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Limited transfer of visual skill in orientation discrimination to locations treated by pre-testing and subliminal exposure

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A R T I C L E I N F O

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A B S T R A C T

Substantial transfer of perceptual skill learning can be achieved across large distances in the visual field by a brief pre-test, training-plus-exposure, or a double-training paradigm (Xiao et al., 2008; Zhang, Xiao, et al., 2010; Zhang, Zhang, et al., 2010). Additionally, subliminal exposure has been shown to be beneficial for subsequent perceptual learning. Here, we tested the generalization of orientation discrimination learning from a fully trained location towards four other test locations, either in the same or opposite hemifield as the training location, which each were subjected to a different type of pre-conditioning. In one test location, there was brief pre-testing in the first session. Two other locations were stimulated by masked stimuli similar or identical to concurrently presented stimuli in the training location. In the fourth test location, no stimuli were presented during training. Generalization of training to test locations was measured in the session immediately following the completion of training in the training location. Moreover, to test the robustness of transfer, training was continued in all four test locations. The experiment as a whole consisted of 15 sessions of orientation discrimination learning at the training location, followed by 15 sessions of training in the test locations. We found only limited generalization from the trained to the test locations. Performance in pre-tested and stimulated test locations showed a small advantage compared to the unstimulated test location. However, this advantage disappeared within a few sessions of further training in the test locations.

1. Introduction

Perceptual learning is defined as the acquisition of a perceptual skill over time. This learning process is characterized by fast improvements during early training and subsequent learning that gradually slows down until reaching asymptotic performance levels (Karni, 1996; Karni & Bertini, 1997; Karni & Sagi, 1993; Karni et al., 1998). Once a skill is learned, performance is retained for extended periods without further training (De Weerd, Pinaud, & Bertini, 2006). Especially during this asymptotic learning phase, learning has been reported to become specific to stimulus characteristics (Fahle, 1997; Karni & Bertini, 1997; Karni & Sagi, 1991; Schoups, Vogels, & Orban, 1995; Schwartz, Maquet, & Frith, 2002).

Recently, a series of experiments has cast doubt upon the idea that specificity is a defining characteristic of perceptual learning (Wang, Zhang, Klein, Levi, & Yu, 2012; Wang, Zhang, Klein, Levi, & Yu, 2014; Xiao et al., 2008; Zhang et al., 2010; Zhang, Xiao, Klein, Levi, & Yu, 2010). Xiao et al. (2008) showed that a double-training procedure consisting of feature and location training resulted in near-complete transfer of learning across far-removed retinal locations. Subsequently, a training-plus-exposure procedure was introduced (Zhang et al., 2010). Here, training was performed on a feature of interest in a training location. In the test location, initial training on the relevant feature was followed by a task on an irrelevant stimulus feature, while the stimulus feature of interest was simply exposed (assumedly unattended). Again, this experimental procedure resulted in substantial transfer.

Wang et al. (2012) extended these findings by showing that task relevance and task demand modulate the amount of transfer obtained in a double-training procedure using a Vernier task. They reported that passive exposure alone was insufficient to elicit transfer in a Vernier acuity task (Wang et al., 2012). More recent studies provide mixed results regarding the effect of passive exposure on location transfer. While Xiong, Zhang, and Yu (2016) reported that location transfer in a Vernier task requires either bottom-up stimulation or top-down transfer, Mastropasqua, Galliussi, Pascucci, and Turatto (2015) reported no transfer for passive stimulation with task-irrelevant stimuli. This latter finding might be seen as support for an effect of attention in generalization. In line with this, a brief pre-test, involving greater

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attentional allocation, led to substantial periphery-to-periphery transfer in an orientation discrimination task (Zhang et al., 2010). The data can also be seen as support for the idea that location specificity is strongly task-dependent. Some tasks such as orientation discrimination were demonstrated to work as actuators in double-training paradigms, enabling transfer of Vernier learning, whereas other tasks including contrast discrimination tasks failed to induce complete transfer (Wang et al., 2014).

A further modulator of transfer is the amount of training at threshold. Using the double-training procedure of Zhang, Wang, Klein, Levi, and Yu (2011), Hung and Seitz (2014) showed that increasing the number of trials at threshold for the Vernier task at the trained location (where there was also orientation discrimination training) eliminated transfer towards the test location. Despite the limited length of learning curves used in Hung and Seitz (2014) (7 sessions), they also demonstrated that increasing the number of trials at threshold increased specificity in orientation discrimination, even in the absence of a double training or a training-plus-exposure procedure. These findings are in line with older studies in which experience with 'difficult' discriminations or asymptotic learning is proposed as a precondition for specificity (Ahissar & Hochstein, 1997; Jeter, Dosher, Petrov, & Lu, 2009).

Although Wang et al. (2012) have shown that passive exposure alone was insufficient to elicit transfer in a Vernier acuity task, there is strong evidence that stimulus repetition leads to adaptation (for a review, see Grill-Spector, Henson, & Martin, 2006), which for some stimulus features has been associated with increased discrimination capabilities. For example, Regan and Beverley (1985) have shown a link between adaptation and improved orientation discrimination. Other studies also found enhanced discrimination of contrast, speed, and direction of motion following adaptation (Abbonizio, Langley, & Clifford, 2002; Clifford & Wenderoth, 1999; Phinney, Bowd, & Patterson, 1997).

Adaptation has also been linked to generalization of skill learning. It has been shown that by removing adaptation, complete generalization can be achieved in a texture discrimination task (Harris, Gliksberg, & Sagi, 2012). Moreover, repeated exposure to unattended stimuli can result in perceptual learning (Gutnisky, Hansen, Iliescu, & Dragoi, 2009; Watanabe, Náñez, & Sasaki, 2001). In addition, a study by Tsushima, Seitz, and Watanabe (2008) showed that the beneficial effect of exposure disappeared when the stimuli could be attended. They suggested that passively exposed stimuli of which the observer is aware during performance of another task may be suppressed by attention, so that an unconscious form of exposure might provide a more effective tool to test a potential contribution to learning (Seitz & Watanabe, 2003) and generalization.

In the light of the conflicting literature, we wished to test generalization in an orientation discrimination task designed to achieve strong perceptual learning. To that aim, we presented sufficiently clear examples of large orientation differences (Ahissar & Hochstein, 2004) especially at the beginning of learning (see Section 2). At the same time we maximized numbers of trials performed near threshold, by starting measurements from the second session onward not too far away from threshold, and by extensive asymptotic training (15-session learning curves) (Ahissar & Hochstein, 1997; Hung & Seitz, 2014; Jeter et al., 2009; Karni & Sagi, 1991). These conditions favoring perceptual learning were combined with testing conditions that have been shown to induce transfer. The first transfer condition consisted of a test location pre-tested with a single orientation discrimination training session (similar to Zhang et al., 2010). Second, we used two transfer conditions in which a test location was passively exposed to Gabor stimuli, which were ignored and masked with the aim of pre-conditioning these locations for subsequent generalization from the trained location. The idea of using exposure was inspired by Xiao et al. (2008), although our procedure was more similar to the approach of Watanabe et al. (2001). We used two slightly different passive exposure conditions to which transfer was tested: In one condition, participants were exposed to masked, unattended stimuli that were identical to those used in the actively trained task, such that visual feedback on correctness in that task in the trained location applied correctly to the unseen stimuli in the exposure location. In the other exposure condition, the unseen oriented stimuli were randomized in orientation (for details see Section 2) so that the feedback signal became irrelevant and any passive learning would only reflect the effects of exposure. We anticipated that these procedures might lead to significant transfer from a trained location to one or possibly both of the masked exposure test locations. Third, for all the different test locations, we wished to verify how robust the advantage would be after pre-testing or after masked exposure compared to a location where no stimuli had been shown. Whereas in all prior studies generalization testing was limited to a single session, in the present study additional prolonged training was performed in all test locations to verify the robustness of any advantages afforded by masked exposure and pretesting.

2. Methods

2.1. Participants

Eight participants (mean age 22.27 years, *sd* 1.41, 7 female), naïve to the purpose of the study participated in the experiment and the control condition. All participants had normal or corrected-to-normal visual acuity. Informed, written and verbal consent was obtained according to the Helsinki Declaration, after full information about all procedures and about the right to withdraw participation at any time. Participants agreed to the full length of the experiment, to be tested at least three times a week at approximately the same time of day, and to show up well-rested at each session. Prior to the first session, the task and required responses were explained to the participants with the help of instructions and illustrations on paper. All procedures were approved by the local Ethical Committee of the Faculty of Psychology and Neuroscience (ECP). For their participation in the study participants received either monetary reward or credits to fulfill course requirements.

2.2. Task, stimuli, and apparatus

Participants performed a forced-choice orientation discrimination task with two response options in which participants had to compare a single stimulus to an implicit oblique reference orientation. They indicated the direction of the orientation offset of a Gabor stimulus from the oblique reference by pressing either the left or right arrow key for counterclockwise and clockwise rotations respectively (Fig. 1A). Each trial started with a 950 ms window in which participants had the opportunity to initiate fixation. Without fixation, this waiting period was restarted. Successful initiation of fixation was followed by a 300 ms period in which steady fixation was required (within 1.5° from the fixation point) to trigger stimulus presentation. Stimulus presentation lasted 33 ms and was followed immediately in some conditions by a mask of 49 ms. Fixation errors during pre-stimulus period and stimulus presentation led to abortion of the trial. The response window started from the beginning of stimulus onset and was 1500 ms long. Upon response, feedback was provided by a color change of the fixation spot to either green or red, for correct and incorrect responses respectively. The color change remained visible for 250 ms after which the trial was terminated and the next trial started. The inter-trial-interval depended on the speediness of responses and on how quickly participants regained fixation.

