Vision Research 106 (2015) 1–6

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Reference-frame specificity of perceptual learning: The effect of practice

Tommaso Mastropasqua [a], Massimo Turatto [a,b,*]

[a] Center for Mind/Brain Sciences, University of Trento, Corso Bettini 31, 38068 Rovereto, Italy
[b] Department of Psychology and Cognitive Sciences, University of Trento, Corso Bettini 31, 38068 Rovereto, Italy

ARTICLE INFO

Article history:
Received 20 August 2014
Received in revised form 23 October 2014
Available online 27 November 2014

Keywords:
Perceptual learning
Specificity
Decision criterion
Reference frame
Training
Selective reweighting

ABSTRACT

One of the hallmarks of perceptual learning is specificity, the lack of transfer of the improved discriminative ability when the trained stimulus changes retinal location, orientation or other basic visual attributes. Specificity has been found also for the trained task and the corresponding attended stimulus feature. Here, we provide evidence for a new form of specificity, called *reference-frame specificity*, which does not follow from changes in the sensory input or the attended stimulus feature. In our paradigm, specificity was the consequence of the mental frame of reference (vertical or horizontal) used to perform the orientation discrimination task. In addition, we found that reference-frame specificity was exacerbated by prolonged practice. Overall the present findings are in agreement with the "selective reweighting" hypothesis of perceptual learning.

1. Introduction

With practice, human beings (and other animals) can improve their discriminative ability, a phenomenon known as perceptual learning (Fahle & Poggio, 2002). A key feature of perceptual learning is that it is often specific for the trained stimulus feature, such as spatial frequency (Fiorentini & Berardi, 1980, 1981), orientation (Crist et al., 1997; Schoups, Vogels, & Orban, 1995), position (Crist et al., 1997; Karni & Sagi, 1991) or direction of motion (Ball & Sekuler, 1982), although cases of transfer of learning have been reported in the literature (Ahissar & Hochstein, 1997; Fahle & Poggio, 2002; Mastropasqua & Turatto, 2013).

The specificity of perceptual learning for low-level stimulus features inspired the "representation modification" hypothesis, according to which the neural populations affected by training would be localized in primary visual cortex (V1), where neurons present, for example, small receptive fields and narrow orientation sensitivity (Fiorentini & Berardi, 1997; Karni & Sagi, 1991). Behavioral indications of specificity for the trained stimulus attribute are not, however, necessarily diagnostic of corresponding changes in early visual areas. Learning, indeed, might entail some degree of plasticity in high-order neural populations that analyze the stimulus sensory representations (Mollon & Danilova, 1996). Accordingly, it has been shown that perceptual learning is better represented by changes in the response properties of neurons in higher-order areas involved in decision making process (Law & Gold, 2009; Shadlen & Newsome, 2001) than by changes in V1 neurons (Crist, Li, & Gilbert, 2001; Ghose, Yang, & Maunsell, 2002; Schoups et al., 2001).

In line with this view, Dosher and Lu (1998, 1999) proposed the "selective reweighting" hypothesis as a possible mechanism to explain perceptual learning and its specificity. Instead of postulating changes in the early stimulus representations, perceptual learning would arise from the weighting of the "readout" connections between a task-decision unit and the stimulus representation (for a similar idea also see, Herzog & Fahle, 1998). Petrov, Dosher, and Lu (2005) have presented, and empirically tested, a detailed computational model completely based on a selective reweighting mechanism (Dosher et al., 2013; Huang, Lu, & Dosher, 2012). With training, the selective reweighting mechanism progressively potentiates the connections with the relevant stimulus features for the task at hand, while at the same time lower weights are assigned to the irrelevant features, with no substantial changes in the stimulus sensory representation. Within this framework, specificity is not the consequence of the constrains imposed by the properties of neurons in the early visual areas, but rather, specificity is due to the process of optimization of the readout connections between the decision unit and the trained stimulus representation. In agreement with this view, Otto, Oğmen, and Herzog (2010) have found perceptual learning to be specific for the perceived rather than actual stimulus orientation, a result that gives support to the idea that learning would occur in nonretinotopic representations and that involves changes in attentional readout processes.

---

* Corresponding author at: Center for Mind/Brain Sciences, University of Trento, Corso Bettini 31, 38068 Rovereto, Italy.

E-mail address: massimo.turatto@unitn.it (M. Turatto).

http://dx.doi.org/10.1016/j.visres.2014.10.035
0042-6989/© 2014 Elsevier Ltd. All rights reserved.

An alternative view on specificity (and transfer) of perceptual learning has been offered by the Reverse Hierarchy Theory (RHT; Ahissar & Hochstein, 1997, 2004). The core idea of RHT is that perceptual learning can take place at different stages of analysis in the visual system. With easy tasks, learning would occur at higher levels of the visual hierarchy, where neurons have larger receptive fields and show little or no specificity for basic stimulus attributes. In this case, perceptual learning is more likely to transfer across different retinal locations and stimulus orientations. By contrast, with difficult tasks, learning would take place at lower levels of the visual hierarchy, and would therefore exhibit the specificity imposed by the properties of neurons at early stages of visual analysis.

