

Contents lists available at [ScienceDirect](http://ScienceDirect.com)

Vision Research

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

Specificity of fast perceptual learning in shape localisation tasks based on detection versus form discrimination

Antje Kraft^a, Cathleen Grimsen^b, Dennis Trenner^b, Stefanie Kehrer^{a,c}, Anika Lipfert^a, Martin Köhnlein^a, Manfred Fahle^{b,d,1}, Stephan A. Brandt^{a,*,1}

^a Department of Neurology, Universitätsmedizin Charité, Berlin, Germany

^b Department of Human Neurobiology, University of Bremen, Bremen, Germany

^c Institute of Psychology, Humboldt University, Berlin, Germany

^d The Henry Wellcome Laboratories of Vision Sciences, City University London, UK

ARTICLE INFO

Article history:

Received 6 August 2009

Received in revised form 6 November 2009

Keywords:

Luminance

Color

Motion

Texture

Figure-ground segmentation

Threshold

ABSTRACT

Perceptual learning is defined as a long-lasting improvement of perception as a result of experience. Here we examined the role of task on fast perceptual learning for shape localisation either in simple *detection* or based on form *discrimination* in different visual submodalities, using identical stimulus position and stimulus types for both tasks. Thresholds for each submodality were identified by four-alternative-forced-choice tasks. Fast perceptual learning occurred for shape detection-based on luminance, motion and color differences but not for texture differences. In contradistinction, fast perceptual learning was not evident in shape localisation based on discrimination. Thresholds of all submodalities were stable across days. Fast perceptual learning seems to differ not only between different visual submodalities, but also across different tasks within the same visual submodality.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

A sustained improvement of perception as a result of experience is defined as perceptual learning. Performance has an initial fast phase of improvement followed by a slower rate of improvement over periods of more than ten testing sessions (e.g. Karni & Sagi, 1993). The improvement can be specific to the precise visual field position (Fahle, Edelman, & Poggio, 1995) or to attributes of the trained stimulus, e.g. different orientations and spatial frequencies, or to vernier discriminations (Ahissar & Hochstein, 1993; Fahle, 1997; Poggio, Fahle, & Edelman, 1992). The underlying neuronal changes may be at least partly realized on the level of early visual cortices (Fahle, 2004) and controlled by specific high-level top-down mechanisms (Ahissar & Hochstein, 1993; Herzog & Fahle, 1998).

Visual processing is based on a physiological hierarchy of visual areas with multiple feedforward and recurrent projections (Lamme & Roelfsema, 2000). Low-level visual areas are characterized by small receptive fields and a specialization for basic visual features such as orientation, while higher areas with larger receptive field sizes show a stronger generalization over spatial positions but

are selectively involved in complex stimulus features. Selective tuning to visual features and positions is realized on each level of processing. According to the “Selective Tuning Model” of Tsotsos (1990) a suppressive surround to the relevant dimension arises when recurrent processing is initiated after an initial feedforward sweep of processing (Boehler, Tsotsos, Schoenfeld, Heinze, & Hopf, 2008).

Studies investigating training effects in low-level features such as orientation (Fahle, 1997) and position (Fahle et al., 1995) revealed that this improvement is highly stimulus- and position-specific (see also Fahle and Morgan (1996)). This training effect pertains as well to the eyes (Karni & Sagi, 1991). The improvement can only be partly transferred after small changes in stimulus configuration, position or change of the eye, if at all. This suggests that perceptual learning can involve even early (primary) visual processing stages on which such low-level features are processed by different neurons. Because of the highly feature-specific effects in some forms of perceptual learning, Fahle and Poggio (2002) proposed that studies using visual training may provide information regarding the stage of visual information processing. The highly specific learning should take place at processing levels that are stimulus-related and where distinct ranges of stimulus features (e.g. orientation, vernier offset and curvature) are processed separately. Even at very early levels, partly different networks may underlie performance and training of distinct tasks (Fahle, 1997).

* Corresponding author. Department of Neurology, Charitéplatz 1, 10117 Berlin, Germany. Fax: +49 30 450 560 942.

E-mail address: stephan.brandt@charite.de (S.A. Brandt).

¹ Both authors have contributed equally as senior authors.

