Perceptual learning of bisection stimuli under roving: Slow and largely specific

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In perceptual learning, performance often improves within a short time if only one stimulus variant is presented, such as a line bisection stimulus with one outer-line-distance. However, performance stagnates if two bisection stimuli with two outer-line-distances are presented randomly interleaved. Recently, S. G. Kuai, J. Y. Zhang, S. A. Klein, D. M. Levi, and C. Yu, (2005) proposed that learning under roving conditions is impossible in general. Contrary to this proposition, we show here that perceptual learning with bisection stimuli under roving is possible with extensive training of 18000 trials. Despite this extensive training, the improvement of performance is still largely specific. Furthermore, this improvement of performance cannot be explained by an accommodation to stimulus uncertainty caused by roving.

Keywords: bisection task, roving, stimulus uncertainty

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Introduction

In perceptual learning, training improves the ability to discriminate or detect basic features that are assumed to be fundamental for perception (for reviews, see Fahle, 2005a; Fahle & Poggio, 2002). Classical examples are the improvement of the discrimination of vernier (McKee & Westheimer, 1978; Poggio, Fahle, & Edelman, 1992) and bisection offsets (Crist, Kapadia, Westheimer, & Gilbert, 1997; Crist, Li, & Gilbert, 2001; Fahle & Morgan, 1996), stereoscopic depth (Ramachandran & Braddick, 1973), line orientation (Vogels & Orban, 1985), motion direction (Vaina, Sundareswaran, & Harris, 1995; Watanabe, Nanez, & Sasaki, 2001), odd men out (Karni & Sagi, 1991; Schoups & Orban, 1996; Sireteanu & Rettenbach, 1995). waveforms of gratings (Fiorentini & Berardi, 1980), and contrast increments (Adini, Sagi, & Tsodyks, 2002; Yu, Klein, & Levi, 2004).

Usually, in studies on perceptual learning, one stimulus variant is presented and performance improves specifically for this variant. For example, a bisection stimulus is presented consisting of a central element bisecting an interval that is delineated by two outer elements (Figure 1A). The central element is slightly displaced towards one or the other outer element. When observers have to indicate this bisection offset, performance improves within 1 hour of training (e.g., Fahle & Morgan, 1996; Otto, Herzog, Fahle, & Zhaoping, 2006). This learning is usually specific for the stimulus parameters. For example, an improvement for vertical bisection stimuli does not transfer to horizontal ones (e.g., Crist et al., 1997; Otto et al., 2006).

When, instead of one, two or more stimulus variants are presented randomly interleaved, a so-called *stimulus roving* paradigm is used (Berliner & Durlach, 1973; Yu et al., 2004). In some cases, learning is not affected by stimulus roving, for example, when the external noise level (Dosher & Lu, 2006) or when the position of the stimulus is randomly varied (Censor, Karni, & Sagi, 2006; Karni & Sagi, 1991; Otto et al., 2006; Sireteanu & Rettenbach, 1995).

Interestingly, in other cases, stimulus roving can prevent perceptual learning (Adini, Wilkonsky, Haspel,

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Figure 1. (A) Horizontal line bisection stimulus with an outer-linedistance of 20' (arcmin). The interval between the outer lines was bisected into two parts by a central line, which was displaced slightly in the direction of the upper (as in this example) or lower outer line. The task was to discriminate the direction of this displacement by pressing one of two buttons (B1, B2). The actual stimuli were white on black. Here, stimuli with outer-line-distances of 20' and 30' are indicated in blue and red, respectively, matching the colors in the following graphs. (B) Line bisection stimulus with an outer-line-distance of 30' (a displacement to the bottom is shown). (C) Experimental design. The two stimuli shown in A and B were presented randomly interleaved in 10 training sessions of 15 blocks each. Each block contained 60 trials of either stimulus. Before and after training, we determined performance for the two trained and for four untrained bisection stimuli without roving (2 blocks of 80 trials per bisection stimulus).

