

Visual perceptual learning generalizes to untrained effectors

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Visual perceptual learning (VPL) is an improvement in visual function following training. Although the practical utility of VPL was once thought to be limited by its specificity to the precise stimuli used during training, more recent work has shown that such specificity can be overcome with appropriate training protocols. In contrast, relatively little is known about the extent to which VPL exhibits motor specificity. Previous studies have yielded mixed results. In this work, we have examined the effector specificity of VPL by training observers on a motion discrimination task that maintains the same visual stimulus (drifting grating) and task structure, but that requires different effectors to indicate the response (saccade vs. button press). We find that, in these conditions, VPL transfers fully between a manual and an oculomotor response. These results are consistent with the idea that VPL entails the learning of a decision rule that can generalize across effectors.

Huxlin, Martin, Kelly, Riley, Friedman, Burgin, & Hayhoe, 2009; Liao, Gichira, Wang, & Chen, 2015; Maniglia, Cottureau, Soler, & Trotter, 2016; Maniglia, Pavan, Sato, Contemori, Montemurro, Battaglini, & Casco Hayhoe, 2016).

Previous work has shown that healthy populations can be trained to improve their discrimination performance for a wide range of visual features, including orientation (Jehee, Ling, Swisher, van Bergen, & Tong, 2012; Wang et al., 2016; Xiong, Zhang, & Yu, 2016), contrast (Cong, Wang, Yu, & Zhang, 2016; Yu, Zhang, Qiu, & Fang, 2016), motion (Liang, Zhou, Fahle, & Liu, 2015; Zhang & Yang, 2014), and speed (Yehezkel, Sterkin, Lev, & Polat, 2015). However, most studies report that such learning is highly *specific* to the trained task and the composition of the visual stimulus. Following subtle changes in features such as the location of the stimulus (Hung & Seitz, 2014), its orientation (Jehee et al., 2012), or even the eye of training (Batson, Beer, Seitz, & Watanabe, 2011), the improvement is lost and has to be relearned.

Although much research in the field has been devoted to exploring a variety of ways in which visual specificity can be overcome (Ahissar & Hochstein, 1997; Green, Kattner, Siegel, Kersten, & Schrater, 2015; Talluri, Hung, Seitz, & Seriès, 2015), there has been very little work on the question of motor specificity in visual perceptual learning. That is, if observers train on a task that requires one kind of response (e.g., a button press), do the benefits of perceptual learning persist when a different kind of response (e.g., an eye movement) is required? This question is just as important as the question of visual specificity, as a pathological specificity to motor responses would severely limit the practical utility of VPL.

In the motor learning literature, transfer across effectors is a well-documented phenomenon (for reviews, see Halsband & Lange, 2006; Obayashi, 2004). For example, various studies have shown that practicing a motor task with one hand leads to improved reaction

Introduction

Visual perceptual learning (VPL) is a long-lasting improvement in the ability of the visual system to detect, to discriminate, or to identify visual stimuli following training or experience. As a manifestation of plasticity occurring in the adult brain, VPL has significant practical and theoretical implications. For subjects with normal visual acuity, VPL can shed light on fundamental processes, such as perceptual development (Gibson, 1969; Gibson & Pick, 2003) and the formation of visual expertise (Appelbaum & Erickson, 2018; DeLoss, Watanabe, & Andersen, 2015; Deveau, Ozer, & Seitz, 2014; Laamerad, Guitton, & Pack, 2020; Reingold & Sheridan, 2011). There is also evidence that VPL can improve outcomes and be used as a strategy for visual rehabilitation in aging and clinical populations (Campana, Camilleri, Pavan, Veronese, & Lo Giudice, 2014; DeLoss et al., 2015;

Citation: Awada, A., Bakhtiari, S., & Pack, C. C. (2021). Visual perceptual learning generalizes to untrained effectors. *Journal of Vision*, 21(3):10, 1–12, <https://doi.org/10.1167/jov.21.3.10>.



times that transfer to the other hand, with little or no need for further learning (Gordon, Forssberg, & Iwasaki, 1994; Laszlo, Baguley, & Bairstow, 1970; Morton, Lang, & Bastian, 2001). A similar lack of specificity is sometimes observed across very different effectors. For example, training on an eye movement task can improve performance on a hand movement task (Modroño, Socas, Hernández-Martín, Plata-Bello, Marcano, Pérez-González, & González-Mora, 2020), although this does not always occur (Fookan, Lalonde, Mann, & Spering, 2018).