Perceptual learning is of course not restricted to the first levels of visual processing (Ahissar & Hochstein, 1993; Ahissar & Hochstein, 2004; Fahle, 2009). In spite of the high stimulus-specificity of some forms of learning, other forms obviously take place on higher levels of visual processing, and top-down attentional mechanisms might play a role, too (Ahissar & Hochstein, 1997; Herzog & Fahle, 1998; Mollon & Danilova, 1996; Morgan, 1992).

Ahissar and Hochstein (1993) proposed, for instance, that perceptual learning is specific to basic stimulus features but that top-down task-related control affects low-level stimulus-driven mechanisms undergoing changes due to learning. The authors trained subjects either in a global or local identification task. No transfer occurred from the local task to global identification performance, but global identification practice did improve local detection performance to a small extent. Ahissar and Hochstein explained this asymmetry in transfer by a difference in processing hierarchy between the two tasks. Local detection is normally processed in the primary visual cortex (texture discrimination, Karni & Sagi, 1991), where processing is less affected by selective attention, and attentional effects are weaker (but see Juan and Walsh (2003), Lamme and Spekreijse (2000), Somers, Dale, Seiffert, and Tootell (1999)) in V1 than in areas V2 or V3. Here, the global identification task may take place (Ahissar & Hochstein, 1993).

Ahissar and Hochstein (1997) also show that the degree of specificity depends on task difficulty. As learning generalized more strongly across orientations and retinal positions when conditions were easier, the authors suggest that learning occurred in higher visual areas where the spatial scale is broader. On the other hand, learning was more specific under difficult task demands, matching the finer spatial resolution in low-level visual areas. Consequently the authors propose the reverse hierarchy theory of visual perceptual learning, asserting that perceptual learning is a top-down guided process that begins at higher levels of visual processing (Ahissar & Hochstein, 2004) and progresses backwards to earlier visual processing stages depending on actual task demands. According to this theory, higher areas carry out a preliminary analysis of features, but primary cortex supplies a more detailed report of detailed structure and spatial position.

This concept fits well with a recent theory of visual attentional processing by Tsotsos, Rodríguez-Sánchez, Rothenstein, and Simine (2008) that postulates distinct and iterative attentional binding strategies in visual hierarchical processing for distinct visual recognition tasks such as detection, identification, localisation or discrimination. In their model, Tsotsos et al. (2008) suggest that multiple bottom-up and top-down passes within hierarchical visual processing are tuned by using actual task information, thus resulting in four different binding processes, each associated with a different time period during a distinct visual task. According to the theory, a simple detection task without stimulus localisation requires only the initial feedforward sweep (convergence binding) to stimulate a response. In contrast, a detection task with location information (e.g. identifying in which visual field quadrant the stimulus lies) requires partial recurrence binding after the initial feedforward sweep, as the location information is represented in lower level areas. If detailed stimulus information and localisation are necessary for a response (e.g. in which visual field quadrant a target stimulus lies among distractors), at least full recurrence binding – or iterative binding – is necessary to complete the response, as multiple low-level areas (depending on the target and/or distractor features and positions) are involved in target localisation.

The theory's assumptions might have implications for perceptual learning processes in distinct visual recognition tasks. One may hypothesize that visual tasks can be differentially trained depending on the binding strategies utilized. Following this idea, the amount of perceptual learning could vary even when the same

stimulus type is used. For example during the localisation of a circle within the visual field quadrants feedforward processing may be sufficient, whereas during the localisation of the same circle based on form discrimination (e.g. among squares within the visual field quadrants), recurrent processing might be required. Possibly, the extent of perceptual learning is faster or stronger during simple partial or full recurrence binding as compared to iterative recurrence binding when different visual levels and positions are involved.

Following these hypotheses, the current study examined the influence of task (binocular shape localisation based on either detection or form discrimination) on the amount of perceptual learning in different visual submodalities (luminance, texture, motion, and color), using identical stimulus positions and stimulus type.

2. Methods

2.1. Observers

Nine healthy right-handed students (5 female) with normal vision (mean age 24.6 years, standard deviation 3.9) participated in five 30-min sessions, one a day on five days. The interval between sessions did not exceed four days. The study was conducted in conformity with the declaration of Helsinki and was approved by the local ethics committee. Written informed consent was obtained from all participants. All subjects were paid for their participation and were unaware of the purpose of the experiments.