1.1. Types of specificity

Perceptual learning has been shown to be both stimulus specific and task specific. As already mentioned, stimulus specificity is observed when the trained stimulus changes its retinal location, orientation, contrast, or motion direction. Hence, this form of specificity follows large changes in the sensory input between the training phase and the test phase, like when, for example, the same waveform discrimination task is first trained with a vertical stimulus and then tested with an horizontal one (e.g., Fiorentini & Berardi, 1980, 1981), or when the same orientation discrimination task, trained at a given retinal location, is then tested at different locations (e.g., Schoups, Vogels, & Orban, 1995).

Specificity, however, can be observed not only after changes in the trained visual features, but also for the trained task. Shiu and Pashler (1992), and Ahissar and Hochstein (1993) were among the firsts to show that when the visual input is defined by two potentially relevant features, perceptual learning is selectively restricted to the attended one. Other studies have shown no transfer between different perceptual tasks relying on similar visual inputs that likely shared a common early level of visual analysis (Crist et al., 1997; Fahle, 1997; Fahle & Morgan, 1996). Although in some cases the stimuli used in the different tasks were not exactly the same, and hence a role of stimulus specificity cannot be totally excluded, Saffell and Matthews (2003) showed a complete task specificity of perceptual learning with a constant sensory input. Participants were presented with dynamic random-dot motion displays that could have different speeds and directions. Half of participants were trained with the speed discrimination task and then tested on the direction discrimination task, and vice versa for the remaining participants. Despite the stimulus conditions were exactly the same for the two groups, the results showed that perceptual learning was specific for the selected stimulus feature and the corresponding trained task. In sum, although cases of transfer of learning between tasks have been reported (Mcgovern, Webb, & Peirce, 2012; Webb, Roach, & McGraw, 2007), there is consistent evidence that perceptual learning can be not only stimulus specific but also task specific.

Here, we document a new form of specificity of perceptual learning, based only on the frame of reference used to perform the orientation discrimination task. The peculiarity of this *reference-frame specificity* is that it was observed when no changes in the sensory input was introduced, a result in agreement with the selective reweighting hypothesis (also see, Huang, Lu, & Dosher, 2012). According to the model, the final output of the decision unit (i.e. the observer's response) is determined by the input received, through weighted connections, from the stimulus representations, with weights that can be modulated by two top-down factors, feedback and the decision criterion (or bias), with the latter introduced in the model to control for any response bias in a *n*AFC task (Petrov, Dosher, & Lu, 2005). Previous studies have also documented that by means of feedback the decision criterion can be changed and optimized with training, and that this form of learning differs from the standard sensitivity learning (Aberg & Herzog, 2012; Herzog et al., 2006). Our study, however, was not aimed at addressing the effects of training on the optimization of the decision criterion, but rather we wanted to investigate whether it was possible to obtain sensitivity learning specific for the frame of reference used during training. With this regard, it is worth noticing that usually, in perceptual learning tasks, the decision criterion and the reference frame overlap. For example, if the task is to decide whether a given stimulus is tilted clockwise or counterclockwise with respect to the vertical axis, the condition of "verticality" defines the reference frame, but the same mental axis is also used as the optimal decision criterion to perform the task. A completely different reference frame and decision criterion are used when the stimulus is rotated by 90°, and the same task (clockwise vs. counterclockwise) is performed with respect to the horizontal axis. The orthogonal rotation of the stimulus, however, introduces a change in both the reference frame and the decision criterion, along with an unwanted massive change in the sensory input. However, it is conceivable to imagine a perceptual condition in which the reference frame and the decision criterion can be disentangled, so that the reference frame can be radically changed without introducing variations neither in the trained stimulus nor in the decision criterion.

Therefore, to show reference-frame specificity, we devised an experimental protocol in which during training participants learned to perform an orientation discrimination for stimuli tilted around an oblique (45°) axis, using the vertical meridian as the frame of reference (or horizontal, counterbalanced across participants). Then, in the test phase they performed the task, with the same stimuli, using a different reference frame (i.e., the orthogonal axis). Specifically, the task was to decide which stimulus among three stimuli was the most oriented toward the assigned reference frame. During the training phase, participants' performance was controlled by means of an adaptive procedure, whereas during the test phase we presented two brief blocks of trials based on the method of constant stimuli. In the first block, participants performed the orientation discrimination task with the same reference frame as during the training phase, whereas in the second block they performed the task using the orthogonal reference frame (horizontal if trained with vertical, or vice versa).

1.2. Specificity and the effects of training

Training has almost invariably a beneficial effect on the observer's discriminative capacity. Under an appropriate training regime, we can improve our ability to discriminate subtle differences in the sensory input, with longer training leading to better performance, until an asymptotic level is finally reached. But what is the effect of the amount of training on specificity?

In a recent study, Jeter et al. (2010) have expressly addressed this issue with a paradigm largely based on stimulus specificity. Specifically, in a first training session participants performed a high-precision discrimination task in which they had to distinguish the exact orientation of a tilted Gabor for a given retinal location. Then, in the following training session the authors tested transfer of learning to a different retinal location and stimulus (orthogonal) orientation. The length of the first training session was the main variable of interest, and could involve 2, 4, 8 or 12 blocks of trials in consecutive days (2 blocks per day), whereas the second training session lasted 8 blocks. As expected, the results showed that the longer the training the better the orientation discrimination performance achieved. The novel finding, however, was that the benefit of a prolonged training was paralleled by a negative impact on visual performance at the beginning of the second training session, when the stimulus changed its position and orientation. The