The Gabor stimuli used (2.37 cycles/degree spatial frequency, 50% Michelson contrast, 3° diameter, 8° eccentricity, average luminance 56 cd/m^2) showed small clockwise or counterclockwise deviations from 135°. Note that we chose relatively high eccentricities to increase the separation in the visual field between the five locations used in our study. The fixation spot was a small white dot of 0.2° diameter. The mask was of the same size as the Gabor stimuli. It was equiluminant

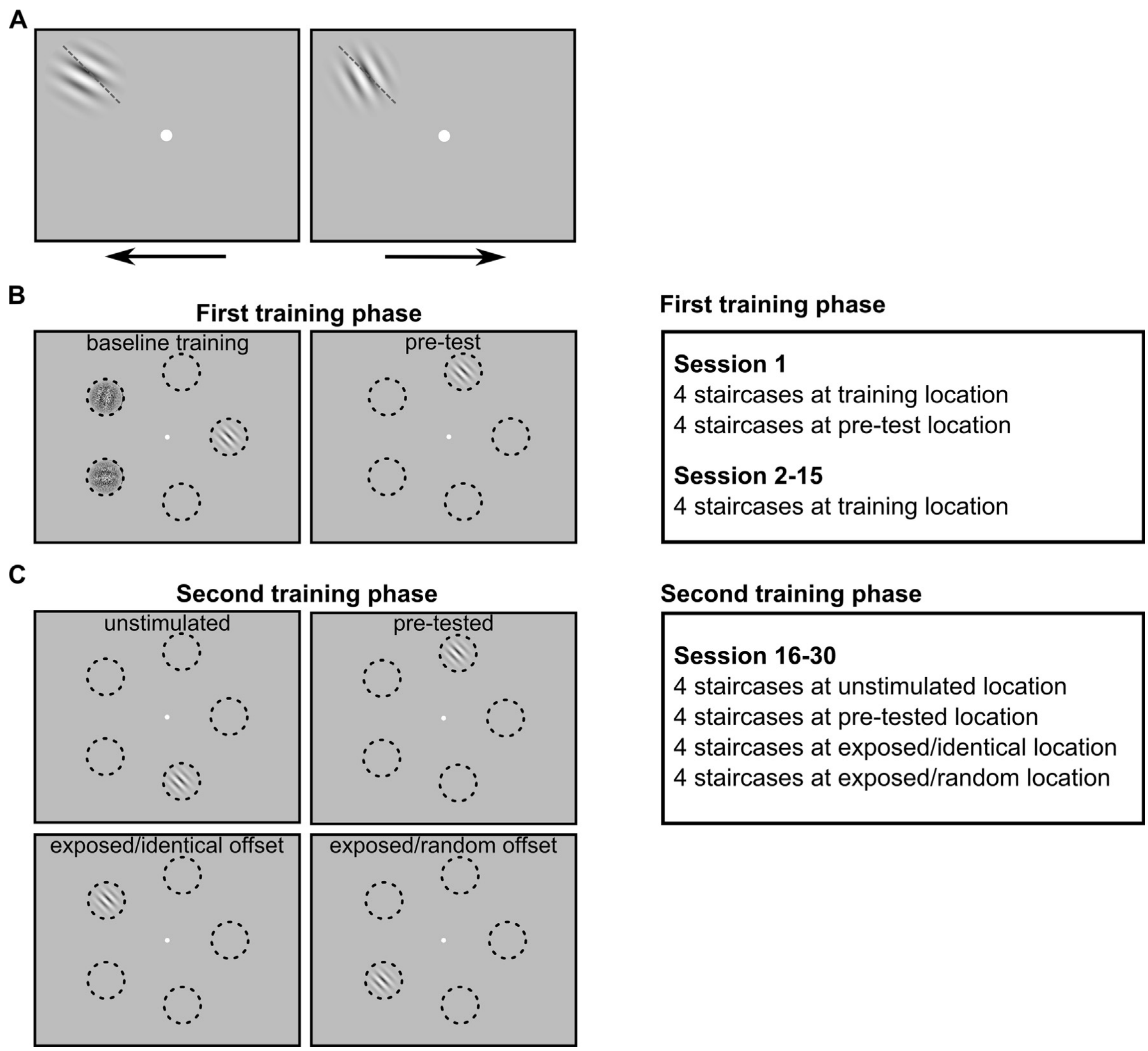


Fig. 1. Orientation discrimination task and experimental design. (A) Stimuli and task. Thresholds were determined using an identification design, with left key responses for orientations with counterclockwise off-set from a 135° reference orientation (dashed line, not shown to participants), and right key responses for orientations with clockwise orientation off-set. Stimuli are enlarged for illustration purpose. (B) First training phase: Participants were trained on a single location for 15 sessions, referred to as baseline training. On two other locations masked, oriented stimuli were shown (135°), one of them with random, the other with identical orientation off-sets as the stimulus at the trained location (details in main text). During the first session, there was one-time additional pre-test on another location. (C) Second training phase: Subsequent training on the remaining four locations for 15 sessions. Dashed circles indicate the five different stimulus locations and were not shown to participants. The location for baseline training was fixed, all other locations were counterbalanced across participants.

with the Gabor stimuli and the background, and consisted of small pixels (0.05° by 0.05°), randomly positioned, and with varying shades of grey, white, and black. The mask was convolved with a Gaussian filter (HWHM = 0.34°). The timing and spatial characteristics of the mask were piloted in the two authors. We deliberately chose to use a non-optimal stimulus termination asynchrony of 49 ms (Macknik & Livingstone, 1998) and a non-optimal spatial frequency (much higher than in the Gabor) to avoid completely preventing the processing of the masked stimulus (Bruchmann, Breitmeyer, & Pantev, 2010), as we reasoned a minimum of processing would be necessary to permit a possible learning effect. In addition, we did not individually calibrate the masks for each participant, as this would have involved presenting the Gabor stimuli prior to the experiment, which would have induced awareness of the Gabor stimuli in the masked conditions, or would have constituted a form of pre-testing that could have interfered with the planned experiment.

Participants were placed in a dimly lit room; their head was supported by a chin and head rest keeping eye-screen distance constantly at 57 cm. Visual stimuli were displayed on a 19″ Samsung SyncMaster 940BF LCD monitor (Samsung, Seoul, South Korea; 60 Hz refresh rate, 1280 × 1024 resolution). The screen was covered by a grey cardboard with an oval aperture so that the screen borders were not visible to participants and thus could not be used as reference for the orientation discrimination task. Fixation control was monitored with a Viewpoint Eyetracker v.2.8.3 (Arrington Research, Inc., Scottsdale, Arizona, USA; 60 Hz sampling rate, 37 pixel/degree spatial resolution). Stimulus presentation and response recording was performed by Cortex v.5.9.6 (NIH freeware for psychophysical and neurophysiological experimentation).

2.3. Training protocol

Over the course of the experiment, participants were trained at five different, equally spaced locations at 8° eccentricity (0°, ± 72°, and ± 144° polar angle; Fig. 1B and C). The experiment was subdivided into two training phases. During the first training phase (session 1–15), baseline training was carried out at one location (0° polar angle) while different types of pre-conditioning (pre-test and the two types of exposure) occurred at the remaining stimulus locations, referred to as test locations (Fig. 1B). During the second training phase (session 16–30) transfer was assessed first in session 16, after which training was continued in all four test locations (± 72°, and ± 144° polar angle, counterbalanced across pre-conditioning treatments) to determine any lasting effects of the different pre-conditioning treatments (Fig. 1C).

In the *first training phase*, participants underwent extensive training in a single location (4 staircase threshold measurements per session) for the duration of 15 daily sessions, resulting in asymptotic learning. Over the course of the 15 sessions, participants performed the orientation discrimination task at a 135° reference orientation, using Gabor stimuli at 8° eccentricity along a 0° polar angle line (referred to as baseline learning; Fig. 1B, left panel). Furthermore, during the entire first learning phase, masked Gabor stimuli oriented around a 135° reference orientation were presented at two additional locations (masked exposure); at one location each stimulus had an orientation off-set from the reference orientation that matched in size and left–right direction with the stimulus in the trained location (masked exposure, identical offset); at the other location the orientation off-set matched in size but its left–right direction was randomized (masked exposure, randomized offset). In addition, during the first session only, participants also performed a block of the orientation discrimination task at one other location (Fig. 1B, right panel; 4 staircases), which is referred to as the pretested location. A fifth location was left unstimulated during the first learning phase, to which we refer as the unstimulated location. The order of baseline learning, and pretest was counterbalanced over participants in the first session. In all sessions, baseline learning was accompanied with masked presentation of Gabors in the two masked exposure locations. The four different treatments of the four test locations are referred to as four different types of 'pre-conditioning'.

After completion of the first training phase, participants were asked to rate visibility (5-point scale) of the masked, unattended stimuli they were exposed to. Two participants reported not having seen anything at the locations used for passive exposure, five participants indicated they had only noticed the mask, and one participant reported to have noticed an oriented Gabor stimulus on occasional trials. The data of the participant who noticed the orientation of the oriented Gabor showed the same trends as in the overall data. Hence in seven of eight participants, there was no awareness of the Gabor stimulus. Altogether, this shows that in the large majority of trials, there was no awareness of the passive stimuli.

During the *second training phase*, participants were trained for another 15 sessions on the four pre-conditioned test locations (each 4 staircases) where no training had yet taken place. That is, second-phase training took place in one location that had been unstimulated during the entire first learning phase, in a second location where masked Gabor stimuli had been shown that had identical orientations as in the baseline-trained location, in a third location where masked Gabor stimuli were shown with random direction of the orientation off-set, and in a fourth location where there had been one-time testing during the first session of the first training phase (Fig. 1B). The different locations were counterbalanced over participants between hemifields in such a way that the two masked exposure conditions were shown in one visual hemifield, whereas the pre-tested location was in the other hemifield together with the previously unstimulated location. Within one hemifield, the pre-conditioning locations in upper and lower quadrant were also counterbalanced across participants. In that way, we excluded any systematic effects of hemifield and upper versus lower visual field on the different generalization conditions. During both training phases, four staircases were done per location, which accumulated to a total of 60 staircases per location in a total of 15 sessions. At least three sessions were completed within a week. The 30 sessions took place at the same time of the day (variations up to 1 h were accepted only exceptionally).