2.2. Stimuli, tasks and procedure

Stimuli were displayed on a 21-in. monitor controlled by a PC with a spatial resolution of 1600×1200 pixels and a refresh rate of 75 Hz. Subjects were seated 60 cm from the screen. To minimize head movements and to ensure a fixed viewing distance the head was stabilized by a chin rest. Participants were instructed to fixate a central dot during all experiments. A software programme developed in-house was used to present stimulus displays and collect performance data.

Circles (210 arcmin in diameter) and squares (186 arcmin side length) covering the same surface area were used as stimuli. Stimulus midpoints were presented at an eccentricity of 5° from central fixation. The stimulus type varied across experimental runs to test shape detection and discrimination thresholds for four visual submodalities (luminance, texture, motion and color). Individual stimulus parameters of each visual submodality are specified in the next section.

All experimental tasks were performed binocularly. A central fixation point (12 arcmin) was presented throughout the entire run. Subjects were instructed to perform the actual task while maintaining central fixation. During each trial the stimulus array was presented for 200 ms (see Fig. 1). For the shape localisation task based on simple detection a single circle was presented in one of the four visual field quadrants. For the localisation task based on form discrimination, three squares were presented additionally in the remaining visual field quadrants. In both conditions the subject's task was to indicate the location of the circle via a manual button press (4-alternative-forced-choice task; AFC). The subject's response was necessary to initiate the next trial. A fixation delay of 500 ms was implemented after the response of the subject.

For both condition (localisation based on detection vs. form discrimination) perceptual thresholds (62.5% correct responses) were defined in each experimental run for each visual field quadrant using the adaptive staircase procedure QUEST (Quick Estimation by Sequential Testing, Watson & Pelli, 1983). As perceptual learning effects are position-specific, we defined separate individual

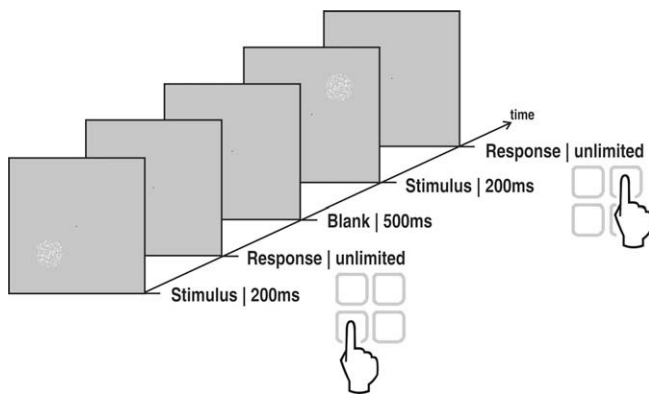


Fig. 1. Experimental procedure.

threshold values for each position in the visual field quadrants. The sequence of the four independent staircases was organized in randomized order within each experimental run. Subjects completed 30 trials per visual field quadrant, i.e. 120 trials per run. Each visual submodality (luminance, texture, motion and color) and task (shape localisation based on detection vs. form discrimination) was tested in a separate run on each testing day, resulting in 8 experimental runs per day. The sequence of tasks was held constant across subjects and days. Subjects first performed the shape localisation tasks based on detection in the order luminance, texture, motion and color. Subsequently the shape localisation tasks based on form discrimination were conducted in the same order.

In a 4AFC task the probability of guessing for each response should be around 25%. A response bias in favor of one visual field quadrant could mimic a lower threshold. Therefore we controlled the probability of guessing for each subject for each visual field quadrant in every testing run, ensuring that the value of guessing was below 32% for all visual field quadrants.

2.3. Submodalities

For the submodality *luminance* 20,000 white dots (maximal luminance, $\sim 108 \text{ cd/m}^2$) with a diameter of 5.6 arcmin each were presented against a gray background ($\sim 54 \text{ cd/m}^2$). The difference between white dots and background was defined as 100% luminance contrast and served as the starting point for the adaptive staircase procedure. QUEST modulated the difference between target and background in percent luminance difference.

For the submodality *texture*, lines of 20 arcmin in length and 1.4 arcmin in width were presented on a virtual grid with an inter-line distance of 14.0 arcmin, randomly jittered by 2 arcmin. Background rotation of line elements was 45° . Starting orientation of target lines was 135° , resulting in a target-background difference of 90° . QUEST modulated the difference between target lines and background lines in degrees.

