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Sensory-motor perceptual learning and motor response specificity

E. Sebastian Lelo de Larrea-Mancera¹, Aaron Seitz¹ and Marcello Maniglia¹

¹ Department of Psychology, University of California at Riverside, CA, USA

In our experience of the World, perception is tightly related to our ability to perform actions on the objects we perceive. And yet, the large majority of studies on perception tend to artificially segregate these two intimately connected processes, and often neglect to explicitly discuss the relationship between perception and action. Only recently studies from the field of the perceptual learning (PL) looked at the role of motricity, showing that, all things kept equal, learning effects can be specific for the motor response used during training. Learning specificity is often used in PL literature to make inference on the mechanisms or the neural regions involved in a training paradigm, and lack of generalization of the motor component seems to suggest its crucial role in the observed effects. However, these studies might be characterized by a crucial confound in the relationship between task and motor response. In this study we first aim to test whether PL transfers to different motor component once the confound is addresses, and then evaluate if a task structure that explicitly links perception and action (adjustment) yields different patterns of generalization of learning with respect to a classic segregated paradigm (categorization). This work will clarify the contribution of the motor aspect in PL. Further, it could potentially shed light on whether motricity is an additional component to consider or whether its inclusion represents a paradigm shift in the way we study perception.

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7 It is still unclear whether details of motor responses are critical to consider when studying
8 perception or designing a model of perception and learning. The goal of this proposal is to
9 understand the role of the often neglected motor component in the study of perception. As a first
10 step, we focus on the field of perceptual learning (PL), which has been mostly construed under a
11 stimulus, then response (S-R) paradigm (Sagi, 2011). PL refers to improvements in a perceptual
12 task as a function of repeated practice. In this literature, evidence suggests that learning is often
13 specific for characteristics of the stimuli and the task the participants were engaged in, while in
14 other cases it can generalize to untrained conditions (Seitz, 2017). Models attempting to provide
15 mechanistic descriptions of PL describe relevant components considering stimulus and task,
16 suggesting that differences at these levels may explain (and predict) specificity or generalization
17 of learning. Despite increasingly complex models which include processes from different levels
18 of perceptual analysis (Ahissar & Hochstein, 1997; Ahissar & Hochstein, 2004; Zhang et al.,
19 2011; Watanabe & Sasaki, 2015), automatic perceptual and cognitive processes (Seitz &
20 Watanabe, 2003; Seitz & Dinse, 2007; Seitz & Watanabe, 2009; Seitz, Kim & Watanabe, 2009)
21 and other cognitive processes distributed across the whole brain (Maniglia & Seitz, 2018), none
22 of these models explicitly addresses the possible involvement of the motor component in
23 perceptual processes.

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37 Thus, the field of PL provides a fertile ground for asking whether a sensori-motor paradigm
38 (SM-R) –where a motor component interacts with the stimulus before a response is provided–
39 would call for a discrete update of current perceptual models (in the modular approach typical of
40 most PL models, an additional ‘box’ for the motor aspect, alongside the ‘task’ and ‘stimulus’
41 boxes, see figure 1), or rather, it would suggest a deeper restructuring of such models, as well as
42 the more general study of perception as suggested by some (Von Uexküll, 1934; Held & Hein,
43 1963; Lettvin et al., 1968; Gibson, 1979; Luria, 1986; Maturana & Varela, 1998; Jonas, 2000;
44 O’Reagan & Nöe, 2001; Stewart et al., 2010; Penny, 2017).

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51 Recently, Grzeczowski et al. (2017; 2019) tried to address the motor component in a series
52 of PL training studies investigating specificity and generalization of learning across motor
53 modalities. Both specificity and generalization have been used extensively in the PL literature as
54 a probe of the mechanisms and neural loci of learning (Poggio, Fahle & Edelman, 1992; Aisshar
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and Hotchstein, 1997, Schoups et al., 2001; Ghose, Yang & Maunsell, 2002; Sagi, 2011; Hung & Seitz, 2014; Watanabe & Sasaki, 2015; Maniglia & Seitz, 2018). Generalization, in which the improvements achieved in a trained task ‘transfer’ to an untrained task or stimulus, is usually seen as an indication of common mechanisms/neural loci across task and/or stimulus properties; conversely, specificity suggests that the training and transfer task and/or stimulus properties rely on different mechanisms. This is shown in Figure 1 (A-D) according to a classic PL model that addresses specificity and transfer (Petrov, Doshier & Lu, 2005). Grzeczowski et al. (2017; 2019) tested two groups of participants on the same task (line bisection), with one group responding with a mouse click (in 2019, keyboard key click in 2017) and the other by swiping the mouse. They found no transfer between groups (motor modalities), thus suggesting that learning can be specific for the motor modality of the response. The authors argue for a discrete update on current models. The model assumption behind the studies by Grzeczowski et al. (2017; 2019) is represented schematically in Figure 1E.