After finishing the main experiment, all participants participated in an additional control session (session 31). Participants performed the orientation discrimination task at five locations (Fig. 2, full black circles, referred to as control locations) intermediate to the original stimulus locations (black dashed circles) and at the same eccentricity. Only three staircases were done per location (so a total of 15 staircases) to ensure that the overall duration of the control session would be similar in length to the sessions of the second training phase (16

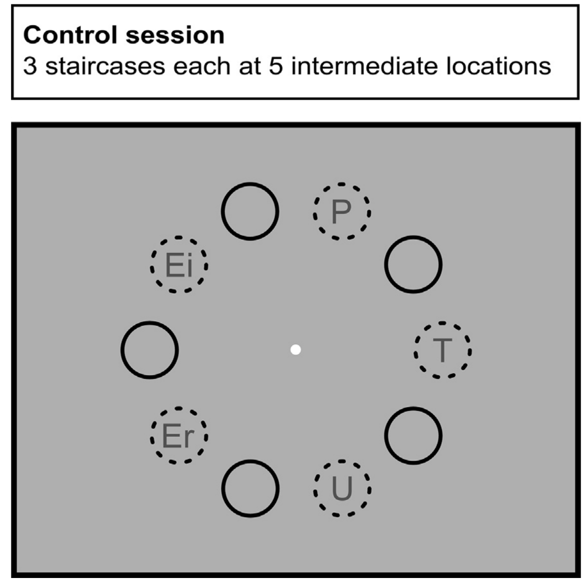


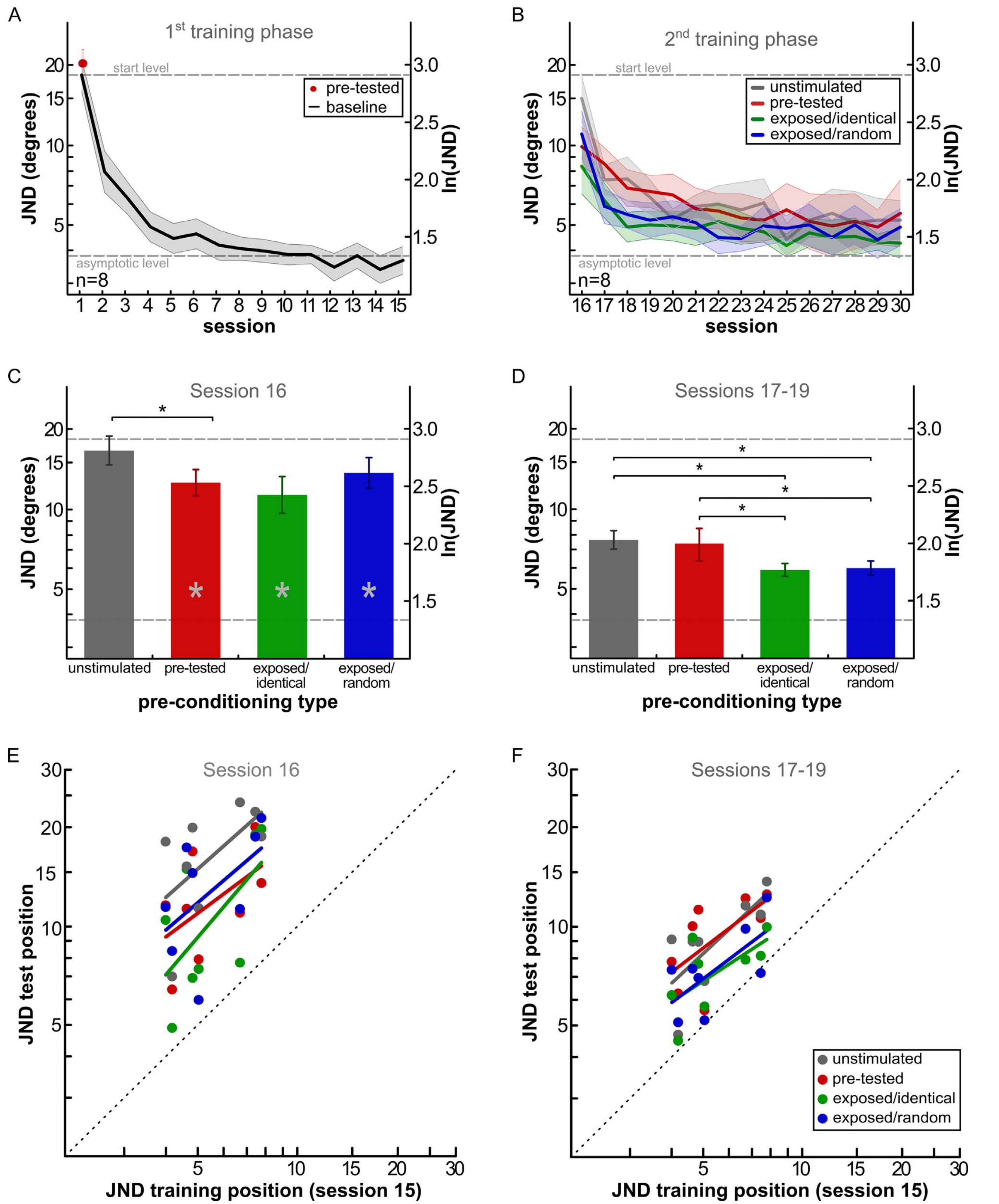
Fig. 2. Stimulus locations for the control session. Blacked dashed circles indicate the five original stimulus locations with the letter indicating the condition presented at that location in this example. P refers to 'pre-tested', Ei refers to 'masked exposure/identical offset direction', Er to 'masked exposure/random offset direction', U refers to 'unstimulated'. Black solid circles indicate the intermediate stimulus locations used in the final control sessions. In each of those five intermediate locations, participants completed three staircases.

staircases). We compared the thresholds at intermediate locations obtained in session 31 with the first three staircase thresholds obtained in session 30 at the four pre-conditioning locations. The aim of that comparison was to assess whether the extensive training at five different locations would have led to complete generalization across the entire visual field.

In both training phases, the starting orientation difference of the staircase in the first session was set to ± 22.5° (i.e., a 45° orientation difference between orientations requiring a 'left' or 'right' response as illustrated in Fig. 1A). Hence, in each location where the first training, pre-testing or testing occurred, all consecutive four staircases started at the ± 22.5° orientation difference. For all subsequent sessions, measuring again four thresholds in the same condition, the average threshold level of the previous session was taken as a starting level for each of the four consecutive staircase measurements. Note that in view of latent consolidation, this provided supra-threshold starting levels for each staircase especially in the first few sessions of the learning curve where overnight performance increments were largest. In addition, also in later stages of the learning, the adaptive nature of the staircase would lead to quick increases in the orientation difference upon few errors, thereby providing supra-threshold differences at any time required during each measurement. These procedures were expected to maximize the amplitude of perceptual learning. The exposure to sufficiently large stimulus differences especially in the beginning of learning has been shown to facilitate perceptual learning (Ahissar & Hochstein, 2004). At the same time, the prolonged exposure to orientation differences around threshold did not preclude exposure to larger differences in light of the adaptive nature of the staircases used.

2.4. Data and statistical analyses

Thresholds were measured using a Wetherill and Levitt (1965) staircase tracking 84% correct performance. This staircase requires four consecutive correct responses to decrease the orientation difference, and increases the difference after each single mistake. The adjustment of the orientation difference was achieved respectively by division or multiplication with a factor of 1.2. The staircase was automatically



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terminated either when 14 reversal points were acquired or 120 trials were completed. The orientations with counterclockwise and clockwise deviation from the reference were presented in each staircase according to a balanced random string. The threshold was calculated by taking the geometric mean of the last ten reversal points from each staircase; the first four reversal points were excluded from threshold calculation, to prevent potential initial mistakes and resulting reversal points at large orientation differences from influencing threshold magnitude. In the context of the present experiments, we use the terms threshold and Just Noticeable Difference (JND) as synonyms. The JNDs yielded by the

Fig. 3. Training and generalization as a function of different types of pre-conditioning. (A) Learning curve from first training phase. During the first training phase participants were trained for 15 sessions, so that they reached asymptotic learning (black line). In session 1 there was additionally a pre-test on one location (red dot). (B) Learning curves from second training phase. After completion of the first training phase participants started training on four test locations for another 15 sessions: pre-tested (red line), exposed/random offset (green line), exposed/identical offset (green line), and unstimulated (grey line). Colored areas in A and B represent SEM. (C) Mean threshold levels for session 16. All thresholds significantly exceeded the asymptotic level (lower grey dashed line). Thresholds in the three pre-conditioned locations (but not the unstimulated location) were significantly lower than the start level (upper, grey dashed line, significance indicated with large grey asterisks). Together these results show limited generalization, specific for the pre-conditioned locations. Direct comparisons among thresholds in unstimulated and pre-conditioned locations showed mixed results (small black asterisk, see text for interpretation). (D) Mean threshold levels for sessions 17–19. Passive exposure conditions yield lower discrimination thresholds than pre-test or unstimulated locations for sessions 17–19. Error bars represent SEM. (E) Averaged thresholds per participant for the test locations in session 16 as a function of the threshold in session 15 (last session of initial training). (F) Averaged thresholds for the test locations in sessions 17–19 as a function of the threshold in session 15. Each data point in E and F is an individual threshold averaged over 4 staircases. Asterisks indicate $p < .05$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

staircase procedure were transformed using the natural logarithm. Per session and per participant, the thresholds for each location were obtained by averaging the JNDs of the four staircases done per session. For the control session, JNDs of only three staircases were averaged.

Data of all five locations were analyzed with a repeated-measures ANOVA with factors session and pre-conditioning (pre-tested, exposed/identical offset, exposed/random offset direction, or unstimulated) to investigate in how far baseline training transferred to any of the exposed locations. In case the sphericity assumption was violated (tested with Mauchly's Test of Sphericity), Greenhouse-Geisser correction was applied. Pairwise comparisons were adjusted for multiple pairwise comparisons using Bonferroni correction unless otherwise indicated.