Given these results, one might expect the benefits of VPL to transfer to different effectors; however, previous studies of motor specificity in VPL have yielded mixed results. Szpiro, Spering, and Carrasco (2014) reported that training on a task that required a manual response transferred to an oculomotor response (smooth pursuit); however, the same authors showed that smooth pursuit training did not influence manual responses. In this experiment, though, there was no significant learning during the pursuit phase, so it is difficult to determine whether these results reflect a lack of transfer per se. Nevertheless, these results are in some ways similar to other dissociations between perceptual and oculomotor responses (Glasser & Tadin, 2014; Lisi & Cavanagh, 2015; Spering & Gegenfurtner, 2007; Zivotofsky, 2005).

Recently, Grzeczowski, Cretenoud, Mast, and Herzog (2019) found that improvements after training on a bisection task that required a response with one hand persisted when observers were asked to perform the same task with the other hand. However, in other tasks that entailed a change in the nature of the response (i.e., from a button press to a mouse movement), the benefits of VPL were lost and there was no transfer across effectors (Green et al., 2015; Grzeczowski, Cretenoud, Herzog, & Mast, 2017; Grzeczowski et al., 2019).

These findings can potentially be reconciled under the hypothesis that the specificity of VPL is a property of the decision rule (Green et al., 2015), but not of the motor response per se (Szumska, van der Lubbe, Grzeczowski, & Herzog, 2016). In this case, training on a task that required a binary decision (e.g., right vs. left) would yield benefits that transferred to any effector, but such learning would not transfer to a task that required a continuous readout (e.g., moving a mouse), even if the same effector was used (Grzeczowski et al., 2019). This is consistent with studies in the motor adaptation domain that have reported specificity for the type of action (forward walking vs. turning) performed by the same effector (Rieser, Pick, Ashmead, & Garing, 1995).

In this work, we have tested this hypothesis more generally, using a paradigm in which the stimuli and decision rules were identical across tasks and that differed solely in the type of effector used for

the response. Observers were trained on a motion discrimination task that required a binary decision (left vs. right), with the motor response being either a saccade (Experiment 1) or a button press (Experiment 2). Training consistently led to improvements in psychophysical performance (VPL), after which the required motor response was changed. In all observers, we found a full transfer of learning between saccades and manual responses, even though the corresponding effectors were distinct functionally and anatomically. We propose that VPL is not necessarily specific to the motor response and that a perceptual decision rule, once learned, can be flexibly attached to different motor responses as needed.

Methods

Observers and apparatus

Twelve observers with normal or corrected-to-normal vision participated in this study (two male observers, ten female observers; age range, 18–25 years). All observers were naïve to the purpose of the study and to visual psychophysics. Observers gave written, informed consent prior to their participation, and the study was approved by the Ethics Committee of the Montreal Neurological Institute and Hospital (NEU-06-033). The experiment was halted by the COVID-19 pandemic, but informative data were successfully collected and analyzed from ten observers who completed the study and two who completed almost all of the protocol. As shown below, the results were highly consistent across observers and across tasks.

Observers sat in a normally lit room 40 cm from the monitor, and their heads were stabilized with a chin rest and a forehead bar. Stimuli were generated through the psychophysics toolbox Psychtoolbox (Brainard, 1997) on MATLAB (MathWorks, Natick, MA) and were presented on a 27-inch BenQ monitor (1680 × 1050 pixels, 60-Hz frame rate; BenQ, Taipei, Taiwan). Eye position and movements were recorded using the EyeLink 1000 Eye Tracker (SR Research, Kanata, ON, Canada). Stimuli were viewed binocularly.

Motion direction discrimination task

Stimulus

The stimulus used in this experiment was a translating drifting grating composed of a Gabor patch with a spatial frequency of 1 cycle per degree and a temporal frequency of 6 cycles per second (Figure 1a). The size of the Gabor patch (2 standard deviations of the Gaussian envelope) was 5°, and the stimulus was

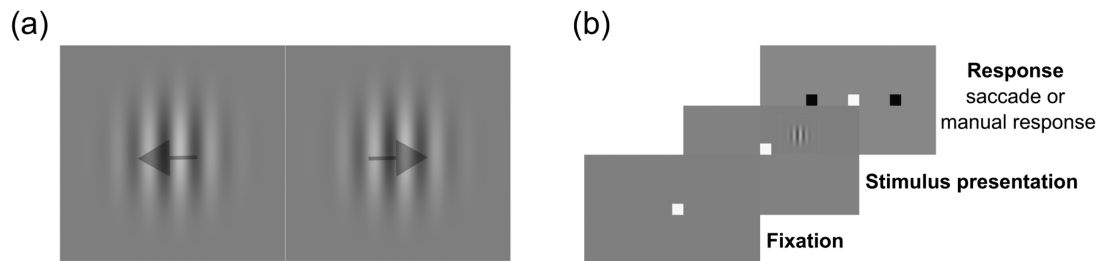


Figure 1. (a) Motion direction discrimination stimulus—Gabor patch drifting to the left or to the right (spatial frequency, 1 cycle per degree; temporal frequency, 6 Hz). (b) On each trial, the observer had to fixate on the fixation square for 500 ms before the stimulus appeared for four frames (66.7 ms), after which two saccade targets appeared, and the observer had to report the direction of the motion with a manual response (keyboard) or a saccade. Each block was composed of 125 trials. One training session was composed of four blocks.