However, we here propose that an alternative explanation for the lack of transfer reported by the authors lies in methodological differences between tasks assumed to be the same: in particular, in their setup, not only is the motor pattern associated to the perceptual task different in each case, but the task as well (categorization vs adjustment, see Figure 1). The mouse (or keyboard) click case was associated to a categorization task (*‘is the bisecting line offset to the left or to the right with respect to the center of the bar?’*) that can be resolved through a simple mapping strategy (Fulvio, Green & Schrater, 2014; Green et al., 2015), in which the perceptual decision can be made during the stimulus phase without the involvement of a motor component, which is only requested in the response phase and is arbitrarily mapped onto the stimulus (see Szumska et al., 2016; Awada, Bakhtiari & Pack, 2021). On the other hand, the mouse swipe case was associated to an adjustment process (*‘move the line to the center of the bar’*) that aligns more with a predictive coding strategy (Fulvio, Green & Schrater, 2014; Green et al., 2015), where the perceptual decision is embedded in a series of sensory and motor interactions, and the stimulation and response phases are overlapping before a final decision (and response) is made. Interestingly, the confound mirrors a failure to recognize the difference between a categorization task that separates stimuli and responses associated to it (classic S-R paradigm) and an adjustment task that better aligns with a sensorimotor paradigm with reciprocal relations between stimulation and action (alternative SM-R paradigm). Thus, not only are the two tasks different at

the perceptual decision level (categorization vs adjustment), but also in their basic interaction with the motor component (S-R vs SM-R).

Grzeczowski et al. (2017) acknowledged the possibility of such task confound in their control experiments, particularly 5 and 6, in which they minimized task differences by converting the keyboard key click case to an adjustment task. In this case they found transfer of learning from the keyboard motor response to the mouse movement adjustment of a bisection task but not the other way around, which suggests the patterns of specificity and transfer of PL might not align with the available theoretical frameworks in this case. However, the authors did not test a case in which they converted mouse movements into a categorization task. The motor differences between swiping a mouse (continuous movement of the effector) and clicking a button (discrete steps for the effector) might still affect the homogeneity of the two modalities. In other words, while the authors reduced the motor (and task) differences between mouse swiping and clicking, it is still unclear how successful this was in eliminating these differences. Further, the sample sizes used in this study invite curiosity about the robustness of their conclusions. Unfortunately, the authors did not pursue further this line of inquiry in later studies (Grzeczowski et al., 2019). It is possible that the learning specificity reported by Grzeczowski et al. (2017 experiments 1-3; and 2019) might not depend upon the motor pattern but on differences in the design of the experimental paradigms, which made the tasks not comparable (see Figure 1F for our interpretation of the results of Grzeczowski et al., 2017; 2019).