Tsodyks, & Sagi, 2004; Kuai, Zhang, Klein, Levi, & Yu, 2005; Otto et al., 2006; Yu et al., 2004). For example, performance in the bisection task does not improve on a short term scale if bisection stimuli with two outerelement-distances are presented randomly interleaved, although learning with either stimulus variant is possible (Otto et al., 2006). Another example is contrast increment detection. Performance improves if one reference contrasts are randomly interleaved during training, no improvement of performance occurs (Adini et al., 2004; Kuai et al., 2005; Yu et al., 2004).

Based on results that show no short term learning under roving conditions, Kuai et al. (2005) proposed that learning is "impossible" in general under these roving conditions because roving interrupts the creation of a long term memory trace. For the bisection task, Zhaoping, Herzog, and Dayan (2003) proposed that different sets of recurrent connections are used to encode different outerline-distances. Under roving, the separate recurrent networks cannot be built up consistently because of mutual interactions. If an improvement of performance is, indeed, impossible under roving conditions, an important aspect of perceptual learning would have been identified: learning with either one of the stimulus variants (e.g., the two outer-line-distances in the bisection task) is possible, only their random combination is not. This issue was investigated here.

General methods

Observers

Data were obtained from one of the authors and paid students of the I. Beritashvili Institute of Physiology, Tbilisi and the Ecole Polytechnique Fédérale de Lausanne (EPFL). All observers (ages between 20 and 36 years) had normal or corrected-to-normal visual acuity as determined by the Freiburg visual acuity test (Bach, 1996). Subjects had to reach a value of 1.0 (corresponding to 20/20) to participate in the experiments. Observers signed informed consent before participation in the experiment.

Apparatus

Stimuli were presented on a Samsung SyncMaster 957DF (320 mm \times 256 mm) or a Philips 201B4 (360 mm \times 288 mm) CRT monitor driven by a standard accelerated graphics card. Screen resolution was 1280 by 1024 pixels. Stimuli were white on a dark background. Stimulus luminance was 100 cd/m² as determined with a GretagMacbeth Eye-One display 2 colorimeter. The room was dimly illuminated (approximately 0.5 lux) and background luminance on the screen was below 1 cd/m². Refresh rate was 75 Hz. Viewing distance was 5 m.

Stimuli and task

Bisection stimuli consisted of two outer elements delineating a horizontal or vertical interval of either 20' (arcmin) or 30' length. This interval was bisected by a central element into two parts (Figures 1A and 1B). For line bisection stimuli, line length was 20'. As controls, we used also dot bisection stimuli. Dots were composed of pixels arranged in a square like fashion, edge length about 40" (arcsec).

The central element of the particular bisection stimulus was slightly displaced in the direction towards one outer element chosen (pseudo)-randomly in each trial. In a binary forced choice task, observers had to discriminate the direction of this displacement; that is, was the central element closer to the upper (left) or lower (right) outer element. We determined bisection acuity thresholds of 75% correct responses with an adaptive staircase method and maximum likelihood estimation of the parameters of the psychometric function (PEST; Taylor & Creelman, 1967).

Each trial was initiated with four markers at the corners of the screen presented for 500 ms followed by a blank screen for 200 ms. No fixation point was presented to prevent observers from judging the position of the central element relative to this fixation point stored in memory. Next, the bisection stimulus was presented for 150 ms in the center of the screen. After stimulus presentation, a blank screen appeared for a maximal duration of 3000 ms, during which observers were required to make a response by pressing one of two buttons. Incorrect responses were followed by an auditory error signal produced by the computer. A new trial was initiated 500 ms after the observer gave a response.

Procedure

Practice session

Three observers had no experience with psychophysical experiments before. To familiarize these observers with bisection stimuli, we provided some training trials with bisection stimuli that differed from the experimental stimuli by their orientation, outer-line-distance, and/or line length.

