

# Motor response specificity in perceptual learning and its release by double training

Lukasz Grzeczowski

Laboratory of Psychophysics, Brain Mind Institute, École Polytechnique Fédérale de Lausanne (EPFL), Switzerland  
Allgemeine und Experimentelle Psychologie, Department Psychologie, Ludwig-Maximilians-Universität München, Germany



Aline F. Cretenoud

Laboratory of Psychophysics, Brain Mind Institute, École Polytechnique Fédérale de Lausanne (EPFL), Switzerland

Fred W. Mast

Department of Psychology, University of Bern, Switzerland

Michael H. Herzog

Laboratory of Psychophysics, Brain Mind Institute, École Polytechnique Fédérale de Lausanne (EPFL), Switzerland

**Perceptual learning is usually feature-specific. Recently, we showed that perceptual learning is even specific for the motor response type. In a three-line bisection task, participants indicated whether the central line was offset either to the left or right by pressing a left or a right button, respectively. We found no transfer when the same participants adjusted the offset by using a computer mouse. Here, we first show that perceptual learning with mouse adjustments transfers to the untrained hand, but only for the trained adjustment condition. There was no transfer to the button press conditions, neither for the trained nor the untrained hand. Second, we show that a double training procedure enables transfer from the mouse adjustment to the button press condition. Hence, the specificity of perceptual learning to the motor response type can be overcome by double training as it is the case for visual features. Our results suggest that during perceptual learning, perceptuo-decisional signals are encoded together with the corresponding actions.**

## Introduction

Perceptual learning improves perception through training. One of the main characteristics of perceptual learning is that improvements with the trained stimuli do not generalize to untrained stimuli. For example, training and improvements with vertical bisection stimuli (Figure 1A) do not transfer to the same

bisection stimulus rotated by 90° (Figure 1B; e.g., Aberg & Herzog, 2009; Crist, Kapadia, Westheimer, & Gilbert, 1997; Crist, Li, & Gilbert, 2001; Grzeczowski, Cretenoud, Herzog, & Mast, 2017; Grzeczowski, Tartaglia, Mast, & Herzog, 2015; Herzog et al., 2012; Otto, Herzog, Fahle, Zhaoping, 2006; Parkosadze et al., 2008; Tartaglia, Balmert, Mast & Herzog, 2009; Tartaglia, Aberg, & Herzog, 2009). Perceptual learning was not only found to be specific for the trained stimulus orientation (Crist et al., 1997; Fahle & Edelman, 1993; Spang, Grimsen, Herzog, & Fahle, 2010; Tartaglia et al., 2009; Vogels & Orban, 1985) but also for contrast (Sowden, Rose, & Davies, 2002; Yu, Klein, & Levi, 2004), motion direction (Ball & Sekuler, 1982, 1987), spatial frequency (Berardi & Fiorentini, 1987), retinal position (Ahissar & Hochstein, 1996), and even in some cases, the eye trained with (Karni & Sagi, 1991; but see Schoups & Orban, 1996).

The specificity of perceptual learning to low-level stimulus features (e.g., orientation), stimulus location, and the specificity for the trained eye were often taken as a strong indicator that perceptual learning takes place in early sensory cortical areas (Adab & Vogels, 2011; Crist et al., 2001; Karni & Sagi, 1991; Raiguel, Vogels, Mysore, & Orban, 2006; Schoups, Vogels, Qian, & Orban, 2001; Yang & Maunsell, 2004), which are mainly retinotopic and where neurons are often monocularly driven (Hubel & Wiesel, 1968; Hubel, Wiesel, & LeVay, 1977). Other studies proposed that perceptual learning occurs beyond primary sensory

Citation: Grzeczowski, L., Cretenoud, A. F., Mast, F. W., & Herzog, M. H. (2019). Motor response specificity in perceptual learning and its release by double training. *Journal of Vision*, 19(6):4, 1–14, <https://doi.org/10.1167/19.6.4>.

<https://doi.org/10.1167/19.6.4>

Received January 14, 2019; published June 7, 2019

ISSN 1534-7362 Copyright 2019 The Authors



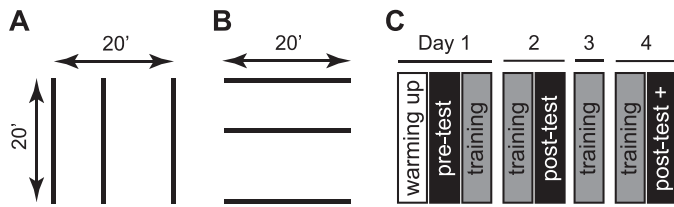


Figure 1. (A) Vertical and (B) horizontal bisection stimuli. (C) Experiment 1 was conducted on 4 consecutive days. On Day 1, participants first were familiarized with the setup by performing 80 practice trials (warming up). Then, participants' pretraining performance was measured, followed by seven blocks of training. On Day 2, participants performed seven blocks of training, which were followed by posttraining tests. On Day 3, participants performed seven blocks of training. The session on Day 4 was the exactly the same as the session on Day 2. The same protocol was used for Experiments 2 and 3, however, without Days 3 and 4.

areas as high- or mid-level processes or distributed, interactive networks but before motor-related areas (Chen, Cai, Zhou, Thompson, & Fang, 2016; Doshier & Lu, 1998, 1999; Ghose, 2004; Ghose, Yang, & Maunsell, 2002; Law & Gold, 2008; Mollon & Danilova, 1996; Petrov, Doshier, & Lu, 2005; Shibata, Watanabe, Sasaki, & Kawato, 2011; Talluri, Hung, Seitz, & Seriès, 2015; Uka, Sasaki, & Kumano, 2012; Xiong, Zhang, & Yu, 2016; J.-Y. Zhang et al., 2010). This view was supported by many studies in the last decade showing that perceptual learning can generalize to different orientations and locations when specific training protocols are used, such as double training and training plus exposure (Mastropasqua, Galliussi, Pascucci, & Turatto, 2015; Wang, Zhang, Klein, Levi, & Yu, 2012, 2014; Xiao et al., 2008; J. Y. Zhang & Yang, 2014; Zhang & Yu, 2018; T. Zhang, Xiao, Klein, Levi, & Yu, 2010; but see Liang, Zhou, Fahle, & Liu, 2015a, 2015b), task-irrelevant perceptual learning (Choi, Seitz, & Watanabe, 2009; Galliussi, Grzeczkowski, Gerbino, Herzog, & Bernardis, 2018; Seitz, Kim, & Watanabe, 2009; Seitz & Watanabe, 2009; Watanabe, Náñez, & Sasaki, 2001), or when the untrained tasks share common features with the trained one (Huang, Lu, Tjan, Zhou, & Liu, 2007; McGovern, Webb, & Peirce, 2012; Wright, Sabin, Zhang, Marrone, & Fitzgerald, 2010).

Nevertheless, most of the perceptual learning theories (for reviews, see Li, 2016; Sagi, 2011; Watanabe & Sasaki, 2015) ensue from the classic information processing framework, which divides perception, cognition, and action in distinct, serial processes (Fodor, 1983; Johnson-Laird, 1988; Keele, 1968; Marr, 1982; Miller, Galanter, & Pribram, 1960; Pylyshyn, 1984). For that reason, regardless of whether perceptual learning occurs at early-, mid-, or late-stage, it is assumed that motor processes do not play a role for

perceptual learning. In fact, in most perceptual studies, observers are presented with stimuli that they have either to detect, categorize, or discriminate, then, take a decision, and finally respond by pressing one of two buttons, accordingly (binary forced choice). Such experimental designs promote segregation and serial processing of the information (i.e., perception > cognition > action). In particular, motor responses seem to play no role for perceptual learning because the output of the decision-making stage can be mapped on any arbitrary action (e.g., Szumska, van der Lubbe, Grzeczkowski, & Herzog, 2016). Nonetheless, in everyday life, many (if not most) of our actions require continuous sensorimotor interactions with the environment rather than “trial-like,” serial interactions that end with a perceptual report preceded by a binary choice (Cisek, 2007; Cisek & Kalaska, 2010; Lebedev & Wise, 2002; Michaels, 2000; Smeets & Brenner, 2001). Accordingly, it was recently shown that perceptual learning with binary and continuous motor responses, such as button presses and mouse adjustment, lead to different procedural-related specificities (Green, Kattner, Siegel, Kersten, & Schrater, 2015; Grzeczkowski, Cretenoud, et al., 2017).

