported to be precisely specific to the trained retinal location. This specificity is often taken as evidence for localizing the site of orientation learning to retinotopic cortical areas V1/V2. However, the extant physiological evidence for training improved orientation turning in V1/V2 neurons is controversial and weak. Here we demonstrate substantial transfer of orientation learning across retinal locations, either from the fovea to the periphery or amongst peripheral locations. Most importantly, we found that a brief pretest at a peripheral location before foveal training enabled complete transfer of learning, so that additional practice at that peripheral location resulted in no further improvement. These results indicate that location specificity in orientation learning depends on the particular training procedures, and is not necessarily a genuine property of orientation learning. We suggest that non-retinotopic high brain areas may be responsible for orientation learning, consistent with the extant neurophysiological data.

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1. Introduction

Among various visual perceptual learning tasks, the neuronal mechanisms of orientation learning have been most intensively studied (Ghose, Yang, & Maunsell, 2002; Raiguel, Vogels, Mysore, & Orban, 2006; Schoups, Vogels, Qian, & Orban, 2001; Yang & Maunsell, 2004). These neurophysiological studies are in large measure inspired by psychophysical evidence that orientation discrimination learning is precisely specific to the trained retinal location (Schoups, Vogels, & Orban, 1995; Shiu & Pashler, 1992). The Schoups et al. (1995) study has been particularly influential, since they showed that orientation learning did not transfer to an untrained retinal location merely 2.5° away from the trained location at 5° retinal eccentricity in the visual periphery. Equally precise location specificity was also reported in learning of a spatial localization (bisection) task which was also specific to the stimulus orientation (Crist, Kapadia, Westheimer, & Gilbert, 1997). Because cortical areas V1/V2 are highly retinotopic, and their small receptive fields are most capable of performing fine orientation discrimination, it is natural that neurophysiological studies first focused on neurons in the early visual cortex, seeking evidence for training induced sharpening of receptive field orientation tuning.
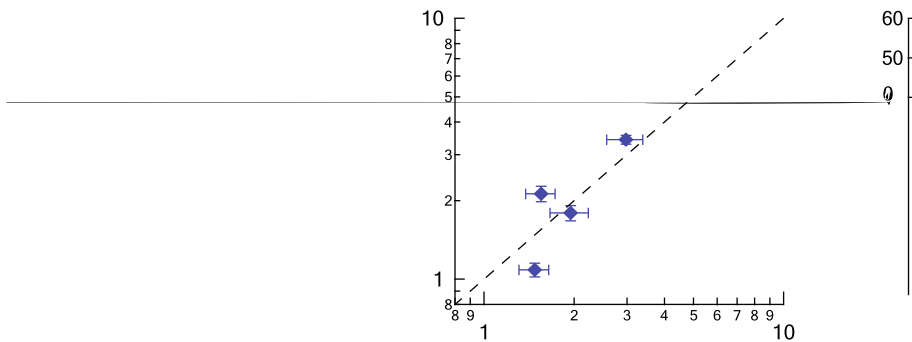
However, to date, the neurophysiological evidence linking orientation learning to V1/V2 neuron orientation tuning sharpening is controversial and weak at best. Schoups et al. (2001), inspired by their own psychophysical findings, found a correlation between improved monkey orientation discrimination and steeper V1 neuron orientation tuning functions; however, Ghose et al. (2002) found no orientation tuning changes in either V1 or V2 neurons. More significant orientation tuning changes have been reported in V4 neurons by the same two research groups (Raiguel et al., 2006; Yang & Maunsell, 2004). Even so, these changes in V4 neurons were still too small to account for behavioral orientation learning (Raiguel et al., 2006).

While neurophysiologists debate the exact brain site of orientation learning, here we demonstrate that the highly cited psychophysical evidence for precise location specificity in orientation learning deserves a second look. Specifically, we show that perceptual learning of orientation discrimination actually transfers substantially across retinal locations, either from the fovea to the periphery, or among peripheral locations. Moreover, we found that location specificity in orientation learning could be eliminated with appropriate training procedures, which suggests that location specificity is not necessarily a genuine property of orientation learning. Our results shed new light on the current neurophysiological debate regarding the brain sites of orientation learning and help illuminate the mechanisms of perceptual learning in general.

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2. Methods

2.1.