Training

Four observers trained with bisection stimuli with horizontal lines (Figure 1) and one observer with vertical lines (i.e., the line bisection stimuli, as shown in Figure 1, were rotated by 90 deg; since results were comparable, we collapsed the data). Line bisection stimuli with outer-line-distances of 20' (Figure 1A) and 30' (Figure 1B) were presented (pseudo)-randomly interleaved trial by trial (stimulus roving). Subjects were informed that bisection stimuli with two different outer-line-distances were presented.

Observers trained in 10 sessions of maximal 1.5 hours (Figure 1C, mean session duration: about 70 min). If an observer participated in two sessions on the same day, there was a break of at least 3 hours between the two sessions (on average, less than 4 session breaks per subject did not include a night). Each session contained 15 blocks of 120 trials (60 for each outer-line-distance). Hence, each observer viewed a total of 18000 trials during training. Observers were allowed to take small breaks between blocks.

Per training block, each outer-line-distance was presented in 60 trials, and two independent adaptive staircase procedures were run (one for each outer-line-distance). The starting value of the adaptive procedures was set to the 1.5 fold of the individual thresholds determined in previous training blocks. This method avoids the presentation of supra-threshold offset values for which performance is already perfect (Ahissar & Hochstein, 1997; Herzog & Fahle, 1998).

Baselines

Before the training phase, we determined baseline performance for the trained line bisection stimuli, for line bisection stimuli oriented orthogonally to the trained stimuli, and for dot bisection stimuli in non-roving conditions (Figure 1C). For all three types of stimuli, we determined thresholds for outer-element-distances of 20' and 30' in separate blocks consisting of 80 trials. For each observer, we measured each condition twice (i.e., 160 trials) and the order of conditions was randomized across observers. After every condition had been measured once, the order of conditions was reversed for the second set of measurements to reduce, at least partly, the influence of possible learning or fatigue effects in the averaged data.

After the training phase, we repeated the baseline measurements to determine post-training performance.

Data analysis

Training

To determine improvement of performance during training, we fitted regression lines to the thresholds of each observer. The slopes of regression lines were subjected to a one sample *t*-test ($\alpha = 0.05$) comparing the slopes of regression lines with the null hypothesis of a slope of zero (no improvement of performance).

Baselines

To determine pre-training performance, we collapsed the two thresholds of each baseline condition for each observer individually. Post-training performance was determined accordingly. Next, we determined the ratio of the collapsed post-training to pre-training thresholds. To test if learning has taken place, we computed one sample *t*-tests ($\alpha = 0.05$) with the null hypothesis of a ratio of one (no change in performance). To compare ratios of different baseline conditions, we computed two tailed, paired *t*-test ($\alpha = 0.05$) with the null hypothesis that ratios are identical.

To compare performance levels in roving and nonroving conditions, we compared the pre-training baseline



Figure 2. Bisection acuity as a function of extensive training. Five observers trained with line bisection stimuli with outer-linedistances of 20' and 30' randomly interleaved (roving). During 150 training blocks (18000 trials), performance improved. Error bars show the SEM.

thresholds (160 trials/observer) with the thresholds determined in the first three training blocks (180 trials/ observer). Post-training performance was analyzed accordingly.

Results

Five observers trained with line bisection stimuli with two outer-line-distances of 20' and 30' randomly interleaved (see Figures 1A and 1B). During 150 training blocks (18000 trials in 10 training sessions), bisection acuity thresholds improved (Figure 2; for the individual training data, see Auxiliary Figure 1). For the outer-linedistance of 30', individually determined regression lines had slopes ranging from -0.19 to -0.07 (mean slope: -0.12; SEM: 0.02; see Auxiliary Table 1). This improvement of performance was significant (one sample t-test, p-value: 0.006). For the outer-line-distance of 20', regression lines had slopes ranging from -0.25 to 0.02 (mean slope: -0.09; SEM: 0.05; see Auxiliary Table 1 for the individual results). The improvement of performance failed to be significant because of one outlier (one sample *t*-test, p-value: 0.168). This observer (slope: 0.02) had already very low thresholds at the beginning of the training (mean threshold during the first three training blocks: 20.8''). This ceiling effect possibly explains the lack of improvement of performance. For baseline conditions, mean ratios of postto pre-training performance are plotted in Figure 3 (for the individual baseline thresholds, see Auxiliary Table 2). A ratio below 1 indicates that performance has improved after