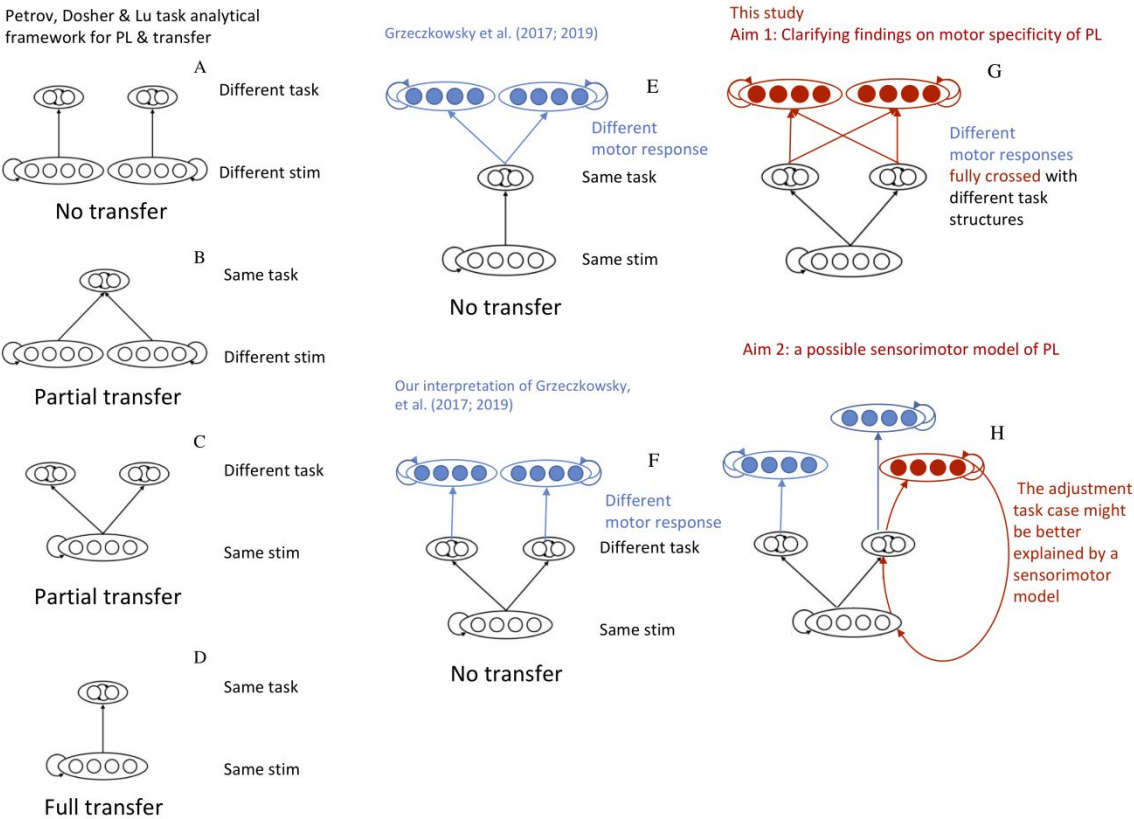


Figure 1: schematic representation of the theoretical framework of the proposed study:

A-D: Petrov et al. (2005)'s model of perceptual learning is composed by representation units, responding to the stimulus, and decision processing units, responding to the task. In this framework, learning of different tasks can happen in one of the 4 possible combinations of type of task and stimulus. While A-C predict partial or no transfer of learning, in case of D, in which task and the stimulus are the same across training, the representation units (below) and the decision units (above) are common between the two types of training, leading to learning transfer. Grzeczkowski et al. (2017; 2019) tested whether learning can be specific for the motor response modality, a level that is not present in the model of Petrov et al (2005), and in most PL models. Their results showed motor modality-specific learning, which led them to theorize that PL can also be specific for the type of motor response used (**Figure 1E**), even when the same task is used. However, in their studies, Grzeczkowski et al. (2017; 2019) modified not only the motor response (mouse click vs mouse swipe), but also the actual task (adjustment vs categorization). Green et al. (2015) proposed that these are different tasks that are differently solved at the level of the decision unit. We then schematized Grzeczkowski's experimental design in **1F**, in which not only the motor response, but also the decision units differ between tasks. We finally propose that, to rigorously test the author's original hypothesis of motor learning specificity, a new design is necessary, which separates the paradigm only at the level of the motor response, while maintaining the same task structure and stimuli (**Figure 1G**). Finally, we propose an alternative model of PL to describe the adjustment (sensorimotor) case. A sensorimotor framework for PL will be needed to the extent that the adjustment case fails to align to the established predictions.