Thirty six observers (undergraduate students in their early 20s at Beijing Normal University) with normal or corrected-to-normal

3. Results

3.1. *Re-examining the results of Schoups et al. (1995)*

The Schoups et al. (1995) study provided the
influential psychophysical evidence for precis~
in orientation learning. In this study, obser~
entation identification at the fovea, w¹
thresholds by approximately 72% or
1.5°, their Fig. 3), before they con~
peripheral locations at 5° eccent~
tice at a peripheral location at ʹ
orientation performance sig~
did not transfer to an unt~
from the trained locatic
ups et al. did not t~
would transfer to ʹ
line measurer~
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the test and the reference was sufficiently large, so that the observers could always make a correct discrimination. The steps of the staircase were separated by 0.05 log units above and below the reference. A classical 3-down-1-up staircase rule was used, which resulted in a 79.4% convergence level. The geometric mean of the experimental reversals was taken as the threshold for each staircase run. An observer typically completed 14–16 staircases in a 2-h training session.
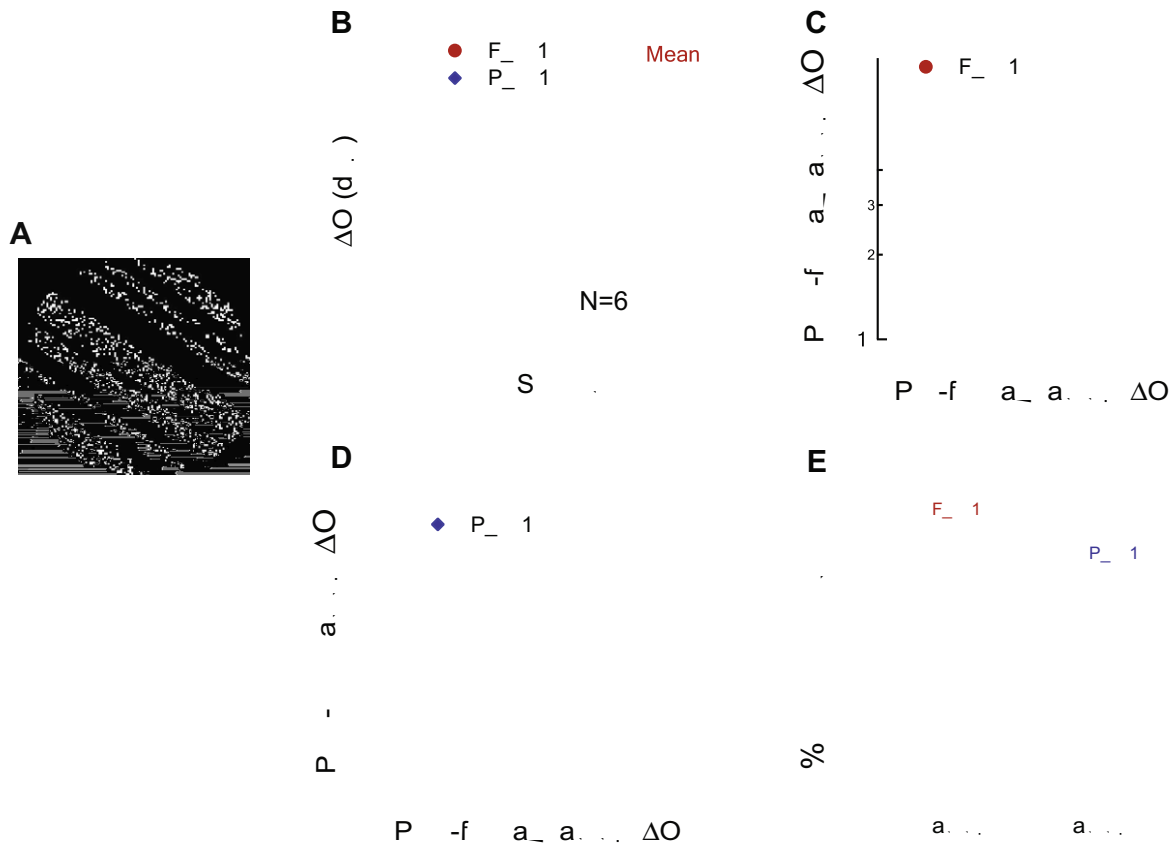
2.3.

