

Perceptual learning of motion direction discrimination transfers to an opposite direction with TPE training



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ABSTRACT

Motion direction learning is known to be specific to the trained direction. However, in this study we used our recently developed TPE (training-plus-exposure) method to demonstrate that motion direction learning can transfer to an opposite direction. Specifically, we first replicated the strict direction specificity of motion direction learning with a group of moving dots. However, when the participants were exposed to the opposite direction in an irrelevant dot number discrimination task, either simultaneously with motion direction training or at a later time, but not in a reversed order, motion direction learning transferred to the opposite direction significantly and sometimes completely. These results suggest that motion direction learning may be a high-level process in which the brain learns the potentially transferable rules of reweighting the motion direction inputs. However, we speculate that high-level learning may not functionally connect to sensory neurons that are tuned to other directions but are not stimulated during training, which leads to direction specificity. It is the stimulus exposure in TPE training that connects high-level learning to the exposed opposite direction to enable learning transfer.

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1. Introduction

Perceptual learning of motion direction discrimination, like learning of many other basic visual features such as contrast, orientation, spatial frequency, and Vernier discrimination (Fiorentini & Berardi, 1980; Schoups, Vogels, & Orban, 1995; Crist et al., 1997; Fahle, 1997; Yu, Klein, & Levi, 2004), has been reported to be specific to the trained retinal location and feature at least under near-threshold conditions (Ball & Sekuler, 1982, 1987; Liu, 1999; Liu & Weinshall, 2000; Shibata et al., 2012). For example, Ball and Sekuler (1982, 1987) reported that training improves the direction discrimination of moving dots, but the learning cannot transfer to an untrained opposite direction, or to an untrained retinal location/hemifield. These and similar specificities in other visual learning tasks have led to the assumptions that visual perceptual learning may occur in early visual areas that are retinotopic and selective to basic visual features (Ball & Sekuler, 1982, 1987; Karni & Sagi, 1991; Schoups, Vogels, & Orban, 1995; Crist et al., 1997; Bejjanki et al., 2011).

Alternatively, as Mollon and Danilova (1996) pointed out, learning specificities do not necessarily imply plasticity in early visual areas. Perceptual learning could be central and high level, but specific to what the brain learns. Indeed, Liu and Weinshall (2000) dis-

covered that although motion direction learning is specific to the trained direction, ensued learning of a new direction becomes faster, suggesting that motion direction learning involves some high-level processes. Moreover, based on their findings that monkey motion direction learning is associated with response changes in decision-related LIP neurons, not the middle temporal area neurons that are known to decode motion signals (Law & Gold, 2008), Law and Gold (2009) proposed a reweighting model in which the decision areas learn to readout the motion inputs from a specific population of MT neurons that respond to the motion stimuli. Because MT is retinotopic and MT neurons are direction selective, this model is able to account for the direction and location specificities in motion direction learning.

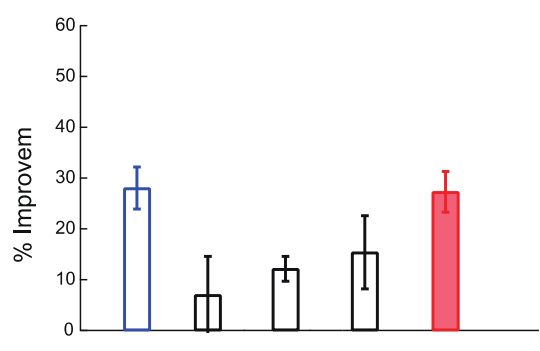
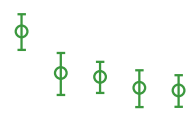
However, even the very concept of perceptual learning being location and feature specific is being challenged. In recent studies we developed new training methods that enable location and orientation specific perceptual learning, such as contrast, orientation, Vernier, feature detection, and texture discrimination learning to transfer to untrained retinal locations (

discrimination task, either simultaneously with training (in alternating staircases) or at a later time, learning transferred com-

phase and once before the exposure phase, which could confound the estimation of the amount of learning transfer. To reduce this confounding effect, six new participants completed a simultaneous TPE procedure in which they practiced $\Delta\text{Dir_dir1}$ and $\Delta\text{Num_dir2}$ simultaneously in alternating blocks of trials (staircases; 10 staircases for each task per session). All other experimental conditions were identical to those in Experiment I. This simultaneous procedure significantly improved motion direction discrimination at the trained direction ($\Delta\text{Dir_dir1}$; $\text{MPI} = 28.0 \pm 4.1\%$, $t = 6.76$, $df = 5$, $p < 0.001$; Fig. 2a, b), as well as at an untrained opposite direction in all participants ($\Delta\text{Dir_dir2}$; $\text{MPI} = 26.9 \pm 3.9\%$, $t = 6.88$, $df = 5$, $p < 0.001$) by a similar amount ($t = 0.16$, $df = 5$, $p = 0.44$). The transfer index TI was 1.2, indicating complete transfer of motion direction learning. Together the successive and simultaneous TPE training results demonstrate that motion direction learning could transfer to an opposite direction quite significantly and sometimes completely.