In a previous study (Grzeczkowski, Cretenoud et al., 2017), participants trained with a classic bisection task discriminating a left from a right offset by pressing a left or a right button, respectively. Before and after training, participants performed a bisection task with the same stimulus by adjusting the position of the central line with a computer mouse. We found a significant improvement following training but no transfer to the untrained type of motor response, i.e., mouse adjustment. The same results were found in a subsequent experiment, where inversely, participants trained with the bisection task by adjusting the position of the central line with the computer mouse while they were tested before and after training with a standard, button press bisection task. Similarly, Green et al. (2015) did not find any significant transfer after perceptual learning from a binary button presses to mouse adjustment condition for an orientation discrimination task and vice-versa. These studies show that perceptual learning is specific for the procedural aspects of the motor response, which suggests that during perceptual learning, visual and motor signals are to some extent, encoded together. Therefore, these results disagree with most of the theories on perceptual learning, which assume that motor processes are of no avail for perceptual learning. Here, we show that this motor response specificity of perceptual learning persists even when the same effectors are used for the trained and the untrained motor response conditions (Experiment 1). However, this specificity can be overcome by double training (Experiments 2 and 3).

## General methods

### Participants

Thirty-eight naive students from the École Polytechnique Fédérale de Lausanne (EPFL) in Switzerland took part in the study (19 females; mean age 21 years, range 18–26 years). Prior to the experiments, participants' visual acuity was measured with the Freiburg visual acuity test (Bach, 1996). Participants had to reach a value of at least 1.0 binocularly to take part in the study (corresponding to a Snellen fraction of 20/20). Participants signed an informed consent and were compensated 20 Swiss francs per hour. The procedures were conducted in accordance with the Declaration of Helsinki and were approved by the local ethics committee.

### Setup and stimuli

Observers sat in a dimly illuminated experimental room at 2 m from the monitor. Head movements were minimized by using a chin rest with a forehead bar. Stimuli were displayed on a Tektronix 608 monitor with a 200 Hz refresh rate controlled by a PC via fast 16-bit D/A converters (1 MHz pixel rate). Bisection stimuli were made of lines that were composed of overlapping dots drawn with a dot pitch of 200  $\mu\text{m}$  at a dot rate of 1 MHz. Vertical and horizontal bisection stimuli were composed of 20' (arc minutes) long bluish lines ( $\approx 80 \text{ cd/m}^2$ ) presented on a dark background ( $< 1 \text{ cd/m}^2$ ). The distance between the outer lines was either 20' (Figure 1A and B) during the main experiments or 40' during the warming up blocks. No fixation point was presented to avoid that observers potentially discriminate whether the central line is to the left or right from this fixation dot. Luminance was measured with a Minolta LS-100 luminance meter. A Logitech B58 optical mouse or wireless push buttons were used for collecting observers' responses.

### Procedure

#### *Bisection task with button presses*

Participants discriminated whether the central line was offset either to the left or right (down or up for horizontal stimuli) by pressing a left or a right button, respectively. In Experiment 1, participants pressed the left and right buttons of a computer mouse using their index and middle fingers. In Experiments 2 and 3, participants used wireless push buttons, one in each hand and used their left and right thumbs for button presses. An adaptive staircase procedure and maximum

likelihood estimation of the parameters of the psychometric function were used to measure thresholds of 75% correct responses (parameter estimation by sequential tracking [PEST]; starting value: 100 arc seconds; min. step, 0.05dB; max. step, 3dB; Taylor & Creelman, 1967). Each trial started with a blank screen presented for 200 ms. Then, the stimulus was presented for 150 ms. Participants had 3,000 ms to respond. An auditory tone indicated erroneous responses. The next trial started after a delay of 500 ms.

#### *Bisection task with mouse adjustment*

Each trial started with a blank screen for 200 ms. Then, a bisection stimulus appeared at the center of the screen. The position of the central line was offset either to the left or to the right (up or down for horizontal stimuli) by 120 arc seconds for the small, 20'-wide vertical and horizontal stimuli and 240 arc seconds for the 40'-wide stimuli. The side of the offset was randomized across trials. The task of the participants was to adjust the central line to the smallest perceptible offset on the side on which the central line initially appeared. Observers were told that adjustments exceeding the central line should be avoided and are erroneous. Participants adjusted the central line by moving the computer mouse horizontally (on its  $y$ -axis). At the end of each adjustment, observers confirmed the position of their adjustment by pressing the left mouse button. An auditory feedback tone indicating the side to which observers adjusted the central line was provided. Adjustments placed on the left side of the center were followed by a 420-Hz tone and those on the right by a 580-Hz tone. Before the next trial, a blank screen was presented after observer's response for 500 ms. Adjustments shorter than 500 ms or longer than 15 s were rejected and replaced by new trials within the same block.

#### *Warming up*

On Day 1, participants first performed 80 practice trials to familiarize with the task (Figure 1C). As mentioned, these practice trials were performed with 40'-wide bisection stimuli. In all three experiments, 40 of those practice trials were performed with the horizontal stimulus and participants judged if the central line was above or below the center by pressing a left or a right button, respectively. In the remaining 40 practice trials, participants adjusted the central line to the smallest perceptible upper or lower (Experiment 1) or left or right (Experiments 2 and 3) offset. Importantly, during practice trials, the combination of the motor response, the orientation of the stimulus, and its width was never the same as during the training or the pre- and the posttraining tests. During the warming up

phase, the experimenter was present in the experimental room and ensured that observers understood the task.

## Data analysis

Learning was assessed by fitting a linear regression to individual training data. One-sample *t* tests were applied to the slopes of the regression lines with a null hypothesis that the mean of the sample is not different from zero. Pre- and posttraining tests performance was calculated by averaging the mean offsets (mouse adjustment) or the thresholds (button presses) from both blocks in each condition.

## Outlier rejection

Because the interest of the study concerned the transfer of learning, participants who did not improve performance during training were rejected from the analysis as no transfer is expected if there is no learning in the first place. Nonlearners were rejected if their performance during training decreased, i.e., if the slope of the fitted linear regression was positive. Participants that underwent two simultaneous trainings during each training session (double training; Experiments 2 and 3), had to have increasing performances (i.e., negative regression slopes) in both training types in order to be included in the data analysis. In total, eight participants were rejected from the analysis (Experiment 1: one participant; Experiment 2: three participants and Experiment 3: four participants).

## Experiment 1

It was recently shown that perceptual learning with a binary forced-choice task does not transfer to an adjustment task and vice versa, even though the stimuli were almost identical (Green et al., 2015; Grzeczowski, Cretenoud, et al., 2017). These results suggest that perceptual learning is specific for the type of motor response. Here, we first examined whether that specificity persists if both types of motor response are performed with the same hand and fingers, thus processed by the same brain hemisphere. Second, we investigated if perceptual learning transfers to the untrained hand for the trained type of motor response (mouse adjustment). Third, although it was proposed that longer training protocols lead to more specificity to the trained stimulus features (Ahissar & Hochstein, 1997, 2004; Jeter, Doshier, Liu, & Lu, 2010), it is still possible that the lack of transfer between the two types

of motor responses was due to an insufficient amount of training. Therefore, we extended the amount of training from two to four training sessions and tested if it yields more transfer.

## Methods

Ten participants took part in the experiment (five females; mean age: 20.9 years; range: 18–24 years). Prior to the experiment, participants' hand dominance was assessed with the Edinburgh handedness inventory (Oldfield, 1971). The experiment was conducted on 4 consecutive days (Figure 1C). Only the vertical bisection stimulus (Figure 1A) was used throughout the experiment (except for the warming up trials). On Day 1, participants were familiarized with the setup by performing 80 practice trials (warming up, cf. General methods). Then, participants' pretraining performance was measured in three conditions, two blocks per condition, 80 trials per block: (1) Participants adjusted the central line to the smallest perceptible offset by using a computer mouse. The mouse adjustment was performed with the hand that was not trained afterwards. (2) Participants judged if the central line was offset to the left or to the right by pressing the left or the right button of a computer mouse with the hand that subsequently was (2) and was not (3) trained. Then, participants performed seven blocks of training, each block containing 80 trials. During training, participants adjusted the central line of the bisection stimulus to the smallest offset they could perceive. On Day 2, participants performed seven blocks of training, followed by posttraining tests, which were composed of the three identical conditions as during the pretraining tests. On Day 3, participants performed seven blocks of training. On Day 4, participants performed the same session as on Day 2, i.e., seven blocks of training, followed by the posttraining tests. Five participants performed the training with their dominant and five with their nondominant hand. All the three test conditions composing the pre- and posttraining tests (pre, post, and post+) were counterbalanced across participants. Participants were free to take short breaks between blocks if they were feeling the need.

## Results

Performance improved over the 4 days of training (Figure 2A; mean slope =  $-0.34 \pm 0.22$ , one-sample *t* test,  $t[9] = 5.01$ ,  $p < 0.001$ ). Hand dominance had no significant effect on learning (dominant hand, mean slope =  $-0.39 \pm -0.29$  vs. nondominant hand, mean slope =  $-0.29 \pm 0.22$ ; paired *t* test,  $t[4] = 0.56$ ,  $p = 0.60$ ).