training. Ratios ranged from 0.39 to 0.81 for an outer-linedistance of 20' and from 0.40 to 0.72 for an outer-linedistance of 30'. The improvement of baseline performance was significant in both cases (Figure 3; L – 20': one sample *t*-test, *p*-value: 0.004; L – 30': one sample *t*-test, *p*-value: 0.003). Hence, performance can improve under roving conditions in a long term fashion although there was no improvement in a similar experiment with 1960 training trials only (see Otto et al., 2006, their Figure 6). However, perceptual learning under roving conditions is rather slow compared to short term learning with only *one* bisection stimulus (i.e., one outer-line-distance).

Improvement of performance after extensive training might be explained by general training effects. Indeed, ratios of pre- and post-training thresholds for the untrained orthogonal line and dot bisection stimuli were on average smaller than 1 indicating that some general learning has taken place (Figure 3; for individual baseline thresholds, see Auxiliary Table 2). For dot bisection stimuli, baseline performance improved significantly (20' D: one sample *t*-test, *p*-value: 0.004; 30' D: one sample *t*-test, *p*-value: 0.018). This improvement of performance might be explained by the fact that the dot bisection stimuli are "contained" in the trained line bisection stimuli. For orthogonal line bisection, the improvement of performance failed to be significant but revealed a trend (Figure 3, O).

On the other hand, for an outer-line-distance of 20', the mean ratio in the trained condition was significantly



Figure 3. Ratios of pre- and post-training thresholds for outerelement-distances of 20' and 30', respectively. A ratio below 1 indicates that performance has improved with training. For the trained line bisection stimuli (L), performance improves significantly. For the untrained orthogonal line bisection (O) and dot bisection stimuli (D), performance also improves with training but much less (except for D 30'). Error bars show the *SEM*.

smaller than the ratio for both the untrained orthogonal line stimulus (Figure 3; two tailed paired *t*-test, *p*-value: 0.005) and the untrained dot stimulus (two tailed paired *t*-test, *p*-value: 0.023). Hence, long-term learning in these conditions shows a stimulus specific component. For the outer-line-distance of 30', these differences failed to be significant.

During the first 30 training blocks (3600 trials in two sessions), bisection acuity thresholds seem even to deteriorate slightly (Figure 4). For the outer-line-distance of 30', regression lines had slopes ranging from -0.89 to 0.72 (mean slope: 0.18; *SEM*: 0.31). For the outer-line-distance of 20', slopes ranged from 0.03 to 0.76 (mean slope: 0.29; *SEM*: 0.13). Hence, learning under roving conditions seems not to start right from the beginning of the training in good agreement with previous findings.

As discussed, baseline performance strongly improves for the trained stimuli (Figure 3). Because these baselines were determined for each outer-line-distance in separate blocks, training with randomly interleaved bisection stimuli (Figure 2) transfers to bisection stimuli that are presented without roving (Figure 3). This finding indicates that the improvement of performance cannot be simply explained by an accommodation to the roving conditions during training. Moreover, before and after training, performance levels in roving and non-roving conditions are comparable (Figure 5). Hence, roving seems to interfere with learning but not with performance in the bisection task *per se*.

In contrast learning under roving conditions, most of the learning from a previous training session is lost at the beginning of a new session (Yu et al., 2004), possibly pointing to an interrupted consolidation process (Seitz,



Figure 4. Bisection acuity as a function of short term training. This graph shows the first 30 training blocks (3600 trials) of Figure 2. Performance seems to deteriorate rather than to improve. Error bars show the *SEM*.



Figure 5. Roving versus non-roving. For both outer-line-distances of 20' and 30', mean thresholds of pre- and post-training baselines (non-roving) are compared with mean thresholds of the first three and last three training blocks (roving), respectively. Performance is comparable in "non-roving" and "roving" conditions indicating that learning but not performance itself suffers from roving. Thresholds in both conditions are reduced after the training under roving conditions. Error bars show the *SEM*.