For the submodality *motion* 20,000 black dots (5.6 arcmin size) moving at a velocity of 3 deg/s were presented on a gray background ($\sim 54 \text{ cd/m}^2$). Background dots moved continuously to the right, whereas the target dots moved to the left, hence motion direction difference was 180° at the beginning of the staircase procedure. QUEST modulated the difference between target and background motion direction in degrees.

For the submodality *color* an Ishihara-like setup was created. Dots of variable size were presented on a virtual grid with an inter-dot distance of 14 arcmin, randomly jittered by 1.5 arcmin. Dot radius varied randomly (on average half of the grid size; 7 arcmin). Dots did not overlap. Target and background wavelengths were chosen by means of corresponding colors in the CIE system. Background dots were set to a color hue corresponding to

550 nm (green) and the starting point for QUEST was the color hue corresponding to 650 nm (red). To avoid discrimination between target and background on the basis of luminance differences, random luminance noise (between 0% and 40% of maximum luminance) was introduced to each stimulus dot. QUEST modulated the difference between target and background in color hue values.

2.4. Data analysis

Perceptual thresholds were conducted using post-hoc fitting procedures (Probit- or likelihood analyses). As the level of guessing in 4AFC tasks corresponds to 25%, the threshold (inflection point of the psychometric function) is defined as 62.5% correct responses.

Statistical data analyses were carried out with SPSS software (Version 16.0). For each submodality (luminance, texture, motion, color) and task (location detection and form discrimination) threshold values were entered in repeated measure 3-way or 2-way ANOVAs with factors “visual field quadrant” (1–4), “testing day” (1–5) and “task” (location detection vs. form discrimination). If necessary, degrees of freedom and p-values were corrected by the Greenhouse-Geisser formula. In all submodalities and tasks Bonferroni-corrected pairwise comparisons were used to evaluate the differences between the threshold level of the first and each following testing day.

For each visual submodality, correlation analyses (Pearson) were conducted between shape localisation based on detection and form discrimination using the individual threshold values of each subject, visual field quadrant and testing day (180 pairs of values).

3. Results

In all visual submodalities tested (luminance, texture, motion and color) thresholds were significantly higher in the localisation task based on form discrimination than in the detection-based localisation tasks (see Fig. 2). This was reflected in significant main effects for the factor “task” in all submodalities [luminance $F(1,8) = 155.43$; $p < 0.001$; texture $F(1,8) = 500.12$; $p < 0.001$; motion $F(1,7) = 49.02$; $p < 0.001$; color $F(1,8) = 183.57$; $p < 0.001$].

Thresholds of visual submodalities were then entered in separate two-way ANOVAs with factors “day” and “visual field quadrant” both for detection-based and form discrimination-based localisation tasks. No visual submodality yielded a significant main effect for the factor “visual field quadrant” ($p > .05$). Thus the results for each visual submodality were collapsed across visual field quadrants in Fig. 2. Additionally the correlation analyses between form discrimination and detection-based localisation tasks were shown for each visual submodality.

For the submodality “luminance” the analysis revealed a significant main effect for the factor “day” during the detection-based task [$F(4,32) = 6.27$; $p < 0.001$], but not for the localisation based on form discrimination [$F(4,32) = 2.71$; $p > 0.05$]. Interactions between the factors day and visual field quadrant were not significant. For the detection task, post-hoc comparisons showed a significantly reduced threshold for the third, fourth and fifth testing day as compared to the first day ($p < 0.01$). Correlation analysis revealed a moderate correlation between the detection of luminance and luminance discrimination (0.475; $p < 0.001$).