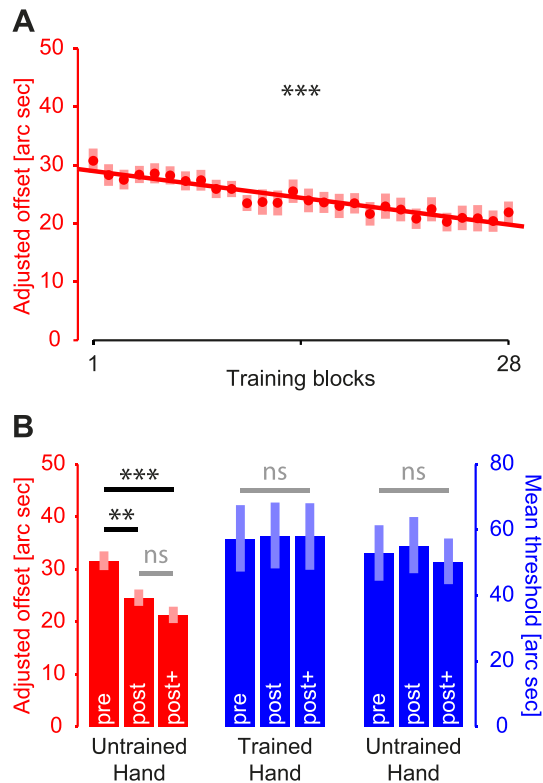


Figure 2. Mouse adjustment and button press bisection tasks are in red and blue, respectively. (A) Participants trained with a vertical bisection stimulus by adjusting the central line to the smallest perceptible offset with a computer mouse. Performance significantly improved over training ( $p < 0.001$ ). (B) Learning transferred to the untrained hand in the mouse adjustment condition (pre vs. post,  $p = 0.002$ ; pre vs. post+,  $p < 0.001$ ) but was not significantly stronger after 4 days of training as compared to 2 days of training (post vs. post+). There was no transfer of learning to the untrained motor response conditions, neither to the trained, nor to the untrained hand. Error bars represent  $\pm$  SEM.

We conducted one-way repeated-measures ANOVAs to assess the transfer of learning on the three conditions tested (adjustment with the untrained hand, button presses with the trained and, the untrained hand) at three different time points (pre, post, and post+). Learning transferred to the mouse adjustment condition performed with the untrained hand (Figure 2B, red;  $F[2, 18] = 20.18$ ,  $p < 0.001$ ; partial  $\eta^2 = 0.69$  [large]). This effect remained significant after Bonferroni correction for multiple comparisons ( $\alpha = 0.05/3 \approx 0.017$ ). Scheffé post hoc tests identified significant differences between the pre- and the posttest (pre vs. post;  $F[2, 18] = 9.00$ ,  $p = 0.002$ ) and between the pretest and the second posttest (pre vs. post+;  $F[2, 18] = 19.32$ ,  $p < 0.001$ ). The difference between the first and the second posttests was not statistically significant (post vs. post+;  $F[2, 18] = 1.95$ ,  $p = 0.17$ ) suggesting that a 4-day training does not induce a stronger transfer as

compared to a 2-day training. Learning did not transfer to the bisection task when participants used the left and right mouse buttons to judge the offsets with the trained (Figure 2B, blue;  $F[2, 18] = 0.005$ ,  $p = 0.99$ ), nor the untrained hand (Figure 2B, blue;  $F[2, 18] = 0.365$ ,  $p = 0.69$ ).

## Experiment 2

In double training, two stimuli features were shown to transfer across different trained locations (Mastropasqua et al., 2015; Wang et al., 2012, 2014; Xiao et al., 2008; J. Y. Zhang & Yang, 2014; J.-Y. Zhang et al., 2010; but see Liang, Zhou, Fahle, & Liu, 2015a, 2015b). For example, Xiao et al. (2008) demonstrated that training, in which observers learn to judge offsets of a vertical Vernier in one location and a horizontal Vernier in a second location, leads to a strong transfer between the two trained locations. In other words, the Vernier discrimination of both the horizontal and the vertical stimuli improved during training at both locations. Interestingly, it was shown that mechanisms underlying double training are also effective in releasing specificity in the visuomotor learning (Yin, Bi, Yu, & Wei, 2016). Here, we tested whether double training can overcome the specificity to motor responses. Observers trained with a vertical bisection stimulus with mouse adjustment and the horizontal bisection stimulus with button presses. In order to test whether double training enables transfer across stimuli and types of motor responses, we tested the untrained combinations of the stimulus orientation – motor response before and after training, i.e., the vertical stimulus with the button presses and the horizontal stimulus with the mouse adjustment.

## Methods

Ten participants were randomly enrolled in the experiment (four females; mean age: 20 years; range: 18–26 years). The experiment was conducted on 2 consecutive days (Figure 1C). On Day 1, participants were familiarized with the setup by performing 80 practice trials (warming up, cf. General methods). Before the training, participants' pretraining baseline performance was measured in two conditions, two blocks of 80 trials each: (1) Participants judged whether the central line of a vertical bisection stimulus (Figure 1A) was offset to the left or to the right by pressing either a left or a right push button, respectively. (2) Participants adjusted the central line of a horizontal bisection stimulus (Figure 1B) to the

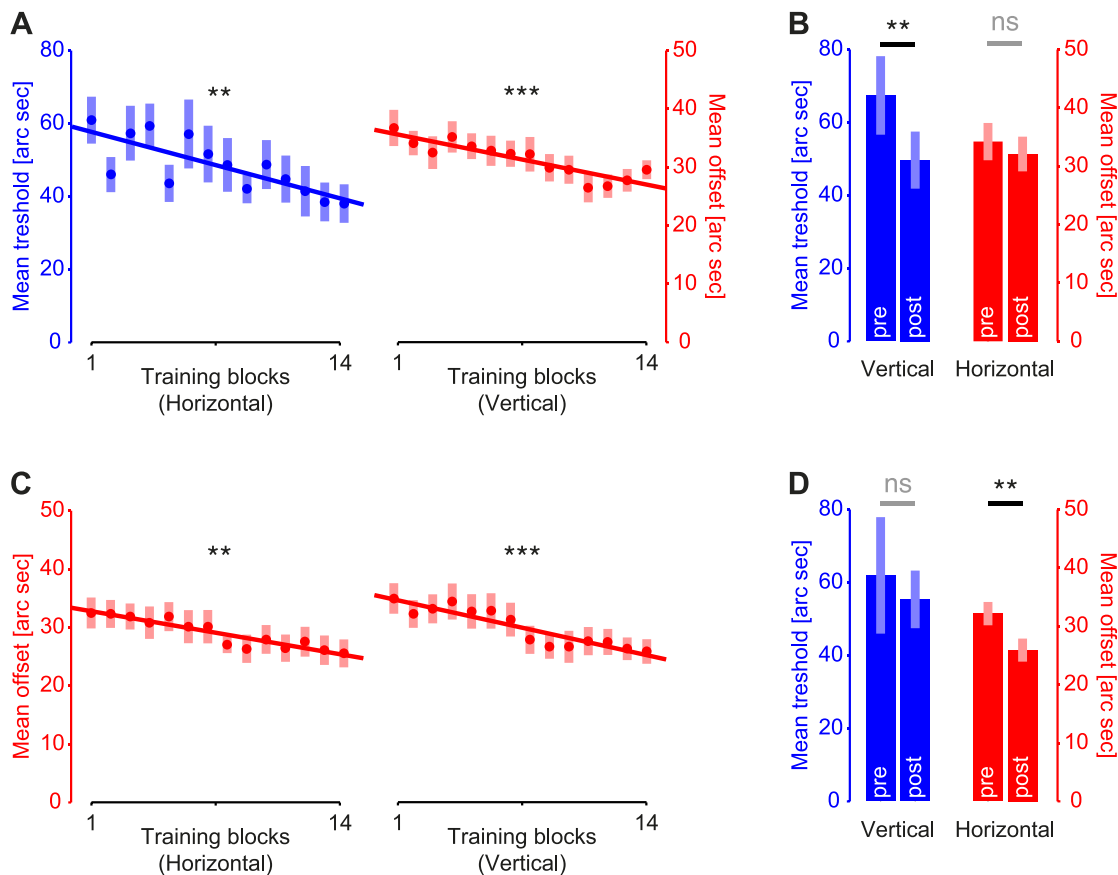


Figure 3. Learning curves for the double training with the horizontal and the vertical stimuli in Experiments 2 (A) and 3 (C). Mouse adjustment and button press conditions are shown in red and blue, respectively. Performance improved significantly in both trained conditions for both experiments. Pre- and posttraining tests in Experiments 2 (B) and 3 (D). In Experiment 2, learning transferred to the vertical, button press condition (blue bars) but not to the horizontal, mouse adjustment condition (red bars). In Experiment 3, learning did not transfer to the vertical, button press condition. The pre- and posttraining tests with the horizontal stimulus were significantly different, confirming that learning occurred. Error bars indicate  $\pm$  SEM.