placed in the upper right quadrant of the visual field at an eccentricity of 5° . This stimulus targets lower-level visual cortical areas with a high degree of specificity in VPL (Bakhtiari, Awada, & Pack, 2020; Fiorentini & Berardi, 1980; Fiorentini & Berardi, 1981; Hubel & Wiesel, 1959; Hubel & Wiesel, 1962; Liu & Pack, 2017). Background luminance was 76.48 cd/m^2 , and the contrast was adjusted on each trial according to the staircase procedure described below.

Task

The experimental task followed a two-alternative, forced-choice paradigm in which the observer reported the direction of the motion of the stimulus (left or right) through either a manual response (button press on a keyboard) or a saccade. Each trial started with a central fixation point that the observer had to fixate for 500 ms before the stimulus appeared on the screen for four frames (stimulus duration = 66.7 ms). For trials in which the required response was a saccade, two targets then appeared 5° to the left and right side of the fixation point, at which point the observer had to report the direction of the motion of the stimulus by making a saccade that landed within 1° of the target (Figure 1b). For trials in which the required response was a button press, the same two targets appeared, but observers had to press the left or right arrow key on the keyboard. After the response was made, the next trial started.

The direction of motion of the Gabor patch was chosen randomly on each trial to be either right or left. Eye position was tracked throughout the trial and was required to be within 1° of the fixation point. If observers broke fixation, the trial was paused until fixation was restored. The starting contrast for the drifting grating was 50%, and the contrast for each subsequent trial was set using a standard two-down/one-up adaptive staircase procedure (Leek, 2001). Observers were compensated at the rate of 1.2 cents (Canadian) per correct response.

Training paradigm

Each experiment was comprised of two phases. The first phase consisted of one session per day for 7 to 10 days, and the second phase consisted of one session per day for 5 days. Each session entailed four blocks of 125 trials each; the total duration of each session was approximately 30 minutes. Experiment 1 included six observers. In the first phase of Experiment 1, the observers reported the perceived direction of motion with a saccade. In the second phase, they reported the direction of motion with a manual response.

In the first phase of Experiment 2, the observers reported the direction of the motion with a manual response. In the second phase, the motor response was changed to a saccade. This experiment included a total of six observers, four of whom successfully completed all phases of the study. Two additional observers successfully completed both phases, with the exception of the last two or three sessions, which were halted because of the COVID-19 pandemic.

At the beginning of each phase in both experiments, the experimenter described the task and response required. Observers were unaware of the change in motor response until the second phase, when they were given new instructions about the required motor response.

Threshold measurement and statistical analysis

Contrast thresholds were computed using the two-down/one-up staircase procedure described above, which resulted in an 83% convergence level. Stimulus contrasts at the last six reversals for each training block were averaged, and the threshold for each training session was computed as the median threshold for the four blocks run per session. To quantify generalization to a different motor output, three threshold measurements were computed (Figure 2): the baseline threshold, the training threshold, and the transfer threshold. The baseline threshold represented