For the submodality “texture” the main effects of the factor “day” were not significant, neither in the detection [$F(4,32) = 0.85$; $p > 0.05$] nor the form discrimination task [$F(4,32) = 0.42$; $p > 0.05$]. The factors “day” and “visual field quadrant”, however, interacted significantly for the texture detection task [$F(12,96) = 2.21$; $p < 0.05$]. The correlation between texture detection and form

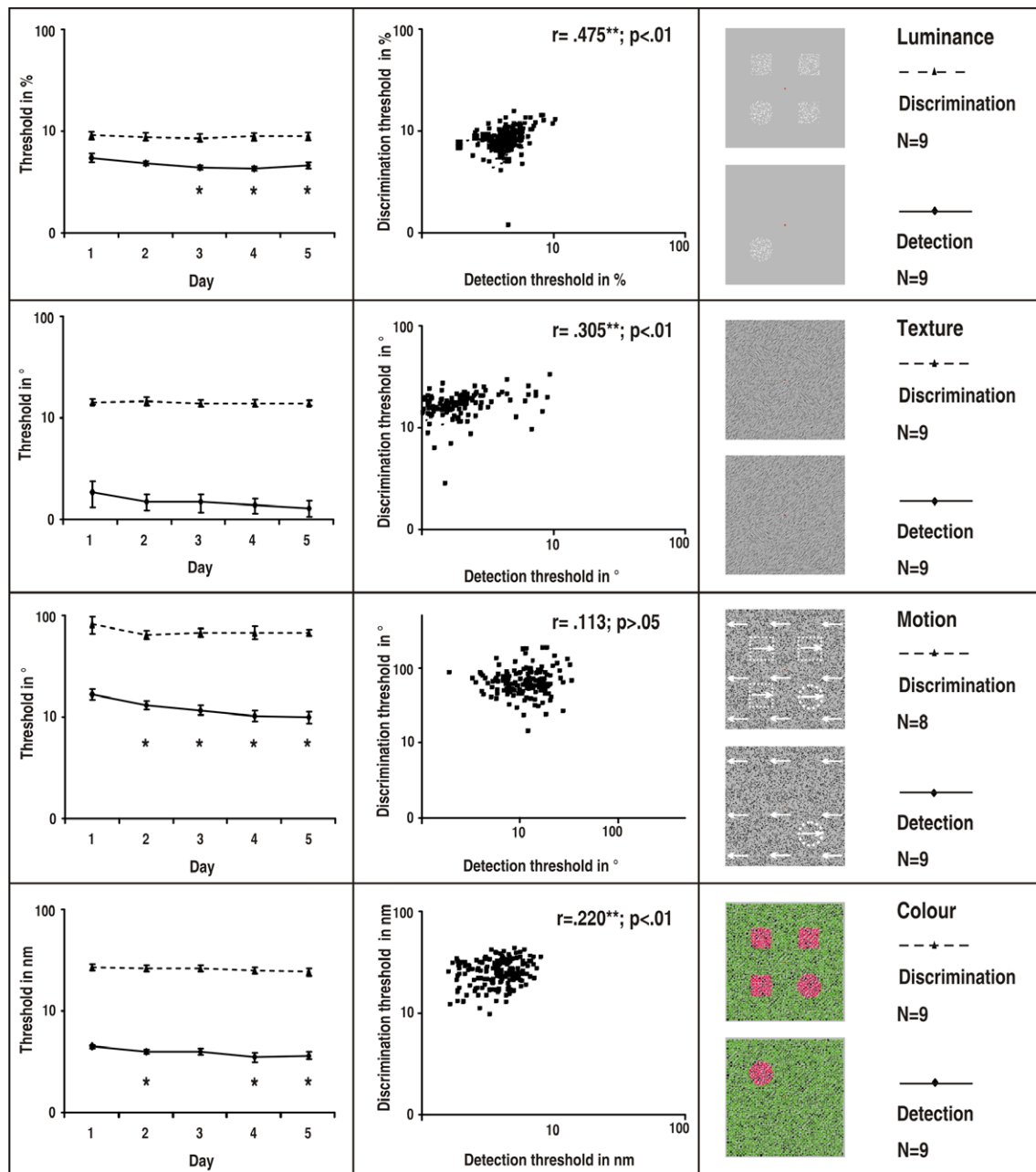


Fig. 2. Specificity of perceptual learning for the visual submodalities and tasks. *First column:* Mean thresholds (luminance contrast in percent (%); texture in visual degree (°); motion in visual degree (°); color in nanometers (nm)) in shape localisation tasks based on detection (solid lines) and form discrimination (dashed lines) as a function of testing day (ordinate) and visual submodality (lines 1–4). *Second column:* Diagrams depict the scatter-plots of correlation analysis between shape localisation based on detection (ordinate) and form discrimination (abscissa) for each visual submodality, respectively. *Third column:* Examples of test displays were illustrated for each visual submodality and task (upper shape localisation based on form discrimination, lower shape localisation based on detection, respectively). * $p < 0.05$, significant difference (Bonferroni-corrected pairwise comparisons between the first and all other testing days).

discrimination was small but significant (0.305 ; $p < 0.002$). For the detection task the threshold was 2.2° (0.64 SE) from the first testing day on. A further perceptual improvement may not be measurable with our experimental setup; due to the design of the stimulus, the minimal presentable difference between shape and background was about 2° .