smallest upper or lower offset with a computer mouse. Next, participants performed 14 blocks of training. For seven training blocks, participants were presented with the horizontal bisection stimulus (Figure 1B) and had to judge the offset of the central line to be below or above the middle by pressing a left or a right push button, respectively. For the remaining seven training blocks, participants trained to adjust the central line of the vertical bisection stimulus (Figure 1A) to the smallest left or right offset using the computer mouse. On Day 2, participants performed again 14 blocks of the same training followed by the posttests which were identical to the pretests. The two trainings were performed sequentially, i.e., participants first performed seven blocks of one type of training and then the seven blocks of the other training. The order of the two trainings was counterbalanced across participants but it was the same for a given participant on both days. The two conditions composing the pre- and posttraining tests were counterbalanced across par-

ticipants. Participants were free to take short breaks between blocks.

## Results

Participants significantly improved performance in both types of training, i.e., the button presses with the horizontal bisection stimulus (Figure 3A, blue; mean slope =  $-1.43 \pm 1.32$ , one-sample  $t$  test,  $t[9] = 3.43$ ,  $p = 0.008$ ) and the mouse adjustment with the vertical bisection stimulus (Figure 3A, red; mean slope =  $-0.67 \pm 0.36$ , one-sample  $t$  test,  $t[9] = 5.9$ ,  $p < 0.001$ ). Learning transferred to the button press condition with the vertical bisection stimulus (Figure 3B, blue; paired  $t$  test,  $t[9] = 3.46$ ,  $p = 0.007$ ) but not to the mouse adjustment condition with the horizontal bisection stimulus (Figure 3B, red; paired  $t$  test,  $t[9] = 0.912$ ,  $p = 0.4$ ). Significant effects remained significant after Bonferroni correction for multiple comparisons ( $\alpha = 0.05/4 \approx 0.013$ ).

## Experiment 3

Experiment 2 showed that double training enables transfer to an untrained, stimulus' orientation—motor response type combination, i.e., the button presses with the vertical bisection stimulus. Inversely, in the following experiment, we investigated if the exposure to the button press motor response (untrained, transfer motor response) during double training is necessary for that transfer to occur.

## Methods

Ten different participants took part in the experiment (eight females; mean age: 21 years; range: 18–26 years). The experimental protocol was the same as in Experiment 2 except that during training, both bisection stimuli, i.e., the vertical and the horizontal stimuli, were trained with the same type of motor response, i.e., mouse adjustment.

## Results

Participants improved performance with the mouse adjustment trainings with both stimuli (Figure 3C; horizontal bisection, mean slope =  $-0.58 \pm 0.43$ , one-sample  $t$  test,  $t[9] = 4.23$ ,  $p = 0.002$ ; vertical bisection, mean slope =  $-0.74 \pm 0.35$ , one-sample  $t$  test,  $t[9] = 6.67$ ,  $p < 0.001$ ). The difference between the pre- and posttraining mouse adjustment condition with the horizontal bisection stimulus was significant, confirming that learning took place (Figure 3D, red; paired  $t$  test,  $t[9] = 4.66$ ,  $p = 0.001$ ). Learning did not transfer to the button press condition with the vertical bisection stimulus (Figure 3D, blue; paired  $t$  test,  $t[9] = 0.52$ ,  $p = 0.6$ ). Significant effects remained significant after Bonferroni correction for multiple comparisons ( $\alpha = 0.05/4 \approx 0.013$ ). Results suggest that during training in Experiment 2, the exposure to the button press condition is necessary for learning to transfer to the horizontal condition.

## Discussion

In the early days, perceptual learning was dominated by the question of where it occurs in the visual hierarchy. Behavioral studies (Fiorentini & Berardi, 1981; Karni & Sagi, 1991; Poggio, Fahle, & Edelman, 1992; Ramachandran, 1976; Ramachandran & Brad-dick, 1973; Vogels & Orban, 1985) and electrophysiological findings (Crist et al., 2001; Schoups et al., 2001)

showing high specificity of perceptual learning were taken as evidence that perceptual learning is mediated by neural changes at the early stages of visual processing such as V1. In the last decades, later sensory and decision-making stages were favored (Doshier & Lu, 1998, 1999; Ghose, 2004; Ghose et al., 2002; Mollon & Danilova, 1996; Petrov et al., 2005) based on findings that task-irrelevant perceptual learning (Choi et al., 2009; Galliussi et al., 2018; Seitz et al., 2009; Seitz & Watanabe, 2009; Watanabe et al., 2001) and double training (Mastropasqua et al., 2015; Wang et al., 2014, 2012; Xiao et al., 2008; J. Y. Zhang & Yang, 2014; T. Zhang et al., 2010) can prevent the specificity of perceptual learning. Other studies showed that perceptual learning can reorganize drastically visual cortical areas functionally (Chen et al., 2016; Shibata, Sasaki, Kawato, & Watanabe, 2016; Shibata et al., 2011), suggesting even more complicated scenarios. However, all theories agree that decision making is the last crucial stage for perceptual learning. One reason seems to be that the stimulus alternatives (left vs. right offset) can be arbitrarily mapped onto any type of motor response (button presses, verbal responses, eye movements, etc.). We recently showed however that perceptual learning can also be specific for the type of motor response (Grzeczkowski et al., 2017).

Here, we first replicated this finding and showed that training with mouse adjustments does not transfer to button presses even if motor effectors (here, the hand and fingers) are the same in both motor response conditions (Experiment 1, Figure 2B, blue). This result shows that even if the motor-related processes are lateralized in the same brain hemisphere, the specificity to the trained motor response persists. This rules out the possibility that perceptual learning is specific for motor-related processes such as motor execution. Green et al. (2015) found no transfer from an estimation (mouse adjustment) to a categorical task (binary button presses) for an orientation discrimination task, but a different explanation was proposed. They proposed that a binary and adjustment tasks differ in the optimal solution the observer must adopt to solve the task. Both tasks thus refer to different learning rules. Because in a categorical task, the reference orientation was constant throughout the experiment, the optimal solution would be to sharpen a discriminant dividing the visual space in two decisional regions. In the estimation task, however, where the orientation of the stimulus to match was varied randomly from trial to trial, the optimal solution would be a regression line that continuously maps stimulus orientation to a motor response. This explanation does not hold for our results because crucially, in our study, the middle of the bisection space was constant in the adjustment condition. Therefore, the optimal solution for both, binary and adjustment conditions would be

the same discriminant that divides the bisection space in two.

Second, we showed that learning transfers to the untrained hand and fingers when the type of the motor response remains the same, namely mouse adjustment (Experiment 1, Figure 2B, red). This result is in accordance with the motor learning literature showing that learned movements are transferred across hands and are thus effector independent (Grafton, Hazeltine, & Ivry, 2002; Perez et al., 2007; Witt, Margraf, Bieber, Born, & Deuschl, 2010). This result demonstrates that perceptual learning with mouse adjustments can elicit transfer to untrained conditions and that the lack of transfer to button press conditions is not due to the insufficient amount of training or lack of statistical power. In other words, we do find transfers when these are expected.

Third, we showed that an extension of training from two to four sessions has no significant effect on transfer, therefore confirming the validity of our two-day protocol.

Fourth, with a double training procedure, we showed transfer to the untrained combination of stimulus orientation and motor response type, i.e., the vertical bisection with button presses (Experiment 2, Figure 3B, blue). In Experiment 3, the improvements in that transfer condition were nonsignificant (Figure 3D, blue) since during double training observers were not exposed to button presses. These results indicate that perceptual learning can transfer to other types of motor response. Importantly however, the visual signals, which undergo plasticity, must be encoded during training to motor response types that will be subsequently used in the posttraining test. Similar reasoning was recently proposed to explain specificity and transfer in visual perceptual learning (rule-based learning; Xiong et al., 2016; T. Zhang et al., 2010). According to that model, transfer of perceptual learning is ensured if functional connections between high-level neurons and low-level neurons coding for untrained stimulus features are established through bottom-up and/or top-down activations. Similarly, we show in Experiment 3 that the exposure to the untrained motor response (button presses) and therefore the underlying neuronal activations are necessary to ensure a significant transfer. Our results, together with the findings that double training can overcome motor learning specificity and that perceptual and motor learning share similar mechanisms (Censor, Sagi, & Cohen, 2012), suggest that not only visual features, but also relevant motor actions could potentially be explained by the rule-based learning.