In addition, we tested the learning transfer to other neither trained nor exposed directions that were 45° , 90° , and 135° from the trained direction, respectively (Fig. 2a and b). Learning trans-

ferred much less to these directions ($\text{MPI} = 11.5 \pm 5.2\%$, $t = 2.19$, $df = 5$, $p = 0.040$, $\text{TI} = 0.47$, pooled over three directions). Previously we found that after TPE training orientation learning also trans-



TPE-enabled learning transfer. That is, whether the mere exposure of the opposite direction through dot-number discrimination train-

ing was sufficient to improve motion direction discrimination at the same direction? Fig. 3 shows that the dot-number discrimina-(a)(b)(c)Fig

tion training ($\Delta\text{Num_dir2}$; $\text{MPI} = 27.3 \pm 5.5\%$, $t = 4.94$, $df = 4$, $p = 0.004$) had no significant impact on the motion direction thresholds ($\Delta\text{Dir_dir2}$; $\text{MPI} = 6.7 \pm 5.6\%$, $t = 1.20$, $df = 4$, $p = 0.15$), indicating that the TPE enabled motion direction learning transfer (Figs. 1 and 2) did not result from the mere exposure of the opposite direction, but from the entire TPE procedure.

The second purpose of this experiment was to replicate an interesting finding with TPE-enabled orientation learning transfer in motion learning tasks. That is, once the TPE order was reversed, the learning transfer to an orthogonal orientation disappeared (Zhang et al., 2010). Fig. 3 shows that in the second phase of the reversed-order TPE training, although training improved motion direction discrimination at a trained direction ($\Delta\text{Dir_dir1}$; $\text{MPI} = 29.3 \pm 4.8\%$, $t = 6.04$, $df = 4$, $p = 0.002$), learning failed to transfer to an opposite direction ($\Delta\text{Dir_dir2}$; $\text{MPI} = 3.5 \pm 11.7\%$, $t = 0.30$, $df = 4$, $p = 0.39$). Therefore the transfer of motion direction learning also disappeared with a reversed-order TPE procedure. The implications of this reversed-order TPE training in understanding the mechanisms underlying motion direction and orientation learning will be discussed later.

4. Discussion

Our results demonstrate that, like orientation learning that can be rendered completely transferrable to an orthogonal orientation with TPE training (Zhang et al., 2010), motion direction learning can become significantly and sometimes completely transferable to an opposite direction with similar TPE procedures. These transfer results suggest that motion direction learning is a high-level learning process.

The neurophysiological study by Law and Gold (2008) is most relevant to our results. They discovered that motion direction learning in monkeys is a high-level process, in that the performance improvements are not correlated to the response changes of direction-selective MT neurons, but to those of LIP neurons that are related to decision making. In a later reweighting model (Law & Gold, 2009), they suggested that motion direction learning results from improved readout of the initial noisy responses of MT neurons responding to the motion stimulus by a high-level decision unit. Our results could improve this high-level reweighting model in a significant way: After learning the decision unit apparently can deal with motion inputs from MT neurons representing other directions with similar and sometimes equal precision. This is a case-based general learning process in which the decision unit learns the general rules of reweighting motion inputs regardless of their specific directions.

As we pointed out earlier, existing psychophysical studies on motion direction learning also hint at the involvement of high-level processes. Liu (1999) reported that the direction specificity in motion direction learning depends on the task difficulty. Learning is transferrable to other untrained directions if the task is easy and suprathreshold. Moreover, even for hard near-threshold learning that shows strong direction specificity, later learning becomes faster when the participants continue to practice at a new direction (Liu & Weinsall, 2000). These results indicate that high-level processes play important roles in motion direction learning. Our results go one step further by showing that even the direction specificity under the near-threshold or “hard” learning conditions can be completely abolished through TPE training. This finding indicates that motion direction learning is mainly a high-level process, since an even partially low-level learning process would not explain complete learning transfer.