Analyses for the submodality “motion” showed a significant main effect for the factor “day” in the detection task [$F(4,32) = 16.61$; $p < 0.001$]. Post-hoc comparisons reflected that the threshold values were reduced on all testing days compared to the first testing day. Perceptual learning cannot be observed in the motion localisation task based on form discrimination. Neither the main effect [$F(4,28) = 1.81$; $p > 0.05$], nor the interac-

tions were significant. Moreover, the correlation between motion detection and form discrimination was not significant (0.113 ; $p > 0.05$).

Analysis for the submodality “color” showed a significant main effect for the factor “day” in the detection task [$F(4,32) = 4.72$; $p < 0.01$] but not for localisation based on color-defined form discrimination [$F(4,32) = 2.33$; $p > 0.05$]. Post-hoc comparisons showed a significant difference between color-defined detection thresholds of the first as compared to the second, fourth and fifth testing day ($p < 0.05$). For both color-defined detection and form discrimination, analysis of interactions between visual field quadrants and testing days revealed no significance. The correlation between color tasks was small but significant (0.22 ; $p < 0.01$).

4. Discussion

4.1. Dependence of learning on task requirements

Fast perceptual learning improved form localisation based on detection of luminance, motion and color differences but not of texture² differences. In contradistinction, *fast* perceptual learning was not evident in localisation based on form *discrimination*; thresholds in all submodalities were stable across the five testing days. The correlations between detection and form discrimination within each modality were small but significant. No differences were evident between visual field quadrants in any modality for both tasks.

The results indicate that *fast* perceptual learning (the first fast phase; Fahle, 2009; Karni & Sagi, 1993) is clearly specific across different tasks within the same visual submodality, even for identical saliency, i.e. identical levels of subjective task difficulty. The *initial* quick phase of improvement only took place for the localisation of a figure-ground difference defined by variable visual cues and did not occur if the localisation additionally required the discrimination between different shapes (circles versus squares).

Perceptual learning has been repeatedly demonstrated in a wide range of visual detection and discrimination tasks within distinct visual submodalities (Tsodyks & Gilbert, 2004; Doshier & Lu, 2006; Fahle, 2009 for an overview). It is known that perceptual learning depends basically on the number of trials (Censor, Karni, & Sagi, 2006) and that the improvement develops progressively. Most studies investigating perceptual learning used a considerably higher number of trials than our study did (e.g. Doshier & Lu, 2006; Fahle, 1997; Karni & Sagi, 1991) and also addressed the later slow phase of perceptual learning. Consequently, we only suggest that perceptual learning occurs *faster* in our localisation task based on detection than based on form discrimination. With prolonged testing, we would also expect perceptual learning effects also in the latter tasks.

4.1. Early versus late selection for perceptual learning

Perceptual learning may take place on multiple cortical levels, from primary, secondary or associative sensory to higher cognitive or attentional cortical processing levels. Different underlying mechanisms are discussed: e.g. representation enhancement, external noise removal and internal noise reduction through channel re-weighting, perceptual learning with and without attentional influences (Ahissar & Hochstein, 1997; Doshier & Lu, 1998; Fahle, 2009; Herzog & Fahle, 1998; Tsodyks & Gilbert, 2004; Watanabe, Náñez, & Sasaki, 2001). Then perceptual learning should differ between different tasks and may reflect distinct mechanisms (e.g. Doshier & Lu, 2006; Fahle, 2009). Thus, analysis of perceptual learning in distinct tasks may inform us about the locus of learning at different stages of cortical processing.

In the current study, *fast* perceptual learning occurs in the detection task but not in localisation task based on form discrimination, indicating that different stages of processing may be involved in these tasks even when the same stimulus types and locations are applied. This effect was evident across all submodalities, even though it is most likely that neuronal populations are predominantly involved in the processing of luminance (V1), texture (V2), motion (V5) and color contrasts (V4, V8).