Interestingly, the transfer to the other combination of untrained stimulus orientation and motor response type, i.e., the horizontal bisection task performed with mouse adjustment, was nonsignificant in Experiment 2

(Figure 3, red). This confirms that unlike for binary actions (e.g., button presses), learned visuomotor contingencies are much stronger for continuous, interactive actions such as mouse adjustments (Cisek, 2007; Cisek & Kalaska, 2010; Grzeczowski, Cretenoud, et al., 2017; Vahdat, Darainy, Milner, & Ostry, 2011). This is in line with the literature showing that for continuous actions (i.e., not binary perceptual reports), sensory and motor signals are strongly related at the behavioral level (Beets, 't Hart, et al., 2010; Beets, Rosler, & Fiehler, 2010; Brown, Wilson, Goodale, & Gribble, 2007; Casile and Giese, 2006; Hecht, Vogt, & Prinz, 2001) and neural level in humans (Engel, Burke, Fiehler, Bien, & Rösler, 2008; Reithler, van Mier, Peters, & Goebel, 2007; Vahdat et al., 2011) and animals (Matyas et al., 2010; Poort et al., 2015; Saleem, Ayaz, Jeffery, Harris, & Carandini, 2013). For example, it was shown that a mere visual exposure to movements activates motor-related brain areas in human (Engel et al., 2008; Reithler et al., 2007). In mice, it was found that motor activity strongly modifies neural responses in primary visual cortex (Poort et al., 2015; Saleem et al., 2013). Thus, it seems that at the neural level, in protocols using continuous motor responses, it is difficult to clearly distinguish between perceptual and motor processes. Furthermore, there is growing evidence showing that, for certain sensorimotor tasks, perception, decision making, motor planning, as well as the transformation of these signals into actions are processed within the same sensorimotor circuits (Cisek & Kalaska, 2005; Pesaran, Nelson, & Andersen, 2008; Romo, Hernández, & Zainos, 2004; Romo, Hernández, Zainos, Lemus, & Brody, 2002). For example, it was shown that posterior parietal cortex (PPC) represents sensory information of objects of interest present in the environment, as well as decision making, and action-related processes (Buneo, Jarvis, Batista, & Anderson, 2002; Dorris & Glimcher, 2004; Kalaska & Crammond, 1995; Sugrue, Corrado, & Newsome, 2004; Yang & Shadlen, 2007; for reviews, see Andersen & Buneo, 2002; Colby & Goldberg, 1999; Stein, 1992).

Accordingly, our present and previous (Grzeczowski, Cretenoud et al., 2017) results suggest that, perceptual, decisional, and, motor signals are encoded together when during perceptual learning continuous actions are performed. This is in accordance with theories (Cisek, 2007; Cisek & Kalaska, 2010; Gibson, 1979; Hommel, Müsseler, Aschersleben, & Prinz, 2001; O'Regan & Noë, 2002; Prinz, 1997) showing that perceptual, decisional, and motor processes are hardly dissociable for continuous actions (for reviews, see Cisek & Kalaska, 2010; Gold & Shadlen, 2007; Lebedev & Wise, 2002; Ostry & Gribble, 2016).

It was proposed that sensory information is simultaneously transformed into several, relevant motor



plans (or affordances; action specification) while one of them is chosen (decision making; action selection) for the final action (affordance competition hypothesis; Cisek, 2007; Cisek & Kalaska, 2005, 2010). Here, we do not claim that stimuli are in general coded together with actions. We propose, that during *intensive training*, sensory information becomes strongly associated with the trained motor plans while other, nontrained motor plans are excluded from the competition for action specification after training. This results in motor response specificity unless other motor plans are still available for action specification during training like in double training.

There seems to be no large common factor for vision (Bosten & Mollon, 2010; Cappe, Clarke, Mohr, & Herzog, 2014; Grzeczowski et al., 2018; Grzeczowski, Clarke, Francis, Mast, & Herzog, 2017). For example, it was found that Vernier acuity correlates only weakly with Gabor detection or Landolt-C acuity (Cappe et al., 2014). Thus, it might be that this hyperspecificity comes from the way we measure visual performance, i.e., by dissociating learned sensory signals from their context-relevant decisional (including intentions) and motor processes. Overney, Blanke, and Herzog (2008) tested visual abilities of tennis players and nonathletes with a battery of seven visual tests, namely coherent motion discrimination, speed discrimination, visual backward masking, tennis ball detection, pattern detection, attentional blink, and flash lag illusion. Surprisingly, except for a few measurements, tennis players had the same performance as the nonathletes. We propose that perceptual learning protocols that aim to be applied in rehabilitation, education, sport, etc., should be designed beyond the classic information processing framework that promotes segregation of perception, cognition, and action, but rather involve context-relevant actions into training protocols that might result in better transfer.

Taken together, our results suggest that perceptual, decisional, and motor associations created during perceptual learning are much stronger than it was thought before. Encoded together during training, perceptual, decisional, and motor signals cannot easily be disentangled.

*Keywords:* perceptual learning, double training, transfer, specificity, bisection, perception-action

## Acknowledgments

We thank Marc Reppow for technical support; Lukasz Grzeczowski was funded by the project “Learning from Delayed and Sparse Feedback” (project number: CRSII2\_147636) of the Swiss National Science Foundation.

Commercial relationships: none.

Corresponding author: Lukasz Grzeczowski.

Email: lukasz.grzeczowski@gmail.com.

Address: Ludwig-Maximilians-Universität, Department Psychologie, München, Germany.

## References

- Aberg, K. C., & Herzog, M. H. (2009). Interleaving bisection stimuli—randomly or in sequence—does not disrupt perceptual learning, it just makes it more difficult. *Vision Research*, *49*(21), 2591–2598.
- Adab, H., & Vogels, R. (2011). Practicing coarse orientation discrimination improves orientation signals in macaque cortical area V4. *Current Biology*, *21*(19), 1661–1666, <https://doi.org/10.1016/j.cub.2011.08.037>.
- Ahissar, M., & Hochstein, S. (1996). Learning pop-out detection: Specificities to stimulus characteristics. *Vision Research*, *36*(21), 3487–3500, [https://doi.org/10.1016/0042-6989\(96\)00036-3](https://doi.org/10.1016/0042-6989(96)00036-3).
- Ahissar, M., & Hochstein, S. (1997, May 22). Task difficulty and the specificity of perceptual learning. *Nature*, *387*(6631), 401–406, <https://doi.org/10.1038/387401a0>.
- Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Sciences*, *8*(10), 457–464, <https://doi.org/10.1016/j.tics.2004.08.011>.
- Andersen, R. A., & Buneo, C. A. (2002). Intentional maps in posterior parietal cortex. *Annual Review of Neuroscience*, *25*(1), 189–220, <https://doi.org/10.1146/annurev.neuro.25.112701.142922>.
- Bach, M. (1996). The Freiburg Visual Acuity test—Automatic measurement of visual acuity. *Optometry and Vision Science*, *73*(1), 49–53.
- Ball, K., & Sekuler, R. (1982, November 12). A specific and enduring improvement in visual motion discrimination. *Science*, *218*(4573), 697–698, <https://doi.org/10.1126/science.7134968>.
- Ball, K., & Sekuler, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research*, *27*(6), 953–965, [https://doi.org/10.1016/0042-6989\(87\)90011-3](https://doi.org/10.1016/0042-6989(87)90011-3).
- Beets, I. A., 't Hart, B. M., Rösler, F., Henriques, D. Y. P., Einhäuser, W., & Fiehler, K. (2010). Online action-to-perception transfer: Only percept-dependent action affects perception. *Vision Research*, *50*(24), 2633–2641, <https://doi.org/10.1016/j.visres.2010.10.004>.
- Beets, I. A., Rosler, F., & Fiehler, K. (2010). Nonvisual