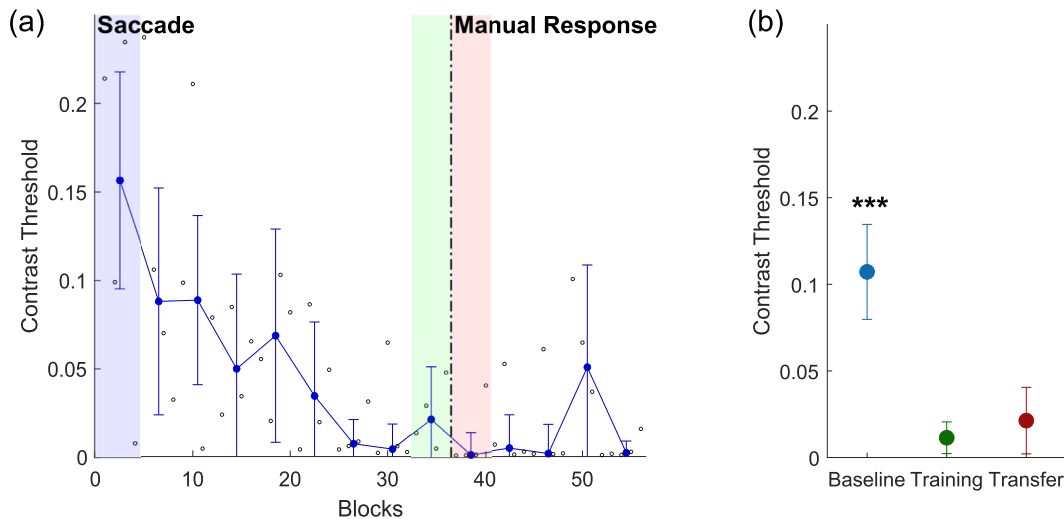


Figure 2. (a) Sample learning curve for one example observer in Experiment 1. The dashed vertical line represents a change in the experimental phase. In phase 1 (left of the dashed line), the observer reported the direction of the motion with a saccade. In phase 2 (right of the dashed line), the observer reported the direction of the motion with a manual response (keyboard). Small black open circles represent the contrast threshold for each block (125 trials). Blue dots represent the contrast threshold for each training session (median threshold for four blocks). Error bars show the standard deviation from the mean contrast threshold for each training session. Shaded regions represent the time periods for each threshold measurement. (b) Average thresholds at baseline, during the first phase of training (training) and the second phase of training (transfer) for the six observers in Experiment 1. Baseline threshold is the threshold during the first training session (blue). Training threshold is the threshold during the last training session of phase 1 (green). Transfer threshold is the threshold during the first day of training of phase 2 (pink/red). Baseline threshold is significantly different from both first-phase training, $t(5) = 4.96$, $p = 0.0043$, and second-phase transfer, $t(5) = 3.23$, $p = 0.0233$, which are not significantly different from each other, $t(5) = -0.923$, $p = 0.398$. Error bars show standard deviation from the mean contrast threshold across observers. *** $p < 0.05$.

the threshold during the first training session. The training threshold was computed as the threshold during the last session of phase 1. The transfer threshold was computed as the threshold during the first session in phase 2. Paired t -tests were performed to compare the three threshold values.

Results

We sought to assess whether training with a motion stimulus that shows high levels of sensory specificity would also show motor specificity.

Experiment 1

In this experiment, we trained six observers on a simple motion direction discrimination task with saccades and evaluated whether the improvement would transfer to a manual response (keyboard). Figure 2a shows a sample learning curve for a single subject, with the dashed line indicating the transition from the first experimental phase to the second. If this observer

exhibited motor specificity, we would expect to see an abrupt increase in the contrast threshold after the transition, but there was in fact little discernible change (Figure 2a). Indeed, quantifying the results of the six observers shows that the contrast threshold in the second phase was not significantly different from that observed at the end of the first phase, $t(5) = -0.923$, $p = 0.398$ (Figure 2b). Both thresholds were significantly different from the baseline threshold taken on the first session—first phase, $t(5) = 4.96$, $p = 0.0043$; second phase, $t(5) = 3.23$, $p = 0.0233$ —indicating that the learning that occurred during the first phase transferred to the second phase. Results for each observer are shown separately in Supplementary Figure S1.

For each observer, we also fit two models for the trajectory of the contrast threshold values over time (Rolf, Murray-Smith, & Carrasco, 2018) (Figure 3). In the transfer model, we fit one exponential curve to the entire dataset. In the no-transfer model, we fit one exponential curve for each phase (one for saccade and one for the manual response) of the experiment. We then compared both models by computing the Bayesian information criterion (BIC) to determine which model was more appropriate. For five of the six observers,