In addition, Monte Carlo simulations were used to test for differences in mean asymptotic performance between training and testing positions. To get an estimate of variability for the averaged thresholds in the test locations, the standard error of the mean was divided by the mean computed across all preconditioned test locations for sessions 7–15. For simulations, the product of the resulting estimate of variability and a pseudorandom number from a normal distribution was added to the mean of a respective condition. Distributions of all four test conditions were compared to the distribution at the trained position. The *p*-value was based on one million simulations.

To quantify generalization, we calculated a generalization index similar to the index of Ahissar and Hochstein (1997)

$$GIp = \frac{T1_{begin} - T2_n}{T1_{begin} - T1_{end}} \times 100 \tag{1}$$

where $T1_{begin}$ and $T1_{end}$ were the first and last orientation threshold of the first training phase (session 1 and 15). $T2_n$ is the threshold of the nth session(s) of interest of the second training phase (i.e., session 16) for a specific type of pre-conditioning (i.e., pre-tested, exposed/identical offset, exposed/random offset, or unstimulated). This generalization index is performance-based (hence GIp) as it expresses the decrease in threshold in the test location compared to the threshold at onset of learning in the training location as a percentage of the full learning amplitude in the trained location. This generalization index indicates the percentage of skill that is preserved when testing the skill in a test location.

However, since the relationship between number of training sessions and performance gains (threshold decreases) is non-linear, the GIp index may overestimate generalization in terms of preserved training time. Hence, a time- or session-based index is useful. For example, a threshold level in the test location may correspond to the threshold in the 3rd training session in the trained location, and might yield a performance-based generalization index of 50%. At the same time, this means that the expertise of only 3 out of 15 training sessions is preserved in the test location, yielding a session-based generalization index of only 20%. Hence, to compute the session-based generalization index, a performance level in a test location was assigned to the interpolated session number with matching performance in the training location. The assigned session-value (S_m) was then expressed as a percentage of the total number of training sessions (N = 15), resulting in generalization index GIs:

$$GIs = \frac{Sm}{15} \times 100 \tag{2}$$

According to the GIs, if the performance during the test session would lie in between performance during session 1 and 2 of initial training, the matched session-value would be 1.5 and the index would thus be 10%. For each pre-conditioning type, average performance during the generalization test (i.e., in session 16) was assigned a corresponding session-value (S_m) in the initial training phase, after which GIs was computed.

3. Results

3.1. Limited generalization from training location to far-removed, pre-conditioned test locations

We investigated the effect of brief pre-testing and of two types of masked exposure on generalization of skill acquired in a single fully trained location. In addition, we used an unstimulated condition as a control. Fig. 3A shows that the first session in the first training phase (sessions 1–15) revealed equivalent performance in the pre-tested location (red dot) and in the baseline training location (black line). Further training in the baseline location revealed strong learning (black line). In the second training phase (sessions 16–30), the main result is that irrespective of the type of pre-conditioning, a considerable amount of re-learning occurs, showing a lack of generalization, and a relatively high degree of specificity in our experiment. The training and test locations were presented on polar axes separated by 72°, and at an eccentricity of 8°, and hence were spread over relatively large distances across the visual field.

In a first approach to statistically evaluate generalization, we compared the thresholds in the test locations in session 16 (i.e., the first session in which transfer is tested in Fig. 3B) with thresholds in session 15 at the training location (final performance) (see Fig. 3A and B), as done in other studies (e.g. Xiao et al., 2008; Zhang et al., 2010; Zhang et al., 2010). When comparing thresholds in the four test locations in session 16 to final performance in the trained location in session 15, a repeated measures ANOVA showed a highly significant main effect of pre-conditioning type (initial training, pre-tested, exposure/identical offset, exposure/random offset, and unstimulated; $F_{(4,28)} = 21.835$, $p < .001$). Pairwise comparisons showed that thresholds in all four test locations significantly exceeded thresholds obtained in the trained location in session 15 (training session 15 vs. pre-tested: $t_{(7)} = -6.723$, $p = .003$; training session 15 vs. exposed/identical offset: $t_{(7)} = -4.345$, $p = .034$; training session 15 vs. exposed/random offset: $t_{(7)} = -6.500$, $p = .003$; training session 15 vs. unstimulated: $t_{(7)} = -9.207$, $p > .001$). This shows that for all four test conditions, thresholds were much higher (and significantly so) than asymptotic performance level in the trained location, demonstrating low generalization.

To be more sensitive to pick up potential differences between pre-conditioning types and the unstimulated control condition, we compared performance at the test-locations in session 16 (i.e., the first session in which transfer is tested in Fig. 3B) to naïve performance during session 1 in the trained location (start level in Fig. 3A, light grey dashed line in 3A-D). There was again a highly significant main effect of pre-conditioning type (initial training, pre-tested, exposure/identical offset, exposure/random offset, and unstimulated) ($F_{(4,28)} = 10.187$, $p < .001$), showing an overall trend for lower thresholds in the transfer locations (session 16) compared to the first session in the training location (session 1). Pairwise comparisons revealed that thresholds at the three pre-conditioned test locations were significantly lower than starting level performance during the first session in the trained location (see white asterisks in Fig. 3C: training session 1 vs. pre-tested: $t_{(7)} = 9.773$, $p < .001$; training session 1 vs. exposed/identical offset: $t_{(7)} = 5.331$, $p = .011$; training session 1 vs. exposed/random offset: $t_{(7)} = 4.317$, $p = .035$), whereas thresholds in the unstimulated location did not differ significantly from first session performance in the trained location (see grey bar without grey asterisks in Fig. 3C: training session 1 vs. unstimulated: $t_{(7)} = 1.718$, $p > .999$). This shows that despite low generalization overall, the observed generalization effect was specific for the pre-conditioning locations (pre-testing and exposure with identical or random offsets conditions), but without differences among the different pre-conditioning types.

3.2. No long-term advantage of pre-conditioning during prolonged learning

In contrast to other studies, we did not stop training after the generalization session (session 16) but continued for 14 sessions to obtain full learning curves at the four test locations. Fig. 3B suggests that in the first few sessions (17–19), there was a beneficial effect for learning of the two types of exposure (green and blue lines Fig. 3B). To statistically analyze the complete learning curves in sessions 16–30, we started by performing a repeated measures ANOVA with pre-conditioning (4 levels comprising the pre-tested and unstimulated conditions, as well as the exposure conditions with identical and random offset) and session (16–30) as within-subjects factors. We found that the main effect of pre-conditioning was not significant ($F_{(3,21)} = 2.343$; $p = .102$), whereas the main effect of session ($F_{(14,98)} = 9.714$; $p < .001$) and the interaction ($F_{(42,294)} = 1.481$; $p = .034$) were significant. This indicated that the differences in thresholds among types of pre-conditioning depended on session number (Fig. 3A–C).

To explore the interaction, we divided the second training phase (sessions 16–30) into three stages. The first stage of interest was session 16 (i.e., first session of second training phase), where we wanted to compare threshold levels among types of pre-conditioning and unstimulated control condition. The second stage we considered included sessions 17–19 (i.e. second to fourth session of second training phase), during which we wanted to assess short-term robustness of any learning transfer. The third stage consisted of the remaining sessions 20–30 (i.e. fifth to fifteenth session of second training phase), roughly corresponding to asymptotic learning. For the three stages, separate analyses were performed. For stage one (Fig. 3C, E), the repeated measures ANOVA with pre-conditioning type (4 levels: pre-tested, exposure/identical offset, exposure/random offset, and unstimulated) as within-subject factor revealed a significant main effect of pre-conditioning ($F_{(3,21)} = 5.080$; $p = .008$). Pairwise comparisons showed that only the difference between pre-tested and unstimulated locations (Fig. 3C) was significant ($t_{(7)} = 4.098$, $p = .028$). All other comparisons failed to reach significance (unstimulated vs. exposed/random offset: $t_{(7)} = 1.883$, $p = .611$; unstimulated vs. exposed/identical offset: $t_{(7)} = 2.938$, $p = .131$; pre-tested vs. exposed/identical offset: $t_{(7)} = 0.980$, $p > .999$; pre-tested vs. exposed/random offset: $t_{(7)} = -0.842$, $p > .999$; and exposed/identical offset vs. exposed/random offset: $t_{(7)} = -1.972$, $p = .535$). Note that the lack of a significant difference in threshold between unstimulated location and exposure locations together with a significant difference between unstimulated and pre-tested locations is somewhat puzzling, but this largely reflects differences in the variance term among the different pairwise t-tests. Generally speaking, the result is compatible with the findings from earlier analysis, in which we found that the thresholds in session 16 differed from the start level in the first training phase for all three pre-conditioned locations, but not for the unstimulated control location (Fig. 3B). Altogether, our analyses certainly underscore that the beneficial effects of the different types of pre-conditioning in session 16 were small.

For stage two (Fig. 3D, F) comprising sessions 17–19, a repeated measures ANOVA with pre-conditioning type (4 levels: pre-tested, exposure/identical offset, exposure/random offset, and unstimulated) and session (17–19) as within-subject factors revealed significant main effects of pre-conditioning type ($F_{(3,21)} = 9.559$; $p < .001$) and session ($F_{(2,14)} = 11.275$; $p = .001$) but a non-significant interaction ($F_{(6,42)} = 1.218$; $p = .317$). Pairwise comparisons among pre-conditioning types showed that the conditions in which masked exposure had been applied in the first training phase differed significantly from the pre-tested and no-stimulation conditions (exposed/random offset vs. unstimulated: $t_{(7)} = -3.795$, $p = .041$; exposed/random offset vs. pre-tested: $t_{(7)} = -3.700$, $p = .046$; exposed/identical offset vs. unstimulated: $t_{(7)} = -3.892$, $p = .036$; exposed/identical offset vs. pre-tested: $t_{(7)} = -4.455$, $p = .018$). The difference between the two passive exposure conditions was not significant (random vs identical: $t_{(7)} = 0.403$, $p > .999$) as was the difference between unstimulated and pre-tested ($t_{(7)} = -0.409$, $p > .999$). The session effect was due to a higher threshold for session 17 compared to session 18 and 19 (session 17 vs. 18: $t_{(7)} = 4.145$, $p = .013$; session 17 vs. 19 $t_{(7)} = 4.050$, $p = .015$; session 18 vs. 19: $t_{(7)} = 1.373$, $p = .636$). So, for sessions 17–19, there were slightly lower thresholds at the location where there had been masked exposure to stimuli during the first training phase, no matter whether the direction of the orientation offset had been identical or random with regard to stimuli shown during baseline training in the trained location during the first training phase. During the second stage of the second training phase, pre-tested and unstimulated locations were significantly worse than the two masked exposure conditions (Fig. 3D). Notably, the advantage a pre-test gave over the unstimulated condition in session 16 (the first session of the second training phase) thus was already lost by session 17. In contrast, masked exposure led to a slightly more robust advantage in the second learning phase (and hence slightly more robust generalization), but this advantage became only visible in sessions 17–19 (i.e. sessions 2–4 of the second training phase, see also Fig. 3F).