We used an Eyelink II eye tracker to assess the impact of eye movements when peripheral orientation discrimination was performed. Five new observers performed a 2AFC orientation discrimination task for 3–5 sessions. During the first interval, the eye positions on the average were within 0.5° and 1° from the fixation in 90.3% and 98.9% of the trials, respectively, similar to those in a fixation-only control condition (p = 0.29 and 0.37, respectively). The eye positions during the second interval were within 0.5° and 1° from the fixation in 78.3% and 96.1% of the trials, respec~ tively, suggesting some involuntary eye drifts (mainl~ −0.5°). Importantly, practice did not reduce the ~ eye drifts to improve visual discrimination. T~ tios of these off-fixation percentages ~ 0.954 (<0.5°) and 0.995 (<1°), s~ after training. Therefore ¹ not significantly a~

~ll
~ study.
~ ioveal orientation learn-
~ the expectation that this would at least

A

B

- ● F_ 1
- ◆ P_ 1

Mean

ΔO (d .)

N=6

S .

C

ΔO

a_ a . . .

P -f

● F_ 1

3

2

1

P -f a_ a . . . ΔO

D

ΔO

a . . .

P -

P

◆ P_ 1

P -f a_ a . . . ΔO

E

F_ 1

P_ 1

%

a . . . a . . .

tell us how much general learning foveal training would generate. Eight observers practiced foveal orientation discrimination of a Gabor stimulus at either 36° or 126° (F_ori1) in 2AFC trials for seven sessions, and all showed improved orientation discrimination (Mean percent improvement (MPI) = 1-post-/pre-training threshold = 39.6 ± 4.4%, p < 0.001, one tail paired -test; mean session-by-session thresholds shown in the left half of Fig. 1B, and individual pre- and post-training thresholds contrasted in Fig. 1C). The error bar corresponds to one standard error of the mean. Before and after foveal training, their orientation thresholds for the same oriented Gabor (P_ori1) and an orthogonal Gabor (P_ori2), both centered in either the lower- or upper-left visual quadrant at 5° retinal eccentricity, were also measured (each averaged over six staircases). The results showed that peripheral orientation thresholds were also significantly reduced for both P_ori1 and P_ori2 (MPI = 29.2 ± 5.6%, p < 0.001, and MPI = 29.6 ± 6.5%, p = 0.002, respectively; Fig. 1B and C). Peripheral performance on the average improved about 75% as much as did foveal performance, but the differences among peripheral and foveal improvements were not statistically significant (p = 0.192, repeated measures ANOVA). Although we expected some improvement of peripheral orientation discrimination because of general learning, the very substantial transfer far exceeded our expectation.

With statistically similarly improved performance at the trained fovea and untrained peripheral locations, we wondered whether the foveal training had taught the periphery all there was to learn. That is, had foveal orientation training already opti-

mized peripheral orientation discrimination, so that additional training at the peripheral location would not further improve the performance? To examine this possibility, the same eight observers performed peripheral orientation training for the fovea-trained orientation (P-ori1) for five to six sessions at the same peripheral location where the transfer was tested. Following peripheral training, orientation discrimination only improved significantly in two observers but not in other six observers (overall MPI = 9.8 ± 7.5%, p = 0.12; mean session-by-session thresholds shown in the right half of Fig. 1B, and individual pre- and post-training thresholds contrasted in Fig. 1D), suggesting that foveal orientation training indeed had optimized peripheral performance in most observers. These data are seemingly inconsistent with Schoups et al. (1995) who reported nearly 50% improvement of peripheral orientation discrimination as a result of additional peripheral training following foveal training (their Fig. 3). Our further experiments will explain why there is this discrepancy.

We first suspected that the discrepancies between the results of ours and Schoups et al.'s might result from stimulus and training procedure differences. Schoups et al.'s test stimuli were large (diameter = 2.5° vs. our σ = 0.29° Gabors), and their training lasted 15–18 sessions, more than two times longer than our 6–7 sessions. So we replicated Schoups et al.'s experiment using the identical stimuli (Fig. 2A) and task (single interval orientation discrimination at either 45° or 135° oblique orientation), and our new training lasted 13 sessions. To measure the fovea-to-periphery transfer of learning, we again pretested orientation thresholds in the