The first goal of the study (Aim 1) is to clarify whether specificity of learning attributed to the motor component observed in Grzeczowski et al. (2017) stems from task-, rather than motor-related differences, (as Green et al. (2015) would suggest) (Figure 1G). We hypothesize that motor modality-specificity would be observed in the adjustment case (SM-R), consistent with Grzeczowski et al. (2017, experiment 5), although we might expect partial transfer (Grzeczowski et al., 2017, experiment 6). In contrast, full motor-modality transfer would be observed in the categorization case (S-R), as expected from a motor component not embedded in a loop with stimulus generation and task processing but only arbitrarily mapped to the perceptual decision, as suggested classically (e.g., Marr, 1982), and shown recently with saccades, voice and hand responses (Szumska et al., 2016; Awada, Bakhtiari & Pack, 2021). In general terms, our hypothesis is that in the presence of a sensorimotor relationship between stimulus and response, the motor aspect is intimately involved in the perceptual process so that learning should be largely specific to the sensorimotor components used.

The second goal of this study (Aim 2) is to evaluate whether the more ecological adjustment (SM-R) task yields fundamentally different patterns of transfer of PL in terms of task and stimulus with respect to the categorization (S-R) task, whose structure is reflective of the classic systemic view of PL (Doshier & Lu, 1998). Following Petrov, Doshier & Lu (2005) model predictions, we expect learning to be specific for stimulus and task properties in the categorization case (S-R). However in the adjustment case (SM-R), we expect to observe partial transfer. The rationale is that participants in the SM-R paradigm are presented with a larger number of stimulus exemplars and are more actively involved in the perceptual/generative aspects of the stimulus. This sensorimotor loop in which the motor response is co-generated with (variations of) the stimulus may more broadly engage a biological system that has evolved with this type of interaction, thus providing higher probability for adaptive learning. Additional support for this hypothesis comes from Green et al. (2015) and Fulvio, Green & Schrater (2014), in which the authors proposed that in categorization cases (S-R), participants adopt a simple mapping strategy which leads to specific learning in terms of stimuli and task, as classically expected, while for the adjustment case (SM-R), participants are more prone to adopt predictive coding strategies, which lead to more generalized learning. Of note, Green et al. (2015)'s description and their support of the hypothesis of larger transfer for the adjustment case, pertain

to the stimulus and task domains only and are not in contradiction with the predicted specificity in the motor component.

To test our hypotheses, we will use a line bisection stimulus and replicate the conditions used by Grzeczowski et al. (2017) while considering the categorization case (S-R) as an independent task from the adjustment (SM-R) case. The categorization task (S-R) will be attached to either a mouse-click or a mouse-swipe movement motor response. The adjustment task (SM-R) will also be attached to either mouse-clicks or a mouse-swipe movement motor response similar to the setup in Grzeczowski et al., 2017 (experiment 5 & 6) but with mouse clicks instead of keyboard button presses. Task type (categorization vs adjustment) and motor response (mouse-swipe vs mouse-click) will be fully crossed over four training conditions (see Figure 1G). Generalization of PL will be evaluated using pre- and post-training assessments at the level of motricity (Aim 1), stimulus and task (Aim 2). Motor transfer will be evaluated in each condition using the trained task (categorization vs adjustment) and the untrained motor response (mouse-swipe or mouse-click). Task transfer will be evaluated for each condition using the untrained task with the trained motor response. Stimulus transfer will be evaluated in all conditions in the same manner replicating Grzeczowski et al. (2017) with both an orthogonal and a wider version of the bisection stimuli trained on.

The results of this study can clarify the contribution of the motor aspect in PL (Aim 1) and could potentially advance the broader question of whether an increment in the complexity of the current models or a more radical departure from the way we think of PL in particular (Figure 1H) and perception science in general is necessary (Aim 2). Although we acknowledge the present set of tasks might not be the best to address the broader controversy implicated in our Aim 2, we believe that the solid work of Grzeczowski et al. (2017; 2019) is the best place to start investigating the issues we sought to clarify.

Methods

We plan to closely follow the methodology of Grzeczowski et al. (2017; 2019) with slight modifications to test the effects of interest. The main difference concerns the formation of the four groups detailed below to address the confound we identified in the original work on motor specificity in PL (see Procedure).

Participants

Participants will be UCR students recruited, consented and tested under the guidelines and supervision of the University of California Human Subject Research Review Board. They will either be paid \$10 per hour or receive course credit for their participation.