For stage three (Fig. 3B), a repeated measures ANOVA with pre-conditioning factor (4 levels: pre-tested, exposure/identical offset, exposure/random offset, and unstimulated) and session (20–30) revealed a non-significant main effects of pre-conditioning ($F_{(3,21)} = 1.116$; $p = .365$), a non-significant main effect of session ($F_{(10,70)} = 0.838$; $p = .594$) and non-significant interaction ($F_{(4,36)} = 0.912$; $p = .602$). Thus, from session 20 onwards there were no significant differences among the four different types of pre-conditioning.

Fig. 3E and F show the large variability of thresholds in the four test locations, which shows that the small differences among test locations we report here – even if some turned out statistically significant – should be interpreted with some reservations. At the same time, Fig. 3E shows that overall, there is a strong lack of generalization in session 16 (complete generalization would place the data around the diagonal in Fig. 3E), and that just a few sessions of further training (Fig. 3F) quickly brings the thresholds towards the level obtained at the end in training phase 1.

Note that in the last part of the second training phase (Fig. 3B sessions 20–30), the level of performance tended to remain somewhat higher than the asymptotic level in the initial learning curve (sessions 1–15, Fig. 3A). This could have been related to the much longer daily training sessions and a contribution of fatigue in the second training phase, with 16 staircases per session, as opposed to four in the first training phase. However, a repeated measures ANOVA including the last nine sessions with pre-conditioning (5 levels: initial learning, pre-tested, exposed/random offset, exposed/identical offset, and unstimulated) as within-subject factor revealed no significant effect

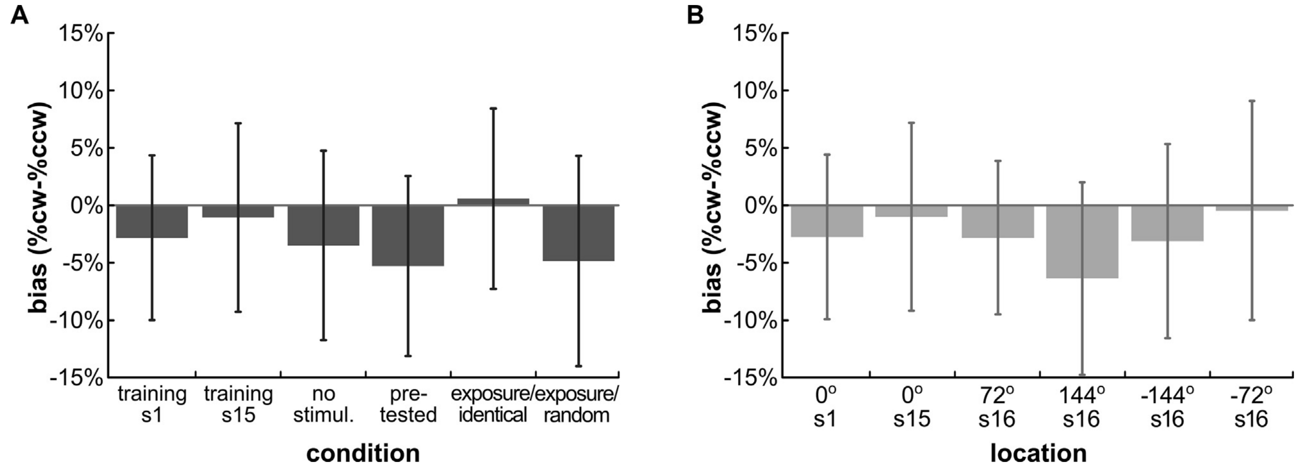

Fig. 4. Approximately equal magnitude of very small biases when plotted as a function of condition (A) and location (B). (A) Bias estimates for the trained location (initial training) in session 1 and 15, followed by values for session 16 for the preconditioning treatments (no stimulation, pre-tested, exposure-identical, and exposure-random). (B) Bias estimates for the trained location (0°) in session 1 and 15, followed by values for right upper (72°), right lower (−72°), left upper (144°), and left lower (−144°) locations in session 16. Bias is estimated as the percentage responses deviating clockwise from the reference orientation (%CW) minus the percentage deviating counter clockwise (%CCW). Error bars represent SEM.

($F_{(1.609,11.262)} = 2.430$; $p = .139$) after applying Greenhouse-Geisser correction. We also simulated asymptotic performance, on a reviewer's suggestion, to assess whether asymptotic performance differed between training and testing locations. According to the reviewer, as the training location was on the horizontal meridian, whereas all other test positions were not, the statistical distributions of performance might not have been equal, thereby rendering ANOVA a non-optimal approach to test differences between the asymptote in the first training phase and asymptotes in the second training phase. Accordingly, we also did Monte Carlo simulations (for details see Section 2.4) with one million simulated samples. This additional analysis confirmed the results of the ANOVA showing that asymptotic performance between training and test positions did not significantly differ ($p = .107$). Thus, the learning curve in the first training phase and all four learning curves in the second training phase all converged towards statistically the same performance level. This result can also be seen as confirming the absence of a long-term disadvantage of any of the pre-conditioning treatments. It also excludes the possibility that the relative lack of generalization in session 16 was a side effect of having collected thresholds in all test positions in a single session.

A reviewer of our paper argued that generalization is more likely between more 'familiar' locations. Since in our experiment the training location was always on the horizontal meridian, which could be considered more familiar, and since the test locations were removed from the horizontal meridian and potentially less familiar, this could have counteracted generalization to some extent. In our design, however, there were always two test locations relatively close to the horizontal meridian and two other locations far from the horizontal meridian. If the above reasoning were correct, one would predict better generalization from the trained location to the close locations than the far locations irrespective of pre-conditioning treatment. We tested this by sorting data according to distance from the horizontal meridian, rather than pre-conditioning treatment, and found that the distance factor did not affect generalization. This was confirmed by the absence of a main effect of distance (4 levels: close upper, close lower, far upper, far lower: $F_{(1.298,9.086)} = 1.391$, $p = .273$; Greenhouse-Geisser correction) and the absence of an interaction between distance and session ($F_{(4.648,32.538)} = 0.688$, $p = .626$; Greenhouse-Geisser correction). This analysis also indicates that potential differences between upper and lower visual fields (Pourtois, Rauss, Vuilleumier, & Schwartz, 2008) did not affect generalization in our experiment.

Following the above reasoning that it matters that the training location was on the horizontal meridian whereas the test positions were not, one might argue that training at the horizontal meridian could result in an advantage in performance for counterclockwise compared to clockwise orientation offsets (from now on referred to as 'bias'), which should be stronger for positions closer to the horizontal meridian. Differences in bias between the horizontal training position and non-cardinal test positions could accordingly diminish generalization. Note that there could also be other biases, which at the horizontal may be trained away, but may persist at the test positions at the beginning of testing. In testing this idea, it is important to keep in mind that except for the training condition, which was always placed on the horizontal meridian, the ± 72° and ± 144° locations were counterbalanced over conditions (i.e. types of 'pre-conditioning') in different participants. So, to the extent there would be systematic effects of location on bias, these effects would be smeared out over the different transfer conditions. In principle, the possibility remains however that this would on average lead to high bias for the four transfer conditions in session 16, and a low bias for the trained condition in session 15.

First, bias in both training and transfer test conditions was computed as the difference in percentage correct for the two response alternatives (% clockwise–% counterclockwise) for the sessions that were used for calculation of the GIp indices (i.e. sessions 1 and 15 for training and session 16 for preconditioned test conditions). We found only very small response differences for the different pre-conditioning treatments, ranging from −5.2% to 0.6% with the value of −2.8% for the trained session falling within that range (Fig. 4A). Note that none of these values differed significantly from zero (all $p > .105$), and that none of these values differed significantly from each other (paired samples t-tests: all $p > .720$). This analysis does not support the idea that a large bias in the transfer conditions would be responsible for a lack of generalization from the trained to the test locations.

Second, it could be argued that it is critical to consider whether bias is similar in the trained and in the transfer conditions. Thus, if a particularly strong and consistent bias persisted in a given transfer condition (despite the above mentioned counterbalancing), it would help generalization if the bias were similar in training and transfer conditions. If one first looks at the trends without considering statistics, again, our data do not agree with this notion. For example, on the one hand we find a bias of −2.8% for the trained location, and of −3.4% in the unstimulated transfer condition, yielding an (absolute) bias difference between these two conditions of 0.7%. This small and non-significant bias difference (BD = 0.7%, $p > .999$) should facilitate generalization, but our data show this is precisely the condition where we have the greatest specificity, or lack of generalization (G = 12%, performance based index). On the other hand, we find that for the three other transfer conditions a relatively higher bias difference (BD) is associated with more generalization, again against expectations (pre-test: BD = 2.5%, G = 40%; exposure/identical: BD = −3.4%, G = 51%; exposure/random: BD = 2%, G = 33%). These trends go clearly against the idea that a similar amount of bias in training and transfer locations predicts larger generalization. More importantly, the variations in the bias differences across conditions are not statistically significant (paired samples t-tests: all $p > .719$), making clear that the discussed trends are not robust enough to give them any interpretation.

Third, to test whether there is any merit to the idea that there are biases specific to stimulus location, we also tested whether there were average differences in bias among locations, after averaging in each location over the different conditions. An analysis of the result (see Fig. 4B) showed again there were no significant biases, and no significant differences among biases among positions (t-tests, all $p > .200$). This excludes the idea that biases or differences in biases between training and test locations would have contributed to lack of generalization.