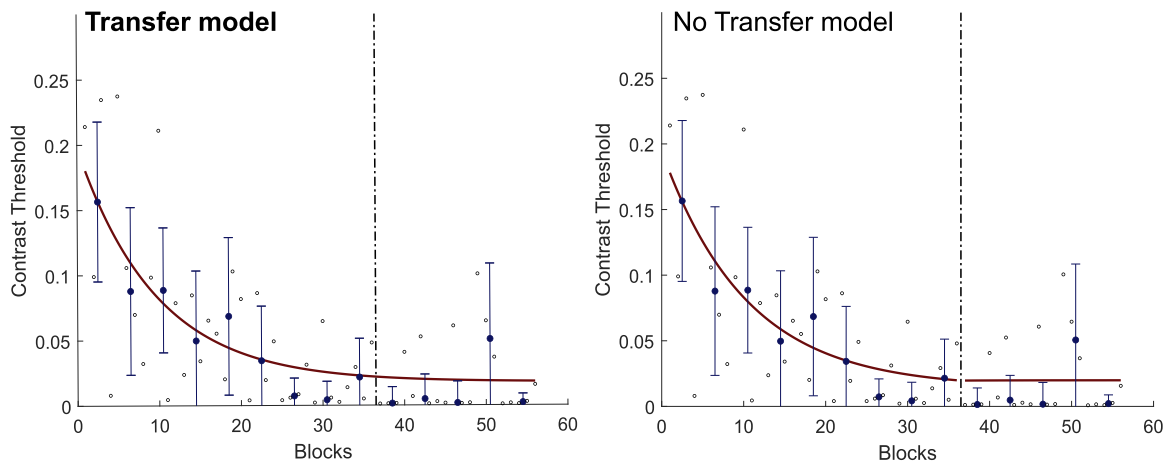


Figure 3. Sample data and model fitting for the example observer in as in Figure 2a. The dashed vertical line represents a change in the experimental phase (from saccade to manual response). Small black open circles represent the contrast threshold for each block (125 trials). Blue dots represent the contrast threshold for each training session (median threshold for four blocks). Error bars show the standard deviation from the mean contrast threshold for each training session. The red curve represents the model fitting curve in the transfer model (left) and the no-transfer model (right). The better model is shown in bold. In five of the observers (including this one), the transfer model significantly fit the data better than the no-transfer model ($\Delta\text{BIC} = 7.5$; range, 7–8).

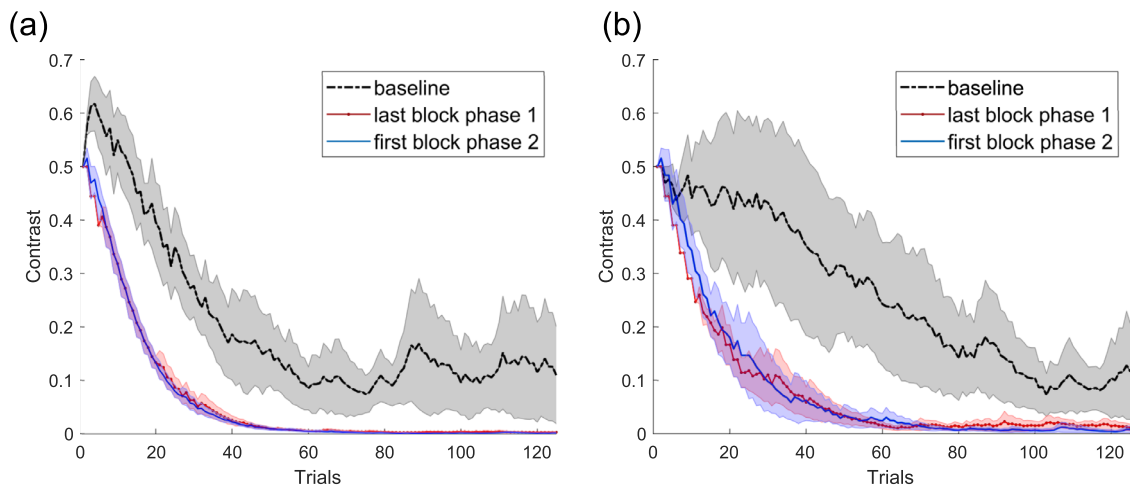


Figure 4. (a) Experiment 1: staircase pattern at baseline (first block of training with saccade), the last block of training with saccade (phase 1), and the first block of training with a manual response (phase 2). The different colored lines represent the average contrast at each trial for the six observers. The shaded region represents the standard error for each measurement. (b) Experiment 2: staircase pattern at baseline (first block of training with a manual response), the last block of training with a manual response (phase 1), and the first block of training with saccade (phase 2). The different colored lines represent the average contrast at each trial for the six observers who completed the study. The shaded region represents the standard error for each measurement.

the transfer model significantly fit the data better ($\Delta\text{BIC} = 7.5$; range, 7–8). The data and model fits for each subject in Experiment 1 are shown in Supplementary Figure S2. Overall, these results indicate that visual perceptual learning transfers when the readout is changed from a saccade to a manual response.

This conclusion is further supported by a comparison of the staircase pattern within different blocks of trials, averaged across observers. As shown in Figure 4a, the staircase during the first (baseline) block shows a slow decline in contrast levels, as observers gradually improved on the task (black dashed line). The last block before the transition from phase 1 to phase 2