Why is motion direction learning specific to the trained direction in the first place with conventional training, and why does it transfer much less to other unexposed directions after TPE train-

ing? The same questions apply to orientation learning with similar results (Zhang et al., 2010). The transfer results indicate that the brain learns the rules of performing a specific task such as motion direction or orientation discrimination that are potentially transferrable. However, these rules may not apply to other untrained directions or orientations because high-level learning may not be able to functionally connect to neurons that are tuned to these directions or orientations but are not stimulated during training. It is the exposure to a new direction or orientation in TPE training that stimulates relevant direction or orientation neurons to promote the connections from high-level learning to allow learning transfer. This account is consistent with the reversed-order TPE training results with the transfer of motion direction learning (Fig. 3) and orientation learning (Zhang et al., 2010). These results suggest that the only possible role of direction or orientation exposure is to activate and connect untrained direction or orientation to high-level learning that either has been or is being developed (Treue & Martinez Trujillo, 1999; Martinez-Trujillo & Treue, 2004).

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References

- Ball, K., & Sekuler, R. (1982). A specific and enduring improvement in visual motion discrimination. *Science*, 218(4573), 697–698.
- Ball, K., & Sekuler, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research*, 27(6), 953–965.
- Bejjanki, V. R., Beck, J. M., Lu, Z. L., & Pouget, A. (2011). Perceptual learning as improved probabilistic inference in early sensory areas. *Nature Neuroscience*, 14(5), 642–648.
- Crist, R. E., Kapadia, M. K., Westheimer, G., & Gilbert, C. D. (1997). Perceptual learning of spatial localization: Specificity for orientation, position, and context. *Journal of Neurophysiology*, 78(6), 2889–2894.
- Fahle, M. (1997). Specificity of learning curvature, orientation, and vernier discriminations. *Vision Research*, 37, 1885–1895.
- Fiorentini, A., & Berardi, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature*, 287, 43–44.
- Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences of the United States of America*, 88(11), 4966–4970.
- Law, C. T., & Gold, J. I. (2008). Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. *Nature Neuroscience*, 11(4), 505–513.
- Law, C. T., & Gold, J. I. (2009). Reinforcement learning can account for associative and perceptual learning on a visual-decision task. *Nature Neuroscience*, 12(5), 655–663.
- Liu, Z. (1999). Perceptual learning in motion discrimination that generalizes across motion directions. *Proceedings of the National Academy of Sciences of the United States of America*, 96(24), 14085–14087.
- Liu, Z., & Weinsall, D. (2000). Mechanisms of generalization in perceptual learning. *Vision Research*, 40(1), 97–109.
- Martinez-Trujillo, J. C., & Treue, S. (2004). Feature-based attention increases the selectivity of population responses in primate visual cortex. *Current Biology*, 14(9), 744–751.
- Mollon, J. D., & Danilova, M. V. (1996). Three remarks on perceptual learning. *Spatial Vision*, 10(1), 51–58.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Schoups, A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: Retinotopy, orientation specificity and monocularity. *Journal of Physiology*, 483(Pt 3), 797–810.
- Shibata, K., Chang, L. H., Kim, D., Nanez, J. E., Sr., Kamitani, Y., Watanabe, T., & Sasaki, Y. (2012). Decoding reveals plasticity in V3A as a result of motion perceptual learning. *PLoS One*, 7(8), e44003.
- Treue, S., & Martinez Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature*, 399(6736), 575–579.
- Wang, R., Cong, L. J., & Yu, C. (2013). The classical TDT perceptual learning is mostly temporal learning. *Journal of Vision*, 13(5), 9, 1–9.
- Wang, R., Zhang, J. Y., Klein, S. A., Levi, D. M., & Yu, C. (2012). Task relevancy and demand modulate double-training enabled transfer of perceptual learning. *Vision Research*, 61, 33–38.

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. *Current Biology*, *18*(24), 1922–1926.

Yu, C., Klein, S. A., & Levi, D. M. (2004). Perceptual learning in contrast discrimination and the (minimal) role of context. *Journal of Vision*, *4*(3), 169–182.

Zhang, J. Y., Zhang, G. L., Xiao, L. Q., Klein, S. A., Levi, D. M., & Yu, C. (2010). Rule-based learning explains visual perceptual learning and its specificity and transfer. *Journal of Neuroscience*, *30*(37), 12323–12328.