Taken together, our analyses in paragraphs 3.1 and 3.2 show that overall, pre-testing and passive exposure in our experiment did not lead to a high degree of transfer. Nevertheless, there was a limited generalization effect induced by the different types of pre-conditioning, as compared to an unstimulated control location when generalization was tested for the first time. Within a few sessions of training in the transfer and control locations, any pre-conditioning-related advantage however quickly disappeared.

3.3. Generalization indices confirm the limited magnitude of generalization

To quantify generalization (Fig. 5) we present the magnitude of generalization for session 16 only, using both performance-based and session-based generalization indices for the four pre-conditioning locations (see Section 2.4). We first used a performance-based generalization index, expressing the decrease of thresholds in the second-phase learning curve in a pre-conditioning location below the starting point of first phase baseline learning, as a proportion of the improvement over the entire first phase baseline learning (for a similar index see Ahissar & Hochstein, 1997; Jeter et al., 2009). In this generalization index, 0% indicates a complete absence of transfer, and higher values indicate transfer. Computing the indices for the first session in the second training phase, Fig. 5A (dark grey bars) showed no transfer to the unstimulated location (GIp = 12%), but we found significant transfer to all three other pre-conditioned locations (41% on average) as established by three one sample t-tests testing the increase compared to 0% (all conditions: $p < .008$). This was also confirmed by a repeated measures ANOVA, which revealed a significant main effect of pre-conditioning ($F_{(3,21)} = 4.699$; $p = .012$), and is in line with analysis related to Fig. 3, in which thresholds in the test locations in session 16 were directly compared with thresholds in the training location in session 1 (paragraph 3.1). As the above performance-based generalization index does not take into account the non-linear decline of performance increments as a function of session during skill learning, a session-based generalization index was additionally calculated (see Section 2). This index shows how much of the training time is preserved when switching from the fully trained location to a test location. Fig. 5B shows that performance in the four test locations was equivalent with performance in the trained location in roughly session 2. At all four test locations the session-based generalization index was significantly larger than 0%, as established by one sample t-tests (all conditions: $p < .007$). A repeated measures ANOVA with pre-conditioning type as within-subject factor (4 levels: pre-tested, exposure/identical offset, exposure/random offset, and unstimulated) revealed a non-significant main effect of pre-conditioning ($F_{(1.543,10.799)} = 2.527$; $p = .133$) after applying Greenhouse-Geisser correction. Thus, the session-based generalization index shows that by moving from the trained to any of the four test locations, the equivalent of 13 of 15 sessions of training labor gets lost. This index is less sensitive to pick up differences between the unstimulated control and the pre-conditioned locations: We found no evidence that the three different pre-conditioning conditions had an effect different from the unstimulated control location. The analyses based on the two generalization indices confirm that there was not much generalization in our data, and that the effects of the different types of pre-conditioning were small.

With respect to the performance-based generalization index, a reviewer asked to what extent the very first threshold in sessions 1 and 16 may have influenced the magnitude of the index. Especially at the beginning of learning (sessions 1 and 16), it is expected that the very first threshold is higher than subsequent thresholds due to within-session learning (e.g., see Karni & Sagi, 1993). If there were a difference in within-session learning between sessions 1 and 16, this could affect the magnitude of the generalization index. For example, if in session 16, the first threshold in a block of four staircase measurements would be particularly large compared to the following three measurements, but less so in session 1, then inclusion of first thresholds in averaging could have led to an underestimation of generalization. According to the reviewer, an extraordinarily high first threshold in the first of four staircase measurements could be due to a temporary mismatch in response biases in trained and test locations (see Section 3.2). To assess the influence of the first staircases, we compared the average threshold

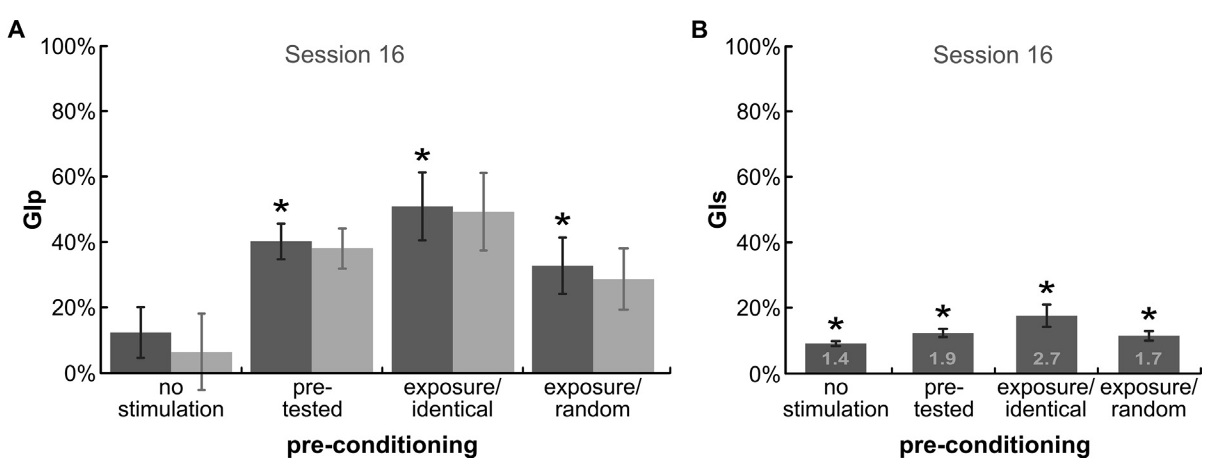

Fig. 5. Generalization quantified by performance and session-based indexes. (A) Performance-based generalization indices (GIp) for the four pre-conditioning locations for session 16. For each pre-conditioning type, dark grey bars on the left show the GIp based on all four thresholds, light grey bars on the right show indices calculated with thresholds 2–4. Stimulated conditions (pre-tested, exposed/identical and exposed/random) showed significant degrees of generalization in session 16 (indicated by asterisks). (B) Session-based generalization index (GIs) for session 16. The index shows that only a small percentage of expertise is preserved in the test locations, corresponding to the first 1.4–2.7 sessions at the beginning of learning (values inside bars). Indices for different pre-conditioning types do not differ significantly from each other. Asterisks indicate a significant difference from 0%. Error bars represent SEM.

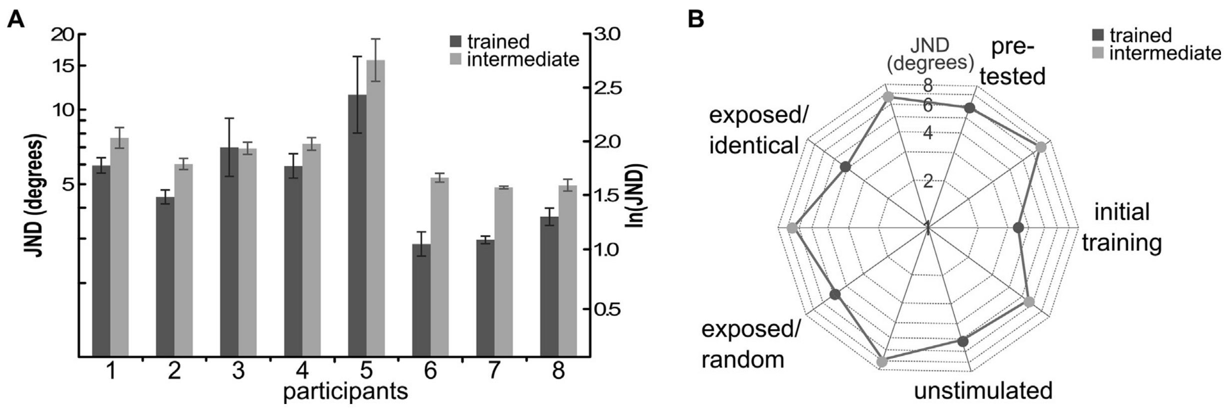

Fig. 6. Data from the control session for the trained (dark grey) and intermediate (light grey) locations. (A) Data for all participants collapsed over individual locations for trained and intermediate locations respectively. We compared thresholds at intermediate locations obtained in session 31 with thresholds obtained in session 30 at the four pre-conditioning locations and the initial training location to assess whether extensive training at five different locations would lead to complete generalization across the entire visual field. (B) Data for the different locations collapsed across participants. For intermediate locations the pooled average of the locations surrounding the original location is depicted. Error bars represent SEM.

based on all four staircases (JND_{1-4}) with the average threshold based on staircases 2–4 (JND_{2-4}). We did so for all sessions and conditions involved in computing generalization. Only in the training location in session 1, at the beginning of initial learning, did we see a small but non-significant increase in the average thresholds when the first threshold was included ($JND_{1-4} = 2.91$, $JND_{2-4} = 2.81$; $t_{(7)} = 2.727$, $p = .177$). The thresholds in session 15, at the end of initial learning in the training location, showed statistically the same average irrespective of the way in which it was computed ($JND_{1-4} = 1.30$, $JND_{2-4} = 1.29$; $t_{(7)} = 0.848$, $p > .999$). Notably, the mean thresholds in the second training phase in session 16 (i.e. at the preconditioned locations) also did not depend on whether the first threshold was included or not. This was true in the unstimulated test location ($JND_{1-4} = 2.71$, $JND_{2-4} = 2.68$; $t_{(7)} = 1.726$, $p = .768$), in the pre-test location ($JND_{1-4} = 2.29$, $JND_{2-4} = 2.26$; $t_{(7)} = 1.429$, $p > .999$), in the passive exposure location with identical offset ($JND_{1-4} = 2.12$, $JND_{2-4} = 2.11$; $t_{(7)} = 0.296$, $p > .999$), and in the exposure location with random offset ($JND_{1-4} = 2.40$, $JND_{2-4} = 2.40$; $t_{(7)} = 0.022$ $p > .999$).