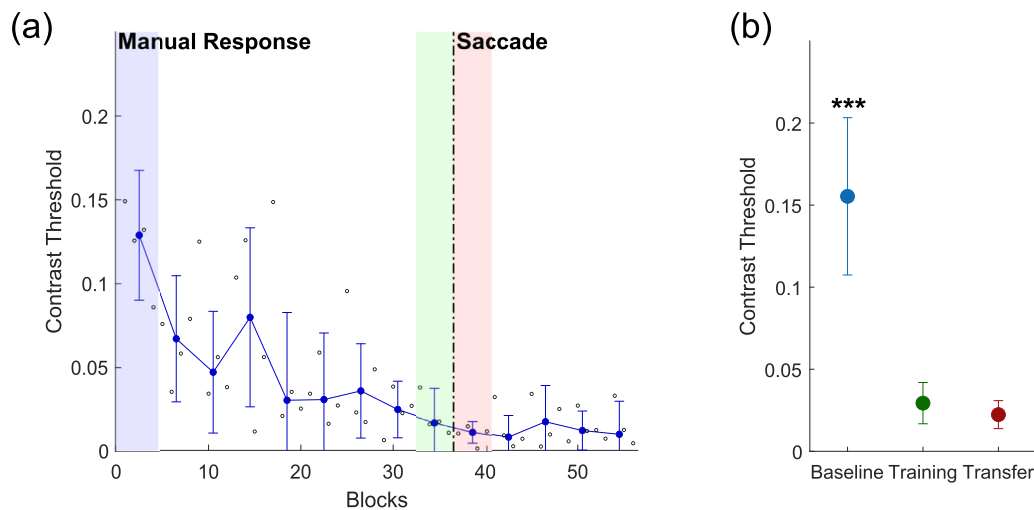


Figure 5. (a) Sample learning curve for one observer in Experiment 2. The vertical dashed line represents the change in experimental phase. In phase 1 (left of the dashed line), the observer reported the direction of the motion with a manual response (keyboard). In phase 2 (right of the dashed line), the observer reported the direction of the motion with a saccade. Small black open circles represent the contrast threshold for each block (125 trials). Blue dots represent the contrast threshold for each training session per day (median threshold for four blocks). Error bars show the standard deviation from the mean contrast threshold for each training session per day. Shaded regions represent the time periods for each threshold measurement. (b) Average thresholds at baseline (blue), during the first phase of training (green), and during the second phase of training (pink/red) for six observers. Baseline threshold is significantly different from both first-phase training, $t(5) = 3.64$, $p = 0.0149$, and second-phase transfer, $t(5) = 3.54$, $p = 0.0166$, thresholds, which are not significantly different from each other, $t(5) = 1.40$, $p = 0.222$. Error bars show standard deviation from the mean contrast threshold across observers. *** $p < 0.05$.

shows a rapid decline in contrast, as observers became proficient at the task (red dotted line). Crucially, the first block after the transition (blue solid line) is nearly identical to the last block before the transition (Pearson's correlation coefficient $r = 0.991 \pm 0.011$), indicating that the proficiency obtained during training transferred almost perfectly to the new motor readout.

Experiment 2

In this experiment, we evaluated whether transfer occurred when changing the motor response from a manual response to a saccade. Six observers completed the training and transition components of the study, although two of these observers were unable to complete the last two or three sessions of phase 2 because of the COVID-19 pandemic. Figure 5a shows a sample learning curve for a single observer, with the dashed line representing the transition from the manual motor response to the saccade. Again, it is clear that the contrast threshold changed very little in the transition from the first to the second phase. As in Experiment 1, we found for the population of observers that thresholds did not change significantly across the transition, $t(5) = 1.40$, $p = 0.222$ (Figure 5b), and that baseline thresholds differed significantly from

those obtained at the end of the first phase, $t(5) = 3.64$, $p = 0.0149$, and the beginning of the second phase, $t(5) = 3.54$, $p = 0.0166$. Similar results were obtained when we excluded the two observers who did not complete the full protocol: baseline threshold versus first-phase training, $t(3) = 2.47$, $p = 0.0903$; baseline versus second-phase transfer, $t(3) = 2.49$, $p = 0.0889$; first-phase versus second-phase thresholds, $t(3) = 1.61$, $p = 0.206$. Results for each individual observer are shown in Supplementary Figure S3.

For each observer, we also fit two models for the trajectory of the contrast threshold values over time (Figure 6). Again, for five of the six observers, the transfer model significantly fitted the data better ($\Delta\text{BIC} = 7$; range, 4–8). The data and model fits for each observer in Experiment 2 are shown in Supplementary Figure S4. As shown in Supplementary Figure S4, for the one observer whose data were better fitted by the no-transfer model, the performance in the second phase of the experiment actually improved, indicating that there was no performance penalty for switching effectors.