Exclusion Criteria

As in Grzeczowski et al. (2017; 2019), we will exclude participants with visual acuity scores below 1.0 logMAR in both eyes and those that fail to show significant improvement after training.

Power Analysis

Because the main focus of this work is to find whether or not the motor component transfers in the four different conditions tested, we based our sample justification on Grzeczowski et al. (2019) using as an effect size estimate the transfer effects found for the double-training case. By converting the t values reported (3.46) into the r equivalent statistic as described by Rosenthal & Rosnow (1991) and using the software G*Power (Faul et al., 2007), we calculated that 15 participants per condition would be enough to achieve 98% power and an equal ratio of type I and II error which is adequate to ensure neutrality on the hypothesis tested of transfer or lack thereof. We consider this sample size sufficient as even after some attrition and exclusion 10 participants would still be enough to achieve 88% power to find an effect.

Apparatus

The study will be conducted in a dimly illuminated room. Participants will see the stimuli on a CRT monitor placed at 2m. A chinrest will be used to control for viewing distance.

Stimuli

The bisection stimulus setup by Grzeczowski et al. (2017) will be replicated as closely as possible in terms of the stimulus and session design. Bisection stimuli will be lines composed of overlapping dots drawn with a dot pitch of 200 lm at a dot rate of 1MHz. Vertical or horizontal stimuli will be composed of 20 arcminutes (') long bluish lines presented on a dark background. The distance between the outer lines will be either 20' or 40' (Figure 2A, B, and C). No fixation point. Participants will be trained with horizontal bisection stimuli (20' apart) (Fig. 2A), they will be tested in terms of stimulus transfer to the vertical case (20' apart) (Fig. 2B), and to the horizontal wide (40' apart) case (Fig. 2C).

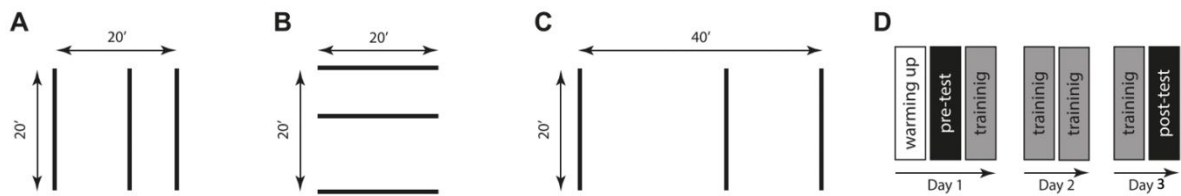


Figure 2. Bisection task in its vertical (A), horizontal (B) and vertical wide (C) versions. The study is programmed for two consecutive days as shown in D. Figure and design taken from Grzeczowski et al. (2017).

Procedure

On the first day, participants will begin the experiment in a warming up phase where 40 trials of a vertical wide (40' apart) will be delivered on each condition. Then participants will be paired based on performance to avoid baseline differences and then randomly assigned to a condition (detailed below) and complete a series of four pre-tests, namely, stimulus transfer to other orientation, stimulus transfer to wider case, task transfer and motor transfer. Each test will comprise a block of 80 trials. Then participants will train for seven blocks of 80 trials after which the first day of the experiment would conclude. On the next day, participants will complete the second and third session of training, while on the last day they will complete the fourth session of training and they will be tested on the same four tests used as pre-tests (stimulus transfer (other & wide), task and motor transfer) but delivered in the reverse order. This procedure is

illustrated in Figure 2D. In order to maximize training effects, we added an additional training day with respect to Grzeczowski et al. (2017).

Categorization (S-R) task structure

Participants will report whether the central line of the bisection stimulus (described below) was offset to the left or to the right from center. We will use the same sequential tracking adaptive procedure as Grzeczowski et al. (2017; 2019) to control stimulus delivery and target a threshold point in the psychometric function of 75% correct responses estimated by maximum likelihood estimation (PEST; Taylor & Creelman, 1967). Each trial will begin with 200 ms blank screen followed by 150 ms of the bisection stimulus. Participants will have 3000 ms to respond. Feedback will be provided by an auditory tone on incorrect responses. The next trial will start after a 500 ms inter-trial-interval.