We nevertheless tested whether dropping the first staircase in the terms that go into the GI_p affected our estimates of generalization. This analysis unambiguously showed that the differences in the resulting generalization indices are negligible (see light grey bars in Fig. 5A). A repeated measures ANOVA with calculation type (based on 4 staircases vs. based on 3 last staircases) and pre-conditioning (no stimulation, pre-tested, exposed/identical and exposed/random) revealed a significant difference in pre-conditioning ($F_{(3,21)} = 4.307$, $p = .016$), but a non-significant effect of calculation method ($F_{(1,7)} = 1.768$, $p = .225$) and a non-significant interaction ($F_{(3,21)} = 0.429$, $p = .734$).

3.4. *Control experiment confirms lack of long-term advantages of pre-conditioning*

It is possible that the lack of a long-term effect of pre-conditioning was due to strong generalization and mixing of the effects of the different treatments and training across the entire visual field during the prolonged training. If this were true, then the lack of a long-term effect of pre-conditioning could be considered an artefact of the experimental design, in which we combined a training location and four pre-conditioning locations in a single experiment. On the other hand, one might find higher thresholds in the locations intermediate to the pre-conditioned and control location. This would indicate that the specific effects of pre-conditioning remained sufficiently separate from each other, to permit the interpretation that the lack of differences among them or with the control location reflected a true lack of a pre-conditioning effect extending until the end of the learning curves. To test these ideas, participants underwent a control session after completion of the second training phase, during which they performed the orientation task in five intermediate locations relative to the original locations used during the main experiment. Participants performed three staircases in each intermediate control location, and we compared the resulting thresholds with corresponding data obtained from the original locations (for details see Section 2.3). For analysis, we included the three pre-conditioned locations, the unstimulated test location and the location where initial training took place. For each of these five locations performance was compared with that in intermediate locations in three ways: by comparing to the pooled average of both neighboring intermediate locations, or to the clockwise intermediate location, or to the counterclockwise intermediate location (referred to as three ways of calculation). A repeated measures ANOVA with pre-conditioning (5 levels: initial training, pre-tested, exposed/identical, exposed/random, unstimulated) and stimulus location (original vs. intermediate) as within-subjects factor showed a significant main effect of location (for all three ways of calculation: $p < .002$), but a non-significant main effect of pre-conditioning (all $p > .165$) and a non-significant interaction (all $p > .149$). Pairwise comparisons confirmed that performance at the original locations (mean ln-transformed threshold = 1.54, *sd* 0.42) was better than at the control locations (mean ln-transformed threshold = 1.89, *sd* 0.33, when calculated as the pooled average of both neighboring intermediate locations). Thus, performance improvements did not transfer completely (for all three ways of calculation $p < .004$). A repeated measures ANOVA in which only the pre-conditioned and control locations (i.e., excluding the location at which training during the first learning phase had taken place) were compared with the four intermediate locations yielded similar results and the same conclusions. The data indicate that the lack of potential maintained advantages of specific kinds of pre-conditioning was not due to a full spread (and mixing) of expertise from the different trained locations (Fig. 6). This is in agreement with data showing location specific learning after training fine orientation discrimination at multiple locations (Le Dantec & Seitz, 2012).

4. Discussion

The present study investigated to what extent different pre-conditioning strategies led to spatial transfer of orientation discrimination learning from a previously trained location to relatively far-removed test locations in the same or opposite hemifields, and how long-lasting the potentially advantageous effects of pre-conditioning were. The initial learning was done over 15 daily sessions. Generalization was tested in four test locations that each had undergone a different treatment: (1) pre-exposure with stimuli whose orientation matched that of stimuli used in the training location; (2) pre-exposure with stimuli of which the magnitude of orientation offset, but not the direction, matched that of stimuli used in training location; (3) pre-testing in a single session; and (4) no stimulation (details in Section 2).

In the first session of generalization testing, we found thresholds in the two pre-exposed conditions and the pre-tested condition to be significantly lower than thresholds in the very first session of the original learning curve in the training location. We did not find this effect for the unstimulated control location, indicating that all three pre-conditioning types helped generalization. At the same time, we found that thresholds in all four testing locations were significantly elevated compared to final performance in the trained condition, indicating that the generalization effect was limited in size. This was confirmed by generalization indices, which showed that only 41% of the learning amplitude at the training location, approximately corresponding to only two sessions of training, was preserved in the test locations (averaged over the three pre-conditioning treatments, not including the control condition). Further analysis did not support any differential effects among the three pre-conditioning treatments.

To determine the robustness of any advantages of the pre-conditioning conditions upon further learning, we determined full learning curves in the four generalization test locations, following the first session of generalization testing (i.e., 14 sessions following the first generalization session). Although during a few sessions, there appeared to be a small advantage of some of the pre-conditioning treatments, these advantages disappeared quickly and were irrelevant during asymptotic learning.

Altogether, our data show that in the present experiment, pre-conditioning by exposure to stimuli of which participants had no or little awareness, and by pre-testing, induced statistically significant generalization, which was however small in magnitude, and not robust enough to influence later asymptotic learning in the generalization test locations. Hence, in the present study of orientation discrimination learning, we did not find evidence for substantial generalization after pre-testing or exposure.

4.1. The effect of a pre-test

Zhang et al. (2010) used a pre-test procedure close to ours. Their study demonstrated that a brief pre-test could result in substantial periphery-to-periphery transfer of orientation discrimination skill to another retinal location. Instead, we found that there was a strong trend towards specificity in the first session of the second training phase, with evidence only for a limited amount of generalization. The number of trials we used for the pre-test was very similar to what that used in Zhang et al. (2010): we had ~240 trials in 4 staircases, compared to their ~200 trials in 6 staircases. However, there are also numerous differences between our study and theirs. To begin, there are important differences in design. First, their study did not include an unstimulated peripheral control location, making it difficult to ascribe generalization specifically to the pre-test. Our study did include an unstimulated control location permitting a more specific interpretation of the small generalization effect we observed. Furthermore, there is a multitude of differences in task, stimulus parameters and procedures. With respect to task, Zhang et al. (2010) required participants to compare two successive stimuli, whereas in our task, participants compared a single stimulus to an internal reference. In addition, various stimulus parameters were different between Zhang et al. (2010) and our study, including viewing distance (57 cm vs. 1 m, respectively), stimulus duration (33 ms vs. 92 ms, respectively), and eccentricity (8° vs 5°). There were various procedural differences as well, such as feedback modality (visual vs. auditory, respectively), staircase rules (4-down-1-up rule resulting in 84.09% convergence vs. 3-down-1-up rule resulting in 79.4% convergence, respectively), threshold estimation (4 preliminary reversals and 10 experimental reversals vs. 4 preliminary reversals and 6 experimental reversals, respectively), and size of orientation difference at start of each staircase beyond the first session (threshold of previous session in our study vs. large orientation difference, respectively). Moreover, whereas in our study, the training in the trained location was continued for 15 daily sessions of roughly 400 trials, the above-cited study typically ended training after seven sessions of roughly 500 trials. Given this extensive list it should be clear that any of these differences might contribute to the difference in observed transfer. However, many of the parameters used in our study might have increased task difficulty (e.g., nature of the task, greater stimulus eccentricity, briefer stimulus duration, more training at threshold, and overall length of training in terms of both trials and daily sessions), which is argued to favor specificity in perceptual skill learning (Ahissar & Hochstein, 1997; Karni & Bertini, 1997; Karni & Sagi, 1993; Liu & Weinshall, 2000; Rubin, Nakayama, & Shapley, 1997). Similarly, specificity effects have been reported for motor skill learning after multi-session training but not single-session training (e.g. Korman, Raz, Flash, & Karni, 2003). We therefore suggest, in line with these older studies, that the extended training at or near threshold increased the specificity of the skill in our study. As it has been shown that prolonged training at threshold promotes location specificity (Hung & Seitz, 2014), the limited generalization in our experiment is likely due to the extensive training during the first training phase (15 sessions) resulting in asymptotic learning.

4.2. The effect of passive exposure

In our study, extended exposure to masked, unattended stimuli gave a slight advantage over pre-tested and unstimulated locations for early learning (session 2–4). This contrasts with another study that has suggested large, near-complete generalization of orientation discrimination learning after training-plus-exposure (Zhang et al., 2010). However, their procedure was different from our masked exposure conditions, since participants performed a task at the transfer location on an irrelevant feature (e.g. contrast) while that stimulus still contained the (future) relevant feature (e.g. orientation). There were no control experiments in Zhang et al. (2010) that assessed the visibility/awareness of, or attention to, the to-be-relevant stimulus feature during this form of exposure. Hence, it is difficult to interpret generalization in this study purely in terms of exposure. In general, it is difficult to compare studies that use different procedures, even more so because there is evidence showing that differences in task, procedure, and other factors can strongly affect generalization (Hung & Seitz, 2014; Wang et al., 2014).

Another study by Xiong et al. (2016) investigated the contribution of bottom-up stimulation (i.e. passively presented Gabor stimuli) and top-down attention (i.e., in the absence of stimuli) to the transfer of training to untrained conditions. Orientation transfer was shown using an orientation discrimination task and location transfer using a Vernier acuity task. We limit ourselves here to their location transfer experiment, which is most relevant for our study. It is important to emphasize nevertheless the limited nature of any conclusions to be drawn from this study regarding our study, as Vernier acuity is a very different task with different transfer properties. In the transfer location, Xiong et al. (2016) used continuous flash suppression to ensure that Gabor stimuli were presented sub-consciously, and used specific task instructions to achieve pure bottom-up stimulation or top-down attention. They reported significant transfer for transfer locations primed by bottom-up stimulation and top-down attention, and hypothesized that specificity results from under-activation of untrained neurons by either top-down or bottom-up influences. In contrast to the significant transfer elicited by passive stimulation in Xiong et al. (2016), Mastropasqua et al. (2015) reported that passive stimulation at the transfer location is insufficient to induce transfer. Here, the passive stimulation at the transfer location consisted of a black annulus shown after the task-relevant Gabor stimulus in the trained location, which presumably favored allocation of attention towards it. Passive stimulation in this study thus refers to the absence of any task. It is not clear why the two studies report opposite results related to the effectiveness of transfer to locations stimulated passively. Both of these studies used sequential training and exposure designs. In Xiong et al.'s (2016) study, blocks of training and exposure were alternated; in Mastropasqua et al. (2015), training and exposure stimuli were shown sequentially within a single trial. In our study, we opted for simultaneous presentation of training and exposure stimuli, thereby limiting attentional resources to the exposure stimuli. Further limiting the possibility to compare among studies are the circumstance that Xiong et al. (2016) did not look at location transfer in an orientation discrimination task, and that both Xiong et al. (2016) and Mastropasqua et al. (2015) used substantially fewer training sessions (seven and four respectively) than the present study. Nevertheless, we follow the interpretation by Xiong et al. (2016) that our finding of limited generalization upon passive exposure points to a limited effect of bottom-up stimulation during the absence of top-down attention.