Yamagishi, Werner, Goda, Kawato, & Watanabe, 2005). To investigate if a comparable effect is present in our data, we compared thresholds at the end of one session with thresholds achieved at the beginning of the next session. On average, performance at the beginning of a new session was not deteriorated (Figure 6A). Analogous results hold when the session breaks were considered that either did or did not include a night (data not shown). It seems that performance slowly improves both between (Figure 6A; see also, Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994) and within sessions (Figure 6B). However, these effects are small compared to the variance in the data.

Discussion

Bisection discrimination strongly and quickly improves when only one outer-element-distance is presented (e.g., Fahle & Morgan, 1996; Otto et al., 2006). As in other roving studies (Adini et al., 2004; Kuai et al., 2005; Otto et al., 2006; Yu et al., 2004), no short term improvement of performance occurs when two or more stimulus variants, such as bisection stimuli with two different outer line distances, are presented randomly interleaved (Figure 4).

Based on their contrast and motion direction discrimination experiments, Kuai et al. (2005) proposed that these tasks are "unlearnable" under roving conditions in gen-



Figure 6. (A) Changes of performance between sessions. Thresholds of the first two training blocks of a session are subtracted from thresholds of the last two training blocks of the previous session (see also Figure 2). A negative value indicates that performance improves between sessions. On average, performance seems to improve slightly between sessions; however, the variance of thresholds is high. (B) Session slopes. We fitted regression lines to the individual thresholds for each session and outer-line-distance (see also Figure 2). A negative slope indicates an improvement of performance. On average, session slopes are around 0 or slightly negative. The variation of session slopes is high. Error bars show the *SEM*.

eral; that is, if there is no short term learning, there will be no long term learning as well. The authors proposed that the bottom-up sensory inputs interact with the development of top-down memory traces. These interactions enhance and refine the memory traces and, consequently, improve performance. Kuai et al. (2005) argued that this continuous interaction of top-down and bottom-up information is disturbed under roving conditions. Hence, no learning occurs.

A similar explanation was put forward by Zhaoping et al. (2003) earlier. In their model, different sets of recurrent connections are used to encode different outerelement-distances of bisection stimuli. To improve performance, these recurrent connections need to be refined. However, a particular recurrent connection might be excitatory for one outer-element-distance and inhibitory for another. Thus, the network would have to do the impossible: achieving an excitatory connection between two neurons for one outer-element-distance and, simultaneously, an inhibitory connection between the same neural pair for another outer-element-distance. Hence, learning is impossible, or at least diminished, under roving conditions.

Contrary to these predictions, our current results show that, at least for bisection stimuli, performance improves slowly under roving conditions if training is extensive (Figure 2). Hence, learning (with extensive training) is possible under roving conditions with two stimulus variants, although there was no short term improvement of performance. These results are in accordance with a recently proposed model incorporating a task selective top-down modulation of sensory processes (Schäfer, Vasilaki, & Senn, in preparation). While the model confirms that a simultaneous improvement for two stimulus variants is possible, it cannot fully account for the slow down of learning.

In this context, Kuai et al. (2005) proposed that learning is impossible under roving conditions based on their experiments with *four* stimulus variants. It remains an open question whether perceptual learning in the bisection task is further slowed down, or even impossible, when more than *two* outer-line-distances are presented randomly interleaved.

The improvement of performance in our experiment is not caused by an accommodation to the roving paradigm because performance in roving and non-roving conditions is comparable before as well as after training (Figure 5). Moreover, learning cannot be completely explained by unspecific factors because we found only a weak transfer of learning to orthogonal line bisection stimuli (Figure 3). The transfer of learning to the dot stimulus with an outer-dot-distance of 30' might be explained because the dots are "contained" in the trained line bisection stimuli. Hence, stimulus specificities, as usually found in perceptual learning (e.g., Fahle, 2005b), are also present with long term training under roving conditions.

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