Categorization (S-R) motor response

Participants will respond either by mouse button press (Group 1: S-R click) or by mouse directional swipe (Group 2: S-R swipe). Instructions for the mouse button mappings left and right for the horizontal, and up and down for the vertical case will be provided in form of a sign and placed where participants can see it at any point. In the case of the mouse-swipe condition the center button of the mouse will have to be pressed before a swipe would be registered. The mouse position (not shown on screen) will always be mapped at center at the moment the middle button is pressed, and the screen will be divided on quadrants (not shown on screen) so that a swipe on any direction is classified as up, down, right or left. Average direction while button pressed will determine the final direction of swipe.

Adjustment (SM-R) task structure

Participants will adjust the central line of the stimulus without crossing the center, as instructed in Grzeczowski et al. (2019). Each trial will start with 200 ms blank screen followed by the bisection stimuli. The position of the line will be offset of 120 or 240 arcseconds (") for the wide versions of the stimuli. Initial offset side will be randomized from trial to trial. Participants will be asked to adjust the central line of the stimulus and confirm its final position by pressing a mouse button (middle). Crucially, the maximum trial duration will have 7 seconds, half of that of Grzeczowski et al., (2017; 2019). This is because we hypothesize that, even in a SM-R paradigm, long trial time would increase the load on perception rather than on the

interaction between perception and motricity. Movement of the line will be done with either mouse swipes or mouse clicks. Swipes will be mapped to the central line so that it only moves horizontally or vertically depending the case. In the mouse-click case, left and right mouse clicks will move the line on either direction (or up and down). Single click step size will be equivalent to the minimum velocity that can be achieved by the mouse swipe. Holding either button will move the line in a given direction at the median speed of the mouse swipes recorded beforehand by an expert performer (experimenter). Auditory feedback will be provided for incorrect or perfect trials. Adjustments shorter than 500 ms or interrupted by the time limit to respond will be rejected and replaced with new trials so that the testing block will always include 80 valid trials. Once confirmation of the final position is provided a blank screen will be presented as an ITI of 500 ms before the next trial is delivered.

Adjustment (SM-R) motor response

Participants will perform the adjustment either by mouse button press (Group 3: SM-R click) or by mouse directional swipe (Group 4: SM-R swipe). In the button press condition, adjustment is initiated by pressing the central button of the mouse and then by clicking on either the left or right buttons of the mouse to adjust the central line left and right in the horizontal case, and up and down in the vertical case. The same instructions provided for the categorization case mappings are relevant in this adjustment case and will be left in sight throughout the experiment. The final position of the line will be reported by a second click in the middle button of the mouse. In the swiping motor response condition, pressing the middle button of the mouse will initiate the adjustment and a second press in either the middle, left or right buttons will confirm the final position for the adjustment.

Statistical Analysis

As in Grzeczowski et al., (2019), the dependent variable will be the performance threshold for the line bisection task expressed in arcminutes, while the combination of task and response type will constitute the independent variables. Learning specific to the trained task will be measured from a linear regression fit within-subject training data. Significance testing will be conducted using one-sample t-tests on the slopes of the regression fits against zero. Generalization of learning effects will be calculated from the average mean offsets (adjustment tasks) or the calculated discrimination thresholds (categorization tasks) of pre- and post-training

assessments in each condition. Significance testing will be conducted using related-samples t tests for pre- and post-assessments within each condition. Comparisons of the transfer effects between conditions will be conducted on the difference scores (post – pre) using independent samples t-tests. All tests will be corrected for multiple comparisons. An Outlier rejection rule will be applied for baseline, post-training or transfer performances which are 3 SD above or below the mean.

Data availability

The data collected during all the experiments will be publicly available through Mendeley Data repository (<https://data.mendeley.com/>)

Open Practices Statement

The data and materials for all experiments will be available on Github. All the Experiments are preregistered.

References

- Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, 387(6631), 401–406. <https://doi.org/10.1038/387401a0>
- [Ahissar, M. & Hochstein, S. The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Sciences* 8, 457–464 \(2004\).](#)
- Awada, A., Bakhtiari, S., & Pack, C. C. (2021). Visual perceptual learning generalizes to untrained effectors. *Journal of Vision*, 21(3), 1–12. <https://doi.org/10.1167/jov.21.3.10>
- Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, 39, 175–191.
- Fulvio, J. M., Green, C. S., & Schrater, P. R. (2014). Task-Specific Response Strategy Selection on the Basis of Recent Training Experience. *PLoS Computational Biology*, 10(1).