Our masked exposure paradigm to some extent can be compared with the subliminal learning studies from Watanabe and Seitz (Seitz & Watanabe, 2003; Watanabe et al., 2001; Watanabe et al., 2002). In their studies, it is shown that perceptual learning happens even when stimuli are not perceived (Watanabe et al., 2001). Further studies on task-irrelevant perceptual learning have demonstrated that parathreshold but not suprathreshold stimuli lead to this form of learning (Tsushima et al., 2008). This result was interpreted as showing that weak stimuli pass the attentional filter unnoticed and therefore fail to be suppressed by the attentional system, whereas strong stimuli are actively inhibited. The short stimulus duration and masking of the passively presented stimuli in our study might thus have prevented inhibition by the attentional system and allowed partial transfer of learning to the exposed locations. One mechanism enabling task-irrelevant learning is thought to be stimulus-reward pairing, whereby stimulus driven signals from the irrelevant stimulus and task driven signals, including reinforcement signals must coincide (Seitz, Kim, & Watanabe, 2009; Seitz & Watanabe, 2005). One might argue that in the present study feedback on task performance functions as reinforcement signal; in which case one could assume that learning should be greater in the exposure condition with identical orientation off-set as the trained location, because here feedback for correct trials is also 'correct' for the exposed orientations. This is not the case for the exposure condition with random orientation off-set, where feedback for a correct response on the trained stimulus might correspond with equal probability to 'correct' or 'incorrect' orientation directions in the exposed stimulus. This prediction was not confirmed in our data. However, feedback may have a weaker effect than actual reward, and the lack of a difference between the two exposure conditions may be related to the fact that the visual feedback is not a sufficient reward signal. Hence, a real reward might have been more effective (Seitz et al., 2009).

Given the lack of a difference between our two exposure conditions, one might argue that task-irrelevant learning in our study was driven by a form of adaptation. Gutnisky et al. (2009) investigated the effects of a form of adaptation-dependent exposure-based learning. During an exposure phase, which lasted three minutes, gratings (alternating between two orientation) were flashed (200 ms on, 200 ms off) at three different locations of which one was attended, another one unattended, and the third functioned as control condition (exposure to random orientations). At the attended location, participants performed a contrast detection task. Over the course of ten daily sessions the authors looked at performance changes in the orientation discrimination task which was always preceded by the exposure phase. Orientation discrimination performance was best in the attended exposure location, intermediate in the unattended exposure location and worst in the control location. Interestingly, the effects of unattended exposure generalized over orientations, whereas beneficial effects of attended exposure were restricted to the orientation used during exposure. Here, we show that locations preconditioned with unattended exposure receive more generalization from another trained location, than a location preconditioned with attended pre-testing, which can be seen as in line with the findings of Gutnisky et al. (2009). In addition, it is interesting that they reported a form of enhanced specificity during pre-exposure with attention, which can be seen as in line with the idea that generalization requires pre-conditioning with stimuli presented outside awareness (Tsushima et al., 2008). It is noteworthy that differences between visual perceptual learning with and without attention have been reported before in the domain of motor skill learning as differences between implicit and explicit learning (e.g. Honda et al., 1998; Kantak, Mummidisetty, & Stinear, 2012; Taylor, Krakauer, & Ivry, 2014). It should be noted also that a detailed comparison between Gutnisky et al.'s (2009) study and ours is limited by the methodological differences between our studies. In contrast to our study, Gutnisky et al. (2009) used exposure stimuli that were supra-threshold and/or attended, interleaved exposure and training within each session, and measured generalization across reference orientations. To maximize the effect of adaptation, it might have been more effective in our study to present the reference orientation itself without orientation offset. Some models predict that this could lead to better discrimination performance (Teich & Qian, 2003). Despite the fact that our paradigm may not be the best to induce adaptation, our data, given the lack of a difference between the two exposure conditions, are consistent with an effect of adaptation in our data. Taken together, pre-conditioning by subliminal exposure while aiming to either render the feedback more potent, or by presenting only the reference orientation, might render the effect of pre-conditioning stronger.

4.3. Potential limitations of this study

As the chosen experimental design consisted of a within-subject design with five conditions per participant, it was impossible to limit stimulus locations to cardinal or oblique axes. Hence, having five conditions created constraints for stimulus positioning. Test positions in this design were deliberately removed from horizontal and vertical axes and all positions were positioned equidistantly. This meant that the training position ended up on the horizontal meridian, and test positions were removed from the cardinal axes by $\pm$ 9° and $\pm$ 17°, which are relatively small differences. However, if one believes that generalization has a strong dependence on similarity between training and test positions in terms of their distances to cardinal and oblique axes, then it could be argued that our results did not tell the full story.

A first question derived from this is whether the way of stimulus positioning in the present study had an effect on the amount of generalization from the horizontal training position to non-cardinal transfer positions. Specifically, a reviewer suggested a specific status of the horizontal meridian, making generalization more difficult the farther the test positions were removed from the horizontal. In our design, potential differences in generalization due to this, but also due to distance towards the horizontal training position, hemispheric differences, upper and lower field differences, and distance from main axes in general were avoided by using counterbalancing of the positions of transfer conditions across participants (see Results). Second, if one believes that the horizontal meridian has a special status, this may also lead to a bias in which the perception of orientation is attracted to horizontal, leading to a bias towards counterclockwise responses given the use of a left oblique reference orientation in our experiments. The difference in amount of bias in training and test conditions in turn could affect the amount of generalization. This concern could be dismissed, as it was shown that the bias was not different at the five stimulus locations. Third, in a reasoning related to the idea of bias, it can be argued that the amount of generalization we report is strongly affected by a very high threshold in the very first staircase due to a specific bias in each test location, different from that in the trained location. Again, this hypothesis could be refuted by our analyses.

Although our analyses indicate that our results are not affected by our stimulus positioning choices, and that therefore our results are probably valid for other stimulus position configurations, it remains valuable to replicate our study with other stimulus configurations. Nevertheless, regarding the fact that we find much less generalization than many other studies, we consider that this is most likely due to the more extensive training involved in our study, rather than to differences in stimulus positioning between the present and other studies.

4.4. Conclusions

Previous studies investigating effects of pre-test or exposure on learning have used a single session to assess generalization, which precludes an assessment of the robustness of the advantages of these forms of pre-conditioning (Zhang et al., 2010; Zhang et al., 2010). In addition, these studies used brief learning curves that likely represent incomplete learning and showed other design aspects such as less training around threshold and an easier task, which can be expected to favor generalization. Their results illustrate various triggers for generalization in particular conditions of learning known to favor generalization. By contrast, we tested whether pre-testing and exposure procedures that have been reported to trigger strong generalization after brief learning can have a similar effect after more extended training. The extended training aimed to yield a large learning amplitude followed by asymptotic learning near threshold, likely to induce more stimulus and location specific learning. If under those conditions, pre-conditioning would produce near-complete generalization; this would be a remarkable finding. It would show that a much more completely trained perceptual skill could be triggered to generalize by specific forms of pre-conditioning, which would have therapeutically relevant implications in the context of training visual skills in amblyopia and other low vision conditions (e.g. Chen, Chen, Fu, Chien, & Lu, 2008; Fronius, Cirina, Cordey, & Ohrloff, 2005; Levi & Polat, 1996; Li, Provost, & Levi, 2007; Zhou et al., 2006). Our results show however, at least for the paradigm and locations we used, that once a perceptual skill is more fully trained, generalization to pre-conditioned locations is limited. This shows that the pre-conditioning treatments we used were not very efficient in overcoming the specificity that comes with extensive training at small perceptual differences. Moreover, we show for the first time that the small effects of pre-conditioning on subsequent learning disappeared during extended asymptotic learning in the pre-conditioned locations. Our results help to further delineate the conditions under which generalization of a perceptual skill can be expected and when not.

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Corrigendum

Corrigendum to "Limited transfer of visual skill in orientation discrimination to locations treated by pre-testing and subliminal exposure" [Vis. Res. 143 (2018) 103–116]

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The authors regret the incorrect usage of statement of Reference Zhang, Xiao, Klein, Levi, and Yu (2010).

The authors would like to apologise for any inconvenience caused.

In their paper investigating periphery-to-periphery generalization, the authors stated in their Introduction that in Zhang, Xiao et al. (Vision Research, 2010) "a brief pre-test, involving greater attentional allocation, led to substantial periphery-to-periphery generalization in an orientation discrimination task". In Discussion, it was stated that Zhang et al.'s (2010) study "did not include an unstimulated peripheral control location, making it difficult to ascribe generalization specifically to the pre-test". The authors regret that these statements are incorrect in that in Fig. 4E of Zhang et al. (2010), where periphery-to-periphery generalization results were shown, 4 of 18 participants were tested for generalization without pre-test. At the same time, the authors' suggestion that the pre-test may have had a limited role in triggering generalization turned out correct in the light of indistinguishable generalization with or without pre-test, as indicated indeed by the data from four participants reported in Zhang et al. (2010). The authors would like to apologise for any inconvenience caused. The ineffectiveness of pre-testing in contributing to periphery-to-periphery generalization in Zhang et al. (2010) is not incompatible with the statistically significant but small and unstable contributions of pre-testing and pre-exposure to generalization in the authors' study. The main difference between the studies remains however, with Zhang et al. (2010) reporting substantial generalization whereas the authors found substantial specificity.

Reference

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