- motor learning improves visual motion perception: Evidence from violating the two-thirds power law. *Journal of Neurophysiology*, *104*(3), 1612–1624, <https://doi.org/10.1152/jn.00974.2009>.
- Berardi, N., & Fiorentini, A. (1987). Interhemispheric transfer of visual information in humans: Spatial characteristics. *The Journal of Physiology*, *384*, 633–647. Retrieved from <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1192282&tool=pmcentrez&rendertype=abstract>
- Bosten, J. M., & Mollon, J. D. (2010). Is there a general trait of susceptibility to simultaneous contrast? *Vision Research*, *50*(17), 1656–1664, <https://doi.org/10.1016/j.visres.2010.05.012>.
- Brown, L. E., Wilson, E. T., Goodale, M. A., & Gribble, P. L. (2007). Motor force field learning influences visual processing of target motion. *Journal of Neuroscience*, *27*(37), 9975–9983, <https://doi.org/10.1523/JNEUROSCI.1245-07.2007>.
- Buneo, C. A., Jarvis, M. R., Batista, A. P., & Andersen, R. A. (2002, April 11). Direct visuomotor transformations for reaching. *Nature*, *416*(6881), 632–636, <https://doi.org/10.1038/416632a>.
- Cappe, C., Clarke, A., Mohr, C., & Herzog, M. H. (2014). Is there a common factor for vision? *Journal of Vision*, *14*(8):4, 1–11. <https://doi.org/10.1167/14.8.4>. [PubMed] [Article]
- Casile, A., & Giese, M. A. (2006). Nonvisual motor training influences biological motion perception. *Current Biology*, *16*(1), 69–74, <https://doi.org/10.1016/j.cub.2005.10.071>.
- Censor, N., Sagi, D., & Cohen, L. G. (2012). Common mechanisms of human perceptual and motor learning. *Nature Reviews Neuroscience*, *13*(9), 658–664, <https://doi.org/10.1038/nrn3315>.
- Chen, N., Cai, P., Zhou, T., Thompson, B., & Fang, F. (2016). Perceptual learning modifies the functional specializations of visual cortical areas. *Proceedings of the National Academy of Sciences*, *113*(20), 5724–5729, <https://doi.org/10.1073/PNAS.1524160113>.
- Choi, H., Seitz, A. R., & Watanabe, T. (2009). When attention interrupts learning: inhibitory effects of attention on TIPL. *Vision Research*, *49*(21), 2586–2590, <https://doi.org/10.1016/j.visres.2009.07.004>.
- Cisek, P. (2007). Cortical mechanisms of action selection: the affordance competition hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1485), 1585–1599. <https://doi.org/10.1098/rstb.2007.2054>
- Cisek, P., & Kalaska, J. F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: Specification of multiple direction choices and final selection of action. *Neuron*, *45*(5), 801–814, <https://doi.org/10.1016/j.neuron.2005.01.027>.
- Cisek, P., & Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. *Annual Review of Neuroscience*, *33*(1), 269–298, <https://doi.org/10.1146/annurev.neuro.051508.135409>.
- Colby, C. L., & Goldberg, M. E. (1999). Space and attention in parietal cortex. *Annual Review of Neuroscience*, *22*, 319–349, <https://doi.org/10.1146/annurev.neuro.22.1.319>.
- 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, <https://doi.org/10.1152/jn.1997.78.6.2889>.
- Crist, R., Li, W., & Gilbert, C. D. (2001). Learning to see: Experience and attention in primary visual cortex. *Nature Neuroscience*, *4*(5), 519–525, <https://doi.org/10.1038/87470>.
- Dorris, M. C., & Glimcher, P. W. (2004). Activity in posterior parietal cortex is correlated with the relative subjective desirability of action. *Neuron*, *44*(2): 365–378, <https://doi.org/10.1016/j.neuron.2004.09.009>.
- Dosher, B. A., & Lu, Z.-L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proceedings of the National Academy of Sciences*, *95*(23), 13988–13993, <https://doi.org/10.1073/pnas.95.23.13988>.
- Dosher, B. A., & Lu, Z.-L. (1999). Mechanisms of perceptual learning. *Vision Research*, *39*(19), 3197–3221, [https://doi.org/10.1016/S0042-6989\(99\)00059-0](https://doi.org/10.1016/S0042-6989(99)00059-0).
- Engel, A., Burke, M., Fiehler, K., Bien, S., & Rösler, F. (2008). Motor learning affects visual movement perception. *European Journal of Neuroscience*, *27*(9), 2294–2302, <https://doi.org/10.1111/j.1460-9568.2008.06200.x>.
- Fahle, M., & Edelman, S. (1993). Long-term learning in vernier acuity: Effects of stimulus orientation, range and of feedback. *Vision Research*, *33*(3), 397–412, [https://doi.org/10.1016/0042-6989\(93\)90094-D](https://doi.org/10.1016/0042-6989(93)90094-D).
- Fiorentini, A., & Berardi, N. (1981). Learning in grating waveform discrimination: Specificity for orientation and spatial frequency. *Vision Research*, *21*(7), 1149–1158, [https://doi.org/10.1016/0042-6989\(81\)90017-1](https://doi.org/10.1016/0042-6989(81)90017-1).
- Fodor, J. A. (1983). *Modularity of mind: An essay on faculty psychology*. Cambridge, MA: MIT Press.

- Galliussi, J., Grzeczowski, L., Gerbino, W., Herzog, M. H., & Bernardis, P. (2018). Is lack of attention necessary for task-irrelevant perceptual learning? *Vision Research*, *152*, 118–125, <https://doi.org/10.1016/j.visres.2017.10.006>.
- Ghose, G. M. (2004). Learning in mammalian sensory cortex. *Current Opinion in Neurobiology*, *14*(4), 513–518, <https://doi.org/10.1016/j.conb.2004.07.003>.
- Ghose, G. M., Yang, T., & Maunsell, J. H. R. (2002). Physiological correlates of perceptual learning in monkey V1 and V2. *Journal of Neurophysiology*, *87*(4), 1867–1888, <https://doi.org/10.1152/jn.00690.2001>.
- Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston: Houghton Mifflin.
- Gold, J. I., & Shadlen, M. N. (2007). The neural basis of decision making. *Annual Review of Neuroscience*, *30*(1), 535–574, <https://doi.org/10.1146/annurev.neuro.29.051605.113038>.
- Grafton, S. T., Hazeltine, E., & Ivry, R. B. (2002). Motor sequence learning with the nondominant left hand: A PET functional imaging study. *Experimental Brain Research*, *146*(3), 369–378, <https://doi.org/10.1007/s00221-002-1181-y>.
- Green, S. C., Kattner, F., Siegel, M. H., Kersten, D., & Schrater, P. R. (2015). Differences in perceptual learning transfer as a function of training task. *Journal of Vision*, *15*(10):5, 1–14, <https://doi.org/10.1167/15.10.5>. [PubMed] [Article]
- Grzeczowski, L., Clarke, A. M., Francis, G., Mast, F. W., & Herzog, M. H. (2017). About individual differences in vision. *Vision Research*, *141*, 282–292, <https://doi.org/10.1016/j.visres.2016.10.006>.
- Grzeczowski, L., Cretenoud, A. F., Herzog, M. H., & Mast, F. W. (2017). Perceptual learning is specific beyond vision and decision making. *Journal of Vision*, *17*(6):6, 1–11, <https://doi.org/10.1167/17.6.6>. [PubMed] [Article]
- Grzeczowski, L., Roinishvili, M., Chkonia, E., Brand, A., Mast, F. W., Herzog, M. H., & Shaqiri, A. (2018). Is the perception of illusions abnormal in schizophrenia? *Psychiatry Research*, *270*, 929–939, <https://doi.org/10.1016/j.psychres.2018.10.063>.
- Grzeczowski, L., Tartaglia, E. M., Mast, F. W., & Herzog, M. H. (2015). Linking perceptual learning with identical stimuli to imagery perceptual learning. *Journal of Vision*, *15*(10):13, 1–8, <https://doi.org/10.1167/15.10.13>. [PubMed] [Article]
- Hecht, H., Vogt, S., & Prinz, W. (2001). Motor learning enhances perceptual judgment: A case for action-perception transfer. *Psychological Research*, *65*(1), 3–14, <https://doi.org/10.1007/s004260000043>.
- Herzog, M. H., Aberg, K. C., Frémaux, N., Gerstner, W., & Sprekeler, H. (2012). Perceptual learning, roving and the unsupervised bias. *Vision Research*, *61*, 95–99, <https://doi.org/10.1016/j.visres.2011.11.001>.
- Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *The Behavioral and Brain Sciences*, *24*(5), 849–878, <https://doi.org/10.1017/S0140525X01000103>.
- Huang, X., Lu, H., Tjan, B. S., Zhou, Y., & Liu, Z. (2007). Motion perceptual learning: When only task-relevant information is learned. *Journal of Vision*, *7*(10):14, 1–10, <https://doi.org/10.1167/7.10.14>. [PubMed] [Article]
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *The Journal of Physiology*, *195*(1), 215–243, <https://doi.org/papers://47831562-1F78-4B52-B52E-78BF7F97A700/Paper/p352>.
- Hubel, D. H., Wiesel, T. N., & LeVay, S. (1977). Plasticity of ocular dominance columns in monkey striate cortex. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *278*(961), 377–409, <https://doi.org/10.1098/rstb.1977.0050>.
- Jeter, P. E., Doshier, B. A., Liu, S. H., & Lu, Z. L. (2010). Specificity of perceptual learning increases with increased training. *Vision Research*, *50*(19), 1928–1940, <https://doi.org/10.1016/j.visres.2010.06.016>.
- Johnson-Laird, P. N. (1988). *The computer and the mind: An introduction to cognitive science*. Cambridge, MA: Harvard University Press.
- Kalaska, J. F., & Crammond, D. J. (1995). Deciding not to GO: Neuronal correlates of response selection in a GO/NOGO task in primate premotor and parietal cortex. *Cerebral Cortex*, *5*(5), 410–428, <https://doi.org/10.1093/cercor/5.5.410>.
- 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, USA*, *88*(11), 4966–4970, <https://doi.org/10.1073/pnas.88.11.4966>.
- Keele, S. W. (1968). Movement control in skilled motor performance. *Psychological Bulletin*, *70*(6, Pt.1), 387–403, <https://doi.org/10.1037/h0026739>.
- 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, <https://doi.org/10.1038/nn2070>.
- Lebedev, M. A., & Wise, S. P. (2002). Insights into seeing and grasping: Distinguishing the neural correlates of perception and action. *Behavioral and*