- 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.
- Gibson, J. J. (1979). *The Ecological Approach to Visual Perception*. London: Routledge.
- Green, C. S., 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), 1–14.
- Grzeczowski, L., Cretenoud, A., Herzog, M. H., & Mast, F. W. (2017). Perceptual learning is specific beyond vision and decision making. *Journal of Vision*, 17(6), 1–11.
<https://doi.org/10.1167/17.6.6>
- 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), 1–14. <https://doi.org/10.1167/19.6.4>
- Held, R., & Hein, A. (1963). Movement-produced stimulation in the development of visually guided behavior. *Journal of Comparative and Physiological Psychology*, 56(5), 872–876.
- Hung, S. C., & Seitz, A. R. (2014). Prolonged training at threshold promotes robust retinotopic specificity in perceptual learning. *Journal of Neuroscience*, 34(25), 8423–8431.
- Jonas, H. (2001). *The Phenomenon of Life: Toward a Philosophical Biology*. Northwestern University Press. ISBN 0-8101-1749-5
- Lettvin, J., Maturana, H., McCulloch, W., & Pitts, W. (1959). What the Frog's Eye Tells the Frog's Brain. *Proceedings of the IRE*, 47(11), 1940–1951.
- Luria, A.R. (1986) *Higher Cortical Functions In Man: Las funciones corticales superiores del hombre*. Editorial Fontamara, México.
- Maniglia, M. & Seitz, A. R. Towards a whole brain model of Perceptual Learning. *Curr. Opin. Behav. Sci.* **20**, (2018).
- Maturana, H R., Varela, F. J. (1998). *The Tree of Knowledge*. Shambhala Publications, Inc. USA.
- O'Regan, J., & Nöe, A. (2001). What it is like to see: A sensorimotor theory of perceptual experience. *Synthese*, 79–103.

- Penny, S. (2017). *Making sense : cognition, computing, art, and embodiment*. MIT Press. Cambridge, Massachusetts.
- 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.
- Poggio, T., Fahle, M., & Edelman, S. (1992). Fast Perceptual Learning in visual hyperacuity. *Science*, 256(5059), 1018–1021.
- Sagi, D. (2011). Perceptual learning in Vision Research. *Vision Research*, 51(13), 1552–1566. <https://doi.org/10.1016/j.visres.2010.10.019>
- Schoups, A., Vogels, R., Qian, N., & ORBAN, G. . (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, 412(August), 549–553.
- Seitz, A. R., & Watanabe, T. (2003). Is subliminal learning really passive. *Nature*, 422(6927), 36. <https://doi.org/10.1038/422036a>
- Seitz, A. R., & Dinse, H. R. (2007). A common framework for perceptual learning. *Current Opinion in Neurobiology*, 17(2), 148–153. <https://doi.org/10.1016/j.conb.2007.02.004>
- Seitz, A. R., & 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>
- Seitz, A. R., 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>
- Stewart, J., Gapenne, O., and Di Paolo, E. A. (eds.). (2010). *Enaction: Toward a New Paradigm for Cognitive Science*. Cambridge, MA: MIT Press.
- Szumska, I., van der Lubbe, R. H. J., Grzeczowski, L., & Herzog, M. H. (2016). Does sensitivity in binary choice tasks depend on response modality? *Consciousness and Cognition*, 43, 57–65.
- Von Uexküll, J. (1934). A stroll through the worlds of animal and men: A picture book of invisible worlds. In C. H. Schiller (Ed.), *Instinctive Behavior: The Development of a Modern Concept*.

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57
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Watanabe, Takeo; Sasaki, Y. (2015). Perceptual learning: Toward a comprehensive theory. *Annu Rev Psychol*, 3(66), 197–221.

Zhang, J.-Y., Wang, R., Klein, S., Levi, D., & Yu, C. (2011). Perceptual learning transfers to untrained retinal locations after double training: A piggyback effect. *Journal of Vision*, 11(11), 1026–1026. <https://doi.org/10.1167/11.11.1026>

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