A

B

$P - a \ldots \Delta O$

10
9
8
7
6
5

4

3

2

N=1

1

1   2   3   4 5 6 7

$P - a \ldots \Delta O$

D

$P - a \ldots \Delta O$

E
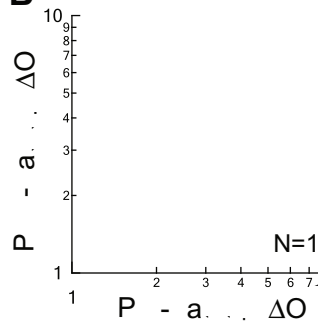
$P - a \ldots \Delta O$

periphery (5° retinal eccentricity on the horizontal meridian, left visual hemifield) before foveal training. However, the new training procedure with new stimuli produced similar data to those with the Gabor stimuli (Fig. 2B–E). First foveal orientation thresholds floored after 5–6 sessions of training, suggesting that significantly more sessions of training was redundant. Second, peripheral orientation discrimination was about equally improved (peripheral MPI = 47.9 ± 2.3%, p < 0.001 vs. foveal MPI = 50.0 ± 4.2%, p < 0.001, approximately a factor of 2 decrease in threshold), similar to the results with Gabor stimuli. Third and most importantly, like our previous data, successive peripheral training did not improve orientation discrimination further (MPI = −4.4 ± 13.8%, p = 0.34), suggesting again optimized peripheral orientation discrimination after foveal training.

So what made the results between the Schoups et al. and the present study so different after the differences of stimuli and training durations were excluded? The only remaining difference between two studies was that before foveal training, we briefly pretested peripheral thresholds (six staircases, or approximately 200 trials) as a baseline to gauge the fovea-to-periphery transfer of learning. Did this brief pretest enable the optimization of peripheral orientation discrimination? To test this we repeated the above experiment without the pretest in six new observers, and this time the results replicate those of Schoups et al. (Fig. 3B). That is, after foveal training (F_ori1) which reduced orientation thresholds in all observers (MPI = 46.7 ± 4.6%, p < 0.001; Fig. 3C), additional peripheral training at 5° retinal eccentricity on the horizontal meridian of the left visual hemifield continued to improve orientation performance at this peripheral location in five out of six observers (MPI = 33.3 ± 10.9%, p = 0.014, (Fig. 3D). The sixth observer had lower peripheral threshold after foveal

training, wh   rther peripheral training
(the far left   l line, Fig. 3D). So this ob-
server's data   he previous experiment with
pretesting (

In summ   ents (Figs. 1–3) allowed us to
decouple lo   orientation learning by showing
that locatio   ps et al.'s classical study can be
abolished w   n Section 4 we will show that this
brief pretes   mplete transfer of foveal learning
to accompli   n of peripheral performance.

3.2.

A more   straightforward way to study location
specificity i   ansfer of learning from a trained to an un-
trained peri   on (without initial foveal training). Using
this training   Shiu and Pashler (1992) in another widely
cited study   significant transfer of orientation learning
from a train   t of the visual field to other untrained visual
quadrants.   Shiu and Pashler's results might have been
tainted by   l cues from uncovered rectangular monitor
edges (Sch   l., 1995). Their line stimulus was presented
near the co   14-in. rectangular monitor screen. The edges
of the moni   d have provided cues for orientation judgment.
Moreover, t   es were different when the line was presented
in a differe   itor corner. For example, the vertical monitor
edge was cl   the other line end when the line was presented
in a diagona   rant. Taking into account this contextual cueing
issue in Sh   d Pashler (1992) and the substantial fovea-to-
periphery t   r of orientation learning demonstrated in Figs. 1

and 2, we decided to reinvestigate the periphery-to-periphery transfer of orientation learning.

Eighteen observers practiced 2AFC orientation discrimination for a Gabor stimulus (36° or 126°) centered in either the upper- or lower-left visual quadrant at 5° retinal eccentricity (ori1_loc1) for six sessions. For testing transfer, different subgroups of observers were tested at different locations and orientations. Fifteen observers were tested for transfer of learning to the same orientation at a new location symmetrically across the horizontal meridian of the visual field (ori1_loc2, Fig. 4B), nine were tested for transfer to an orthogonal orientation at the same trained location (ori2_loc1, Fig. 4C), and eleven were tested for transfer to an orthogonal orientation at the new location (ori2_loc2, Fig. 4D), and four were tested for transfer to the other three untrained quadrants at the same orientation (Fig. 4E) for the purpose of re-examining the results of Shiu and Pashler (1992) while having the monitor edge cues removed with a circular opening of the monitor screen (see Section 2). Orientation thresholds were pretested for the transfer location/orientation in all observers except the last four (Fig. 4E) for whom isoeccentric pretest threshold equality was assumed.