- Cognitive Neuroscience Reviews*, 1(2), 108–129, <https://doi.org/10.1177/1534582302001002002>.
- Li, W. (2016). Perceptual learning: Use-dependent cortical plasticity. *Annual Review of Vision Science*, 2(1), 109–130, <https://doi.org/10.1146/annurev-vision-111815-114351>.
- Liang, J., Zhou, Y., Fahle, M., & Liu, Z. (2015a). Limited transfer of long-term motion perceptual learning with double training. *Journal of Vision*, 15(10):1, 1–9, <https://doi.org/10.1167/15.10.1>. [PubMed] [Article]
- Liang, J., Zhou, Y., Fahle, M., & Liu, Z. (2015b). Specificity of motion discrimination learning even with double training and staircase. *Journal of Vision*, 15(10):3, 1–10, <https://doi.org/10.1167/15.10.3>. [PubMed] [Article]
- Marr, D. C. (1982). *Vision: A computational investigation into the human representation and processing of visual information*. San Francisco, CA: W.H. Freeman.
- Mastropasqua, T., Galliussi, J., Pascucci, D., & Turatto, M. (2015). Location transfer of perceptual learning: Passive stimulation and double training. *Vision Research*, 108, 93–102, <https://doi.org/10.1016/j.visres.2015.01.024>.
- Matyas, F., Sreenivasan, V., Marbach, F., Wacongne, C., Barsy, B., Mateo, C., . . . Petersen, C. C. H. (2010, November 26). Motor control by sensory cortex. *Science*, 330(6008), 1240–1243, <https://doi.org/10.1126/science.1195797>.
- McGovern, D. P., Webb, B. S., & Peirce, J. W. (2012). Transfer of perceptual learning between different visual tasks. *Journal of Vision*, 12(11):4, 1–11, <https://doi.org/10.1167/12.11.4>. [PubMed] [Article]
- Michaels, C. F. (2000). Information, perception, and action: What should ecological psychologists learn from Milner and Goodale (1995)? *Ecological Psychology*, 12(3), 241–258, [https://doi.org/10.1207/S15326969ECO1203\\_4](https://doi.org/10.1207/S15326969ECO1203_4).
- Miller, G. A., Galanter, E., & Pribram, K. H. (1960). *Plans and the structure of behavior*. New York, NY: Holt, Rinehart and Winston. <https://doi.org/10.1037/10039-000>
- Mollon, J. D., & Danilova, M. V. (1996). Three remarks on perceptual learning. *Spatial Vision*, 10(1), 51–58, <https://doi.org/10.1163/156856896X00051>.
- O'Regan, J. K., & Noë, A. (2002). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences*, 24(5), 939–973, <https://doi.org/10.1017/S0140525X01000115>.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113, [https://doi.org/10.1016/0028-3932\(71\)90067-4](https://doi.org/10.1016/0028-3932(71)90067-4).
- Ostry, D. J., & Gribble, P. L. (2016). Sensory plasticity in human motor learning. *Trends in Neurosciences*, 39(2), 114–123, <https://doi.org/10.1016/j.tins.2015.12.006>.
- Otto, T. U., Herzog, M. H., Fahle, M., & Zhaoping, L. (2006). Perceptual learning with spatial uncertainties. *Vision Research*, 46(19), 3223–3233, <https://doi.org/10.1016/j.visres.2006.03.021>.
- Overney, L. S., Blanke, O., & Herzog, M. H. (2008). Enhanced temporal but not attentional processing in expert tennis players. *PLoS One*, 3(6), e2380, <https://doi.org/10.1371/journal.pone.0002380>.
- Parkosadze, K., Otto, T. U., Malania, M., Kezeli, A., & Herzog, M. H. (2008). Perceptual learning of bisection stimuli under roving: Slow and largely specific. *Journal of Vision*, 8(1):5, 1–8, <https://doi.org/10.1167/8.1.5>. [PubMed] [Article]
- Perez, M. A., Tanaka, S., Wise, S. P., Sadato, N., Tanabe, H. C., Willingham, D. T., & Cohen, L. G. (2007). Neural substrates of intermanual transfer of a newly acquired motor skill. *Current Biology*, 17(21), 1896–1902, <https://doi.org/10.1016/j.cub.2007.09.058>.
- Pesaran, B., Nelson, M. J., & Andersen, R. A. (2008, May 15). Free choice activates a decision circuit between frontal and parietal cortex. *Nature*, 453(7193): 406–409, <https://doi.org/10.1038/nature06849>.
- Petrov, A. A., Doshier, B. A., & Lu, Z.-L. (2005). The dynamics of perceptual learning: An incremental reweighting model. *Psychological Review*, 112(4), 715–743, <https://doi.org/10.1037/0033-295X.112.4.715>.
- Poggio, T., Fahle, M., & Edelman, S. (1992, May 15). Fast perceptual learning in visual hyperacuity. *Science*, 256(5059), 1018–1021, <https://doi.org/10.1126/science.1589770>.
- Poort, J., Khan, A. G., Pachitariu, M., Nemri, A., Orsolich, I., Krupic, J., . . . Hofer, S. B. (2015). Learning enhances sensory and multiple non-sensory representations in primary visual cortex. *Neuron*, 86(6), 1478–1490, <https://doi.org/10.1016/j.neuron.2015.05.037>.
- Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology*, 9(2), 129–154, <https://doi.org/10.1080/713752551>.
- Pylyshyn, Z. W. (1984). *Computation and cognition: Toward a foundation for cognitive science*. Psychological Review. Cambridge, MA: MIT Press. [https://doi.org/10.1016/0004-3702\(89\)90062-3](https://doi.org/10.1016/0004-3702(89)90062-3)