As in Experiment 1, a closer examination of the staircase patterns shows that the progression of contrast values was very similar between the last block of phase 1 and the first block of phase 2 (Pearson's correlation coefficient $r = 0.974 \pm 0.037$), with neither block

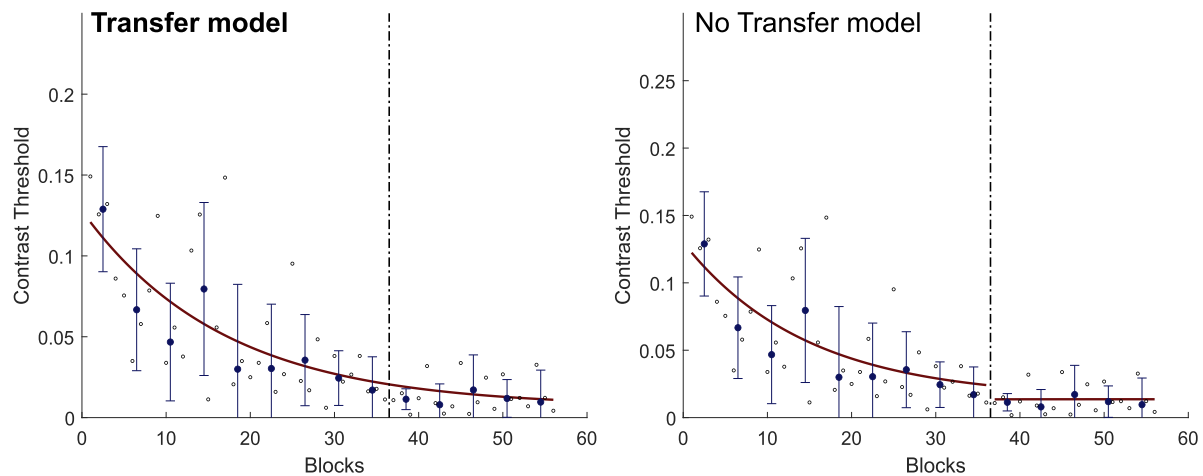


Figure 6. Sample data and model fitting for the example observer in as in Figure 5a. The dashed vertical line represents a change in the experimental phase (from manual response to saccade). Small black open circles represent the contrast threshold for each block (125 trials). Blue dots represent the contrast threshold for each training session (median threshold for four blocks). Error bars show the standard deviation from the mean contrast threshold for each training session. The red curve represents the model fitting curve in the transfer model (left) and the no-transfer model (right). The better model is shown in bold. In five of the observers (including this one), the transfer model significantly fit the data better than the no-transfer model ($\Delta\text{BIC} = 7$; range, 4–8).

being similar to baseline (Figure 4b). Overall, these results indicate that significant transfer can occur when changing the motor response from a manual response to a saccade.

Although our sample size may not have been sufficient to detect a small cost of transferring VPL across effectors, the large differences in thresholds at baseline and at transfer (Figures 2b and 5b) suggest substantial motor generalization.

Discussion

VPL represents a type of adult cortical plasticity that has significant theoretical and practical implications. Indeed, exploring VPL and its underlying mechanisms can shed light on essential brain functions in the adult visual system and can be used to develop training strategies for those seeking visual expertise or visual rehabilitation. Research in the field has thoroughly focused on exploring the sensory aspect of VPL and has identified a hallmark sensory specificity that might limit its practical use (Batson et al., 2011; Doshier & Lu, 2017; Hung & Seitz, 2014; Jehee et al., 2012). However, recent advances have highlighted a variety of ways in which this sensory specificity can be overcome (Ahissar & Hochstein, 1997; Green et al., 2015; Talluri et al., 2015).

At the same time, if VPL is to be of practical utility, it should not be limited to the effector used in the training protocol; yet, to date, little is known about the motoric aspects of VPL. In this work, we propose that the hallmark specificity of VPL does not necessarily extend to motor outputs. Indeed, we show that, following training with a stimulus that often yields VPL with high levels of sensory specificity, the improved performance nevertheless transfers to different motor responses.

Implications for VPL

Our results have a number of implications for a mechanistic understanding of VPL. First, our findings are in line with the proposal that two separate anatomical pathways in the visual cortical system exist for object perception and motor responses (Goodale & Milner, 1992). Indeed, our results suggest that the improved perception of a stimulus in VPL occurs independently of the response to that stimulus. Our results are also consistent with most VPL theories that posit that visual processing follows an information processing framework in which perception occurs before any decision making or action occurs (Li, 2016; Marr, 1982; Watanabe & Sasaki, 2015).

Second, our results shed light on the long-standing debate about the brain locus of VPL. A number of studies have shown that VPL can reweight the readout of visual information, emphasizing the cortical regions most suitable for the trained task (Bakhtiari et al., 2020; Chang, Mevorach, Kourtzi, & Welchman, 2014; Chen, Cai, Zhou, Thompson, & Fang, 2016; Chowdhury & DeAngelis, 2008; Liu & Pack, 2017; Walsh, Ashbridge, & Cowey, 1998). In our experiments, the most suitable brain regions were presumably

low-level visual cortical areas, which optimally encode grating stimuli of the kind used in our training protocol (Bakhtiari et al., 2020; Fiorentini & Berardi, 1980; Fiorentini & Berardi, 1981; Hubel & Wiesel, 1959; Hubel & Wiesel, 1962; Liu & Pack, 2017). Anatomical and physiological evidence suggests that direct connections between these visual areas and motor regions are weak and that these connections exhibit a strong preference for saccades over limb movements (Levy, Schluppeck, Heeger, & Glimcher, 2007; Strigaro, Ruge, Chen, Marshall, Desikan, Cantello, & Rothwell, 2015). This suggests an intermediate stage of processing between sensory and motor regions that is capable of encoding perceptual decision rules independently of the motor response.