Since we measured at threshold both tasks were subjectively equally difficult, but the detection task was objectively easier, as thresholds were two to nine times lower (luminance: 8.7% vs. 4.6%; texture: 16.7° vs. 1.8°; motion 68.5° vs. 12.2°; color:

25.7 nm vs. 4.0 nm). For easy tasks, learning is thought to be restricted to late selection of appropriate signals on higher cortical levels, which seems to be easier and faster to achieve (e.g. Ahissar & Hochstein, 1997; Fahle, 2009). One may speculate that the detection task, being inherently easier, depends more on late selection mechanisms and therefore can be learned faster (Ahissar & Hochstein, 1997).

4.2. Different levels of binding required?

The localisation of the stimulus in our detection task, however, necessitates the involvement of early retinotopic visual areas, assuming an earlier site of improvement. Adding distractor stimuli in the discrimination task should not critically affect the level of cortical processing. It might, however, affect recurrent processes which are controlled by attention (Tsotsos et al., 2008). The theory of Tsotsos et al. (2008) may explain why perceptual learning starts earlier for the detection-based localisation task than for the form localisation based on discrimination: Learning occurs faster for the detection task, which requires only a single recurrent process and not the iterative attentional binding strategies associated with the form discrimination task, where multiple levels and/or pathways for features and spatial position must be tuned. We think that the extent of perceptual learning is delayed during iterative recurrence binding when different visual levels and positions are involved. This is congruent with current theories of visual and visuo-attentional processing, suggesting a dynamic view of cortical processing, with the complexity of a task defining the level of processing and the amount of top-down influences (Ahissar & Hochstein, 2004; Juan & Walsh, 2003). Moreover, for the flexibility of cortical processing, it is suggestive that this *early/fast* form of perceptual learning is under attentional top-down control (Fahle, 2009; Herzog & Fahle, 1998).

4.3. Alternative accounts

The presentation of distractor stimuli (e.g. the additional squares within the form discrimination tasks) may lead to a visual search situation. But we would like to emphasize the fact that the localisation task based on form discrimination is much harder than the simple localisation task based on detection, with thresholds increasing substantially (i.e. the task cannot be solved any more in the presence of the distractors), while distractors usually just increase reaction times (e.g. Treisman & Gelade, 1980) and not thresholds. A future study should investigate if the *initial* period of perceptual learning is also absent for a localisation task based on a form discrimination task without distractors across the visual field quadrants (i.e. is it a circle or a square?) as compared to the localisation task based on simple shape detection.

In our tasks, the response stays the same across tasks; subjects had to indicate the position of the circle in one of the four visual field quadrants by pressing one out of four buttons with their index finger (non-speeded response). Therefore, it is improbable that the motor site of the task is learned in the detection task but not in the form discrimination task.

An alternative explanation for the difference between the results in the detection versus form discrimination task could be the involvement of *stimulus enhancement* and *perceptual template retuning* in any underlying perceptual learning (Doshier & Lu, 2006). Stimulus enhancement increases the input stimulus. Perceptual template retuning optimizes the perceptual template to exclude distractors or external noise. Only stimulus enhancement could be the underlying mechanism of perceptual learning in the present detection task, while in the localisation based on form discrimination both mechanisms could be involved. To our knowledge, a connection between distinct perceptual learning mecha-

² As mentioned in the results section, the missing perceptual learning effect in texture detection task was possibly rather due to the technical restrictions of the screen resolution.

nisms and the *initial* phase or the later slower phase of learning (Karni & Sagi, 1993) has not been reported in the literature.

4.4. Limitations of the study

As described in the results section, in the texture shape localisation based on detection, a further perceptual improvement may not be measurable due to our experimental setup.

Moreover, we performed independent ANOVAs, though observers were the same in all experiments. It remains unknown how the different conditions in the same observers may interact.

4. Conclusion

The *initial* phase of improvement through practice is different in a localisation task based either on detection or form discrimination even if stimuli are identical with respect to visual submodality, stimulus type and stimulus position. An appealing hypothesis is that the number of recurrent attentional binding processes varies between these tasks. In the detection task, only one recurrent binding process is necessary to identify the stimulus position. This process could be easily improved or learned. In the form discrimination task, however, iterative binding is necessary to identify the shape of target and distractor stimuli, as well as their localisation. We therefore suggest that the rate at which learning occurs is decreased if multiple iterative processes have to be learned simultaneously.