- Raiguel, S., Vogels, R., Mysore, S. G., & Orban, G. A. (2006). Learning to see the difference specifically alters the most informative V4 neurons. *The Journal of Neuroscience*, *26*(24), 6589–6602, <https://doi.org/10.1523/JNEUROSCI.0457-06.2006>.
- Ramachandran, V. S. (1976, July 29). Learning-like phenomena in stereopsis. *Nature*, *262*(5567), 382–384, <https://doi.org/10.1038/262382a0>.
- Ramachandran, V. S., & Braddick, O. (1973). Orientation-specific learning in stereopsis. *Perception*, *2*(3), 371–376, <https://doi.org/10.1068/p020371>.
- Reithler, J., van Mier, H. I., Peters, J. C., & Goebel, R. (2007). Nonvisual motor learning influences abstract action observation. *Current Biology*, *17*(14), 1201–1207, <https://doi.org/10.1016/j.cub.2007.06.019>.
- Romo, R., Hernández, A., & Zainos, A. (2004). Neuronal correlates of a perceptual decision in ventral premotor cortex. *Neuron*, *41*(1), 165–173, [https://doi.org/10.1016/S0896-6273\(03\)00817-1](https://doi.org/10.1016/S0896-6273(03)00817-1).
- Romo, R., Hernández, A., Zainos, A., Lemus, L., & Brody, C. D. (2002). Neuronal correlates of decision-making in secondary somatosensory cortex. *Nature Neuroscience*, *5*(11), 1217–1225, <https://doi.org/10.1038/nn950>.
- Sagi, D. (2011). Perceptual learning in Vision Research. *Vision Research*, *51*(13), 1552–1566, <https://doi.org/10.1016/j.visres.2010.10.019>.
- Saleem, A. B., Ayaz, A., Jeffery, K. J., Harris, K. D., & Carandini, M. (2013). Integration of visual motion and locomotion in mouse visual cortex. *Nature Neuroscience*, *16*(12), 1864–1869, <https://doi.org/10.1038/nn.3567>.
- Schoups, A., & Orban, G. A. (1996). Interocular transfer in perceptual learning of a pop-out discrimination task. *Proceedings of the National Academy of Sciences, USA*, *93*(14), 7358–7362, <https://doi.org/10.1073/pnas.93.14.7358>.
- Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001, August 2). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, *412*(6846), 549–553, <https://doi.org/10.1038/35087601>.
- Seitz, A., Kim, D., & Watanabe, T. (2009). Rewards evoke learning of unconsciously processed visual stimuli in adult humans. *Neuron*, *61*(5), 700–707, <https://doi.org/10.1016/j.neuron.2009.01.016>.
- Seitz, A., & Watanabe, T. (2009). The phenomenon of task-irrelevant perceptual learning. *Vision Research*, *49*(21), 2604–2610, <https://doi.org/10.1016/j.visres.2009.08.003>.
- Shibata, K., Sasaki, Y., Kawato, M., & Watanabe, T. (2016). Neuroimaging evidence for 2 types of plasticity in association with visual perceptual learning. *Cerebral Cortex*, *26*(9), 3681–3689, <https://doi.org/10.1093/cercor/bhw176>.
- Shibata, K., Watanabe, T., Sasaki, Y., & Kawato, M. (2011, December 9). Perceptual learning incepted by decoded fMRI neurofeedback without stimulus presentation. *Science*, *334*(6061), 1413–1415, <https://doi.org/10.1126/science.1212003>.
- Smeets, J. B. J., & Brenner, E. (2001). Perception and action are inseparable. *Ecological Psychology*, *13*(2), 163–166, [https://doi.org/10.1207/S15326969ECO1302\\_8](https://doi.org/10.1207/S15326969ECO1302_8).
- Sowden, P. T., Rose, D., & Davies, I. R. L. (2002). Perceptual learning of luminance contrast detection: Specific for spatial frequency and retinal location but not orientation. *Vision Research*, *42*(10), 1249–1258, [https://doi.org/10.1016/S0042-6989\(02\)00019-6](https://doi.org/10.1016/S0042-6989(02)00019-6).
- Spang, K., Grimsen, C., Herzog, M. H., & Fahle, M. (2010). Orientation specificity of learning vernier discriminations. *Vision Research*, *50*(4), 479–485, <https://doi.org/10.1016/j.visres.2009.12.008>.
- Stein, J. F. (1992). The representation of egocentric space in the posterior parietal cortex. *Quarterly Journal of Experimental Physiology*, *15*(4), 691–700, <https://doi.org/10.1113/expphysiol.1989.sp003314>.
- Sugrue, L. P., Corrado, G. S., & Newsome, W. T. (2004, June 18). Matching behavior and the representation of value in the parietal cortex. *Science*, *304*(5678): 1782–1787, <https://doi.org/10.1126/science.1094765>.
- Szumaska, I., van der Lubbe, R. H. J., Grzeczkowski, L., & Herzog, M. H. (2016). Does sensitivity in binary choice tasks depend on response modality? *Consciousness and Cognition*, *43*, 57–65, <https://doi.org/10.1016/j.concog.2016.05.005>.
- Talluri, B. C., Hung, S.-C., Seitz, A. R., & Seriès, P. (2015). Confidence-based integrated reweighting model of task-difficulty explains location-based specificity in perceptual learning. *Journal of Vision*, *15*(10):17, 1–12, <https://doi.org/10.1167/15.10.17>. [PubMed] [Article]
- Tartaglia, E. M., Aberg, K. C., & Herzog, M. H. (2009). Perceptual learning and roving: Stimulus types and overlapping neural populations. *Vision Research*, *49*(11), 1420–1427, <https://doi.org/10.1016/j.visres.2009.02.013>.
- Tartaglia, E. M., Bamert, L., Mast, F. W., & Herzog, M. H. (2009). Human perceptual learning by mental imagery. *Current Biology: CB*, *19*(24), 2081–2085, <https://doi.org/10.1016/j.cub.2009.10.060>.
- Taylor, M. M., & Creelman, C. D. (1967). PEST:

- Efficient estimates on probability functions. *The Journal of the Acoustical Society of America*, *41*(4), 782–787.
- Uka, T., Sasaki, R., & Kumano, H. (2012). Change in choice-related response modulation in area MT during learning of a depth-discrimination task is consistent with task learning. *The Journal of Neuroscience*, *32*(40), 13689–13700, <https://doi.org/10.1523/JNEUROSCI.4406-10.2012>.
- Vahdat, S., Darainy, M., Milner, T. E., & Ostry, D. J. (2011). Functionally specific changes in resting-state sensorimotor networks after motor learning. *The Journal of Neuroscience*, *31*(47), 16907–16915, <https://doi.org/10.1523/JNEUROSCI.2737-11.2011>.
- Vogels, R., & Orban, G. A. (1985). The effect of practice on the oblique inline orientation. *Vision Research*, *25*(11), 1679–1685, [https://doi.org/10.1016/0042-6989\(85\)90140-3](https://doi.org/10.1016/0042-6989(85)90140-3).
- 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, <https://doi.org/10.1016/j.visres.2011.07.019>.
- Wang, R., Zhang, J.-Y., Klein, S. A., Levi, D. M., & Yu, C. (2014). Vernier perceptual learning transfers to completely untrained retinal locations after double training: A “piggybacking” effect. *Journal of Vision*, *14*(13):12, 1–10, <https://doi.org/10.1167/14.13.12>. [PubMed] [Article]
- Watanabe, T., Náñez, J. E., & Sasaki, Y. (2001, October 25). Perceptual learning without perception. *Nature*, *413*(6858), 844–848, <https://doi.org/10.1038/35101601>.
- Watanabe, T., & Sasaki, Y. (2015). Perceptual learning: Toward a comprehensive theory. *Annual Review of Psychology*, *66*(1), 197–221, <https://doi.org/10.1146/annurev-psych-010814-015214>.
- Witt, K., Margraf, N., Bieber, C., Born, J., & Deuschl, G. (2010). Sleep consolidates the effector-independent representation of a motor skill. *Neuroscience*, *171*(1), 227–234, <https://doi.org/10.1016/j.neuroscience.2010.07.062>.
- Wright, B. A., Sabin, A. T., Zhang, Y., Marrone, N., & Fitzgerald, M. B. (2010). Enhancing perceptual learning by combining practice with periods of additional sensory stimulation. *Journal of Neuroscience*, *30*(38), 12868–12877, <https://doi.org/10.1523/JNEUROSCI.0487-10.2010>.
- 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, <https://doi.org/10.1016/j.cub.2008.10.030>.
- Xiong, Y.-Z., Zhang, J.-Y., & Yu, C. (2016). Bottom-up and top-down influences at untrained conditions determine perceptual learning specificity and transfer. *ELife*, *5*, 1–17, <https://doi.org/10.7554/elife.14614>.
- Yang, T., & Maunsell, J. H. R. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *The Journal of Neuroscience*, *24*(7), 1617–1626, <https://doi.org/10.1523/JNEUROSCI.4442-03.2004>.
- Yang, T., & Shadlen, M. N. (2007, June 28). Probabilistic reasoning by neurons. *Nature*, *447*(7148): 1075–1080, <https://doi.org/10.1038/nature05852>.
- Yin, C., Bi, Y., Yu, C., & Wei, K. (2016). Eliminating direction specificity in visuomotor learning. *The Journal of Neuroscience*, *36*(13), 3839–3847, <https://doi.org/10.1523/JNEUROSCI.2712-15.2016>.
- 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):4, 169–182, <https://doi.org/10.1167/4.3.4>. [PubMed] [Article]
- 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, <https://doi.org/10.1523/JNEUROSCI.0704-10.2010>.
- Zhang, J. Y., & Yang, Y. X. (2014). Perceptual learning of motion direction discrimination transfers to an opposite direction with TPE training. *Vision Research*, *99*, 93–98, <https://doi.org/10.1016/j.visres.2013.10.011>.
- Zhang, J., & Yu, C. (2018). Vernier learning with short- and long-staircase training and its transfer to a new location with double training. *Journal of Vision*, *18*(13):8, 1–8, <https://doi.org/10.1167/18.13.8>. [PubMed] [Article]
- Zhang, T., Xiao, L.-Q., Klein, S. A., Levi, D. M., & Yu, C. (2010). Decoupling location specificity from perceptual learning of orientation discrimination. *Vision Research*, *50*(4), 368–374, <https://doi.org/10.1016/j.visres.2009.08.024>.