One possibility is the parietal lobe, more specifically the posterior parietal cortex (PPC), which has been shown to be responsible for sensorimotor transformations in visually guided behaviors in non-human primates (Andersen & Buneo, 2002; Andersen & Cui, 2009; Andersen, Essick, & Siegel, 1987; Andersen, Snyder, Bradley, & Xing, 1997). Indeed, Law and Gold (2008) demonstrated that training non-human primates on a motion perception task with saccades resulted in changes in the neural response in the lateral intraparietal area (LIP) of the PPC and not in the middle temporal visual area (MT), which is responsible for motion perception. There is ample evidence that PPC neurons in non-human primates can respond to both saccades and arm movements, even in specialized areas such as the LIP and the parietal reach region (PRR) (de Lafuente, Jazayeri, & Shadlen, 2015; Snyder, Batista, & Andersen, 1997). Similarly, a recent functional magnetic resonance imaging study in humans found only slight preferences for a specific effector in the human equivalents of areas LIP and PRR (Levy et al., 2007). The authors further demonstrated that a greater effector specificity existed in visual and motor areas outside the parietal cortex, as early visual areas were activated during saccades and motor areas during reaching movements (Levy et al., 2007). Our results thus support a framework in which VPL reflects a change in the efficiency with which sensorimotor structures in the parietal lobe read out visual information from the occipital cortex (Chen et al., 2016; Law & Gold, 2008).

In this regard, the PPC might be the site at which decision rules—mappings from sensory stimuli to perceptual outputs—reside. Recent evidence suggests that perceptual learning can occur at a conceptual level at which abstract rules, rather than specific stimulus mappings, are learned (Green et al., 2015; Wang et al., 2016). Differences in VPL specificity might thus be attributed to differences in a learned decision rule; that is, a rule that encourages flexibility, via a task that exposes the observer to multiple

stimulus conditions and responses, will naturally lead to less specificity, and this has been observed experimentally (Bavelier, Achtman, Mani, & Föcker, 2012; Green et al., 2015). Such rules need not be specific to the motor response, and indeed our results suggest that, when a decision rule has been learned, it can flexibly be mapped onto untrained motor responses. At the same time, binary decision rules might be regarded as a special case (Szumska et al., 2016), and it remains to be seen whether other types of rules would also generalize to different effectors.

Also unknown is the extent of motor specificity in other kinds of visual learning. The phenomenon of task-irrelevant learning illustrates a case in which perceptual training can result in a change of visual perception in the absence of a specific mapping from stimulus to response (Seitz, Kim, & Watanabe, 2009; Shibata, Watanabe, Sasaki, & Kawato, 2011; Watanabe, Náñez, & Sasaki, 2001; Xiong et al., 2016). In this case, one might expect to find that training effects are equal for all effectors, although this has not to our knowledge been tested.

Implications for vision rehabilitation

Our findings have important implications for the practical utility of VPL, namely for rehabilitation. VPL has been shown to be somewhat successful in recovering some visual function in patients with V1 lesions, although the improvements seem to be limited by a high degree of specificity to the stimulus and its location (Cavanaugh & Huxlin, 2017; Das, Tadin, & Huxlin, 2014; Huxlin et al., 2009; Sahraie et al., 2006). Such specificity can to some degree be overcome with the use of training stimuli that target higher level visual areas, for which generalization at the neural level is greater (Das et al., 2014).

Even if stimulus specificity could be overcome, motor specificity could sharply limit the utility of VPL in vision rehabilitation, and in this regard the finding that learning is not necessarily specific to the motor response reinforces its use as a potential therapy. That said, the above considerations on decision rules suggest that rehabilitation protocols should encourage flexibility in mapping stimuli to motor responses. As mentioned previously, VPL appears to be highly sensitive to the decision rules embodied by the training task (Green et al., 2015); specificity often arises because observers learn to link individual stimuli to individual responses. Thus, it is likely useful to make use of protocols that require a continuum of visual stimuli and motor outputs (Achtman, Green, & Bavelier, 2008).

Keywords: visual perceptual learning, effectors, transfer

Acknowledgments

The authors thank Michael Herzog, PhD, for helpful discussions.

Supported by a grant from the Natural Sciences and Engineering Research Council of Canada to CCP.

Commercial relationships: none.

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