Most observers showed improved orientation discrimination after training at ori1_loc1 which on the average asymptoted after four training sessions (Fig. 4A, MPI = 32.7 ± 4.3% over all 18 observers, p < 0.001). Moreover, orientation discrimination for the untrained ori1_loc2 was also improved significantly after training (green dots; MPI = 26.6 ± 4.5%, p < 0.001; Fig. 3B), suggesting substantial transfer of orientation learning at one peripheral location to an untrained peripheral location. Moreover, orientation discrimination for the untrained orthogonal orientation at the same trained location (ori2_loc1) also improved significantly (blue dots; MPI = 22.1 ± 5.4%, p = 0.002; Fig. 4C), suggesting significant learning transfer across orientations in the periphery. However, performance for the untrained orthogonal orientation at the untrained location (ori2_loc2) was not significantly changed (purple dots; MPI = 6.31 ± 5.1%, p = 0.12; Fig. 4D) in 11 participating observers.

In addition, for the four observers whose transfer of learning was tested at the other three untrained quadrants, post-training orientation thresholds at the trained and untrained quadrants were similarly improved (Fig. 4). The mean MPI = 41.0 ± 5.1% (p = 0.002) at the trained quadrant, and MPI = 38.0 ± 3.7% (p = 0.001), 36.8 ± 6.2% (p = 0.005), and 36.1 ± 7.6% (p = 0.009) at the untrained quadrants across the vertical meridian (VM), across the horizontal meridian (HM), and across the fixation (diagonal), respectively, which were not significantly different among each other (p = 0.69, repeated measures ANOVA). For these observers, there was no pretest of orientation thresholds at untrained quadrants, similar to Shiu and Pashler (1992), so post-training thresholds were compared to the pre-training thresholds at the trained quadrant to quantify learning transfer. These results show complete transfer of orientation learning upon the removal of contextual cues, which argues strongly against location specificity and suggests that the previous concerns about Shiu and Pashler's study (Schoups et al., 1995) were warranted.

4. Discussion

In this study we discovered that a brief pretest of orientation thresholds in the periphery (six staircases, or approximately 200 trials, originally planned as a baseline measure to gauge the transfer of learning from foveal orientation training), surprisingly overrode Schoups et al.'s classical results for location specificity in orientation learning and helped optimize peripheral orientation discrimination without additional multi-session training (Figs. 1B and 2B).

Could this brief training, which might likely generate some general and transferable fast learning at the beginning of sensory training (Censor & Sagi, 2009; Jeter, Dosher, Petrov, & Lu, 2009; Karni & Sagi, 1993), alone account for the substantial peripheral improvement after foveal training? From Fig. 4A which shows session-by-session data of Gabor orientation training at the same peripheral location as in Fig. 1B, we were able to estimate the difference between orientation thresholds of the pretest (the first data point from left in Fig. 4A, averaged over six staircases) and of the first six staircases in the next session (the second data point from the left in Fig. 4A was the mean of more than six staircases. We only averaged the thresholds of the first six, equal to the number of staircases in post-training testing in Fig. 1B), which was 15.4 ± 3.9%. Thus fast learning due to the pretest can account for only half the peripheral orientation improvement (MPI = 29.2 ± 5.6%) after foveal training in Fig. 1B (P_ori1). The latter is actually comparable to the overall improvement after six sessions (approximately 3000 trials) of intensive training at the same peripheral location (MPI = 32.7 ± 4.3%) in Fig. 4A. More importantly, the null effect of further peripheral orientation training in most observers (Figs. 1B and 2B) confirmed that the remaining slower and "local" part of orientation learning, which is the interest of most perceptual learning studies, also transferred completely to the peripheral location. So the "local part" of learning is not really local, and with the help of a brief pretesting, the fovea can teach the periphery all there is to learn!