Acknowledgment

This work was supported by the German Research Foundation (BR 1691/5-1 and FA119/17-1).

References

- Ahissar, M., & Hochstein, S. (1993). Attentional control of early perceptual learning. *Proceedings of the National Academy of Sciences USA*, 90, 5718–5722.
- Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, 387, 401–406.
- Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Sciences*, 8(10), 457–464.
- Boehler, C. N., Tsotsos, J. K., Schoenfeld, M. A., Heinze, H.-J., & Hopf, J.-M. (2008). The center-surround profile of the focus of attention arises from recurrent processing in visual cortex. *Cerebral Cortex*, 19, 982–991.
- Censor, N., Karni, A., & Sagi, D. (2006). A link between perceptual learning, adaption and sleep. *Vision Research*, 46, 4071–4074.
- Doshier, 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 USA*, 95(23), 13988–13993.
- Doshier, B. A., & Lu, Z.-L. (2006). Level and mechanisms of perceptual learning: Learning first-order luminance and second order texture-objects. *Vision Research*, 46, 1996–2007.
- Fahle, M. (1997). Specificity of learning curvature, orientation, and vernier discriminations. *Vision Research*, 37(14), 1885–1895.
- Fahle, M. (2004). Perceptual learning: A case for early selection. *Journal of Vision*, 4, 879–890.
- Fahle, M. (2009). Perceptual learning and sensorimotor flexibility: Cortical plasticity under attentional control? *Philosophical transactions of the Royal Society of London, Series B. Biological Sciences*, 364, 313–319.
- Fahle, M., Edelman, S., & Poggio, T. (1995). Fast perceptual learning in hyperacuity. *Vision Research*, 35, 3003–3013.
- Fahle, M., & Morgan, M. (1996). No transfer of perceptual learning between similar stimuli in the same retinal position. *Current Biology*, 6(3), 292–297.
- Fahle, M., & Poggio, T. (Eds.). (2002). *Perceptual learning*. MIT Press.
- Herzog, M. H., & Fahle, M. (1998). Modeling perceptual learning: Difficulties and how they can be overcome. *Biological Cybernetics*, 78(2), 107–117.
- Juan, C.-H., & Walsh, V. (2003). Feedback to V1: A reverse hierarchy of vision. *Experimental Brain Research*, 150, 259–263.
- 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, 4966–4970.
- Karni, A., & Sagi, D. (1993). The time course of learning a visual skill. *Nature*, 365(6443), 250–252.
- Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neuroscience*, 23, 571–579.
- Lamme, V. A., & Spekreijse, H. (2000). Modulations of primary visual cortex activity representing attentive and conscious scene perception. *Frontiers in Bioscience*, 5, 232–243.
- Mollon, J. D., & Danilova, M. V. (1996). Three remarks on perceptual learning. *Spatial Vision*, 10, 51–58.
- Morgan, M. J. (1992). Hyperacuity of those in the know. *Current Biology*, 2, 481–482.
- Poggio, T., Fahle, M., & Edelman, S. (1992). Fast perceptual learning in visual hyperacuity. *Science*, 256, 1018–1021.
- Somers, D. C., Dale, A. M., Seiffert, A. E., & Tootell, R. B. (1999). Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proceedings of the National Academy of Sciences USA*, 96, 1663–1668.
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12(1), 97–136.
- Tsodyks, M., & Gilbert, C. (2004). Neural networks and perceptual learning. *Nature*, 431(7010), 775–781.
- Tsotsos, J. K. (1990). A complexity level analysis of vision. *The Behavioral and brain sciences*, 13, 423–455.
- Tsotsos, J. K., Rodríguez-Sánchez, A. J., Rothenstein, A. L., & Simine, E. (2008). The different stages of visual recognition need different attentional binding strategies. *Brain Research*, 1225, 119–132.
- Watanabe, T., Náñez, J. E., & Sasaki, Y. (2001). Perceptual learning without perception. *Nature*, 413(6858), 844–848.
- Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception and Psychophysics*, 33, 113–120.