It is unclear how the peripheral pretest enables complete transfer of slow foveal learning. One possibility is that the pretest serves as location training to improve peripheral spatial attention to enable learning transfer, as evidenced in contrast and Vernier learning tasks in our recent study (Xiao et al., 2008). However, Fig. 4E which shows complete transfer of orientation learning from a trained quadrant to untrained and un-pretested quadrants indicates that such location training might be unnecessary for orientation learning. On the other hand, in contrast and Vernier learning tasks, six staircases of pretesting are too few to enable learning transfer (Xiao et al., 2008). Because data in Fig. 4E and in Xiao et al. (2008) are related to periphery-to-periphery transfer, we suspect that alternatively the pretest effect may be a result of interactions between foveal and peripheral processing. That is, peripheral presentations of the stimuli, even in a few staircases, could prime the peripheral side of the network, so that foveal learning can transfer over. Because of the retinotopic nature of the early visual cortex, this network should be high level, or at least have strong high-level components. In some way this priming process is like the Eureka effect in learning (Ahissar & Hochstein, 2004) for its requiring only a limited number of trials to take effect. We are currently studying this possible interaction between foveal and peripheral learning. However, regardless of the mechanisms, the nearly complete transfer of foveal orientation learning to a peripheral location in most observers suggests that location specificity is only specific to certain training procedures, and therefore it can be decoupled from orientation learning.

4.1. . . . . d . . . .

The decoupling of location specificity from orientation learning is in line with our recent findings that contrast and Vernier learning, which normally shows location specificity when trained at one retinal location and tested at a new retinal location, can actually completely transfer to the new location that has been trained with a totally different task (Xiao et al., 2008). These results together support the central-site hypothesis of perceptual learning by Mollon and Danilova (1996). Central orientation learning is also supported by our data that the substantial transfer of orientation learning is mainly orientation non-specific (Figs. 1 and 4), consis-

tent with neurons in non-visual high brain areas not being orientation selective (e.g., Mohler, Goldberg, & Wurtz, 1973).

Perceptual learning at central brain sites would easily explain why receptive field tuning changes in visual areas up to V4 can only account for a very small part of behavioral learning data ("at least an order of magnitude smaller than the behavioral changes", Raiguel et al., 2006). We suggest that perceptual learning may reflect training induced improvements in decision making which is modeled by Dosher and Lu (1999), but this process has to occur in non-retinotopic high brain areas, which coincides with recent neurophysiological evidence that perceptual learning is correlated to neuronal changes not in sensory cortical areas, but in higher areas associated with decision making (Law & Gold, 2008). Further experimental and computational evidence is necessary to spell out the possible central mechanisms underlying perceptual learning.

Acknowledgments

References

Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. . .d . . . . , 8(10), 457–464.

Censor, N., & Sagi, D. (2009). Global resistance to local perceptual adaptation in texture discrimination. . . . . , 49(21), 2550–2556.

Crist, R. E., Kapadia, M. K., Westheimer, G., & Gilbert, C. D. (1997). Perceptual learning of spatial localization: Specificity for orientation, position, and context. . . . . , 78(6), 2889–2894.

Dosher, B. A., & Lu, Z. L. (1999). Mechanisms of perceptual learning. . . . . , 39(19), 3197–3221.

Ghose, G. M., Yang, T., & Maunsell, J. H. (2002). Physiological correlates of perceptual learning in monkey V1 and V2. . . . . , 87(4), 1867–1888.

Jeter, P. E., Dosher, B. A., Petrov, A., & Lu, Z. L. (2009). Task precision determines specificity of perceptual learning. . . . . , 9(3), 1–13.

Karni, A., & Sagi, D. (1993). The time course of learning a visual skill. . . . . , 365(6443), 250–252.

Law, C. T., & Gold, J. I. (2008). Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. . . . . , 11(4), 505–513.

Mohler, C. W., Goldberg, M. E., & Wurtz, R. H. (1973). Visual receptive fields of frontal eye field neurons. . . . . , 61, 385–389.

Mollon, J. D., & Danilova, M. V. (1996). Three remarks on perceptual learning. . . . . , 10(1), 51–58.

Raiguel, S., Vogels, R., Mysore, S. G., & Orban, G. A. (2006). Learning to see the difference specifically alters the most informative V4 neurons. . . . . , 26(24), 6589–6602.

Schoups, A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: Retinotopy, orientation specificity and monocularity. . . . . , 483(Pt 3), 797–810.

Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. . . . . , 412(6846), 549–553.

Shiu, L. P., & Pashler, H. (1992). Improvement in line orientation discrimination is retinally local but dependent on cognitive set. . . . . .d . . . . , 52(5), 582–588.

Xiao, L. Q., Zhang, J. Y., Wang, R., Klein, S. A., Levi, D. M., & Yu, C. (2008). Complete transfer of perceptual learning across retinal locations enabled by double training. . . . . , 18(24), 1922–1926.

Yang, T., & Maunsell, J. H. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. . . . . , 24(7), 1617–1626.