Experience-dependent long-term facilitation of skew adaptation

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Adaptation to changes in the environment allows the visual system to achieve optimal perception in a continuously changing visual world. One particular example regarding recurrently encountered changes in everyday vision is geometrical distortions of the environment when wearing spectacles for vision correction, e.g., image shear by skew geometric distortions in progressive additional lenses. For optimal visual performance, it would be beneficial if the visual system uses previous history of recurrent distortions and learns to adapt fast when they are reapplied, yet this has not been systematically shown. The present study evaluates experience-dependent long-term facilitation of fast adaptation to image skew, i.e., a shear from the x- and y- axis, using ecological stimuli. Immediate and long-term facilitation of fast adaptation induced by minutes time scales of extended skew exposures was tested. Fast adaptation was quantified via the magnitude of perceptual bias after a brief exposure to image skew in a constant stimulus procedure. Immediate facilitation was tested by comparing the magnitudes of fast adaptation that are measured on the same day before, i.e., baseline, and after extended skew exposure. The retention of the facilitation was evaluated by comparing the fast adaptation measured after, on average, 57 days of the previous extended skew exposure with the baseline. After one hour of skew exposure, the amount of fast adaptation significantly increased from the baseline measurement indicating immediate facilitation of the fast adaptation. This facilitation was retained at, on average, 57 days after the extended exposure. Thus, the results depicted experience dependent long-term facilitation of skew adaptation that potentially explains visual habituation to distortions of spectacles.

Introduction

Everyday vision constitutes a remarkably wide range of conditions, e.g., continuously varying luminance across a single day. For optimal functioning, it would be efficient if the visual system rapidly adjusts its responses to compensate for recurrent changes in the environment. The visual system might facilitate fast adaptation process to frequently occurring alterations by using a previous history of visual experiences. One real-life scenario of such adaptation dynamics is how people habituate to unfamiliar image modifications introduced by new spectacle lenses. Distortion is one of the artifacts in spectacles that alters features of the visual world and induces loss of visual stability (Vlaskamp, Filippini, & Banks, 2009; Welch, 1969, 1978). Skew geometrical distortion is an example of inevitable distortions in spectacles, such as progressive additional lenses (PALs) (Barbero & Portilla, 2015; Meister & Fisher, 2008). Image skew obliquely magnifies and shears images as illustrated in Figure 1 (Barbero & Portilla, 2015; Fannin & Grosvenor, 2013). This manipulation alters multiple features, e.g., in orientation and dimension symmetry statistics of the natural environment (see Figure 1c). Lack of adaptation to such alterations potentially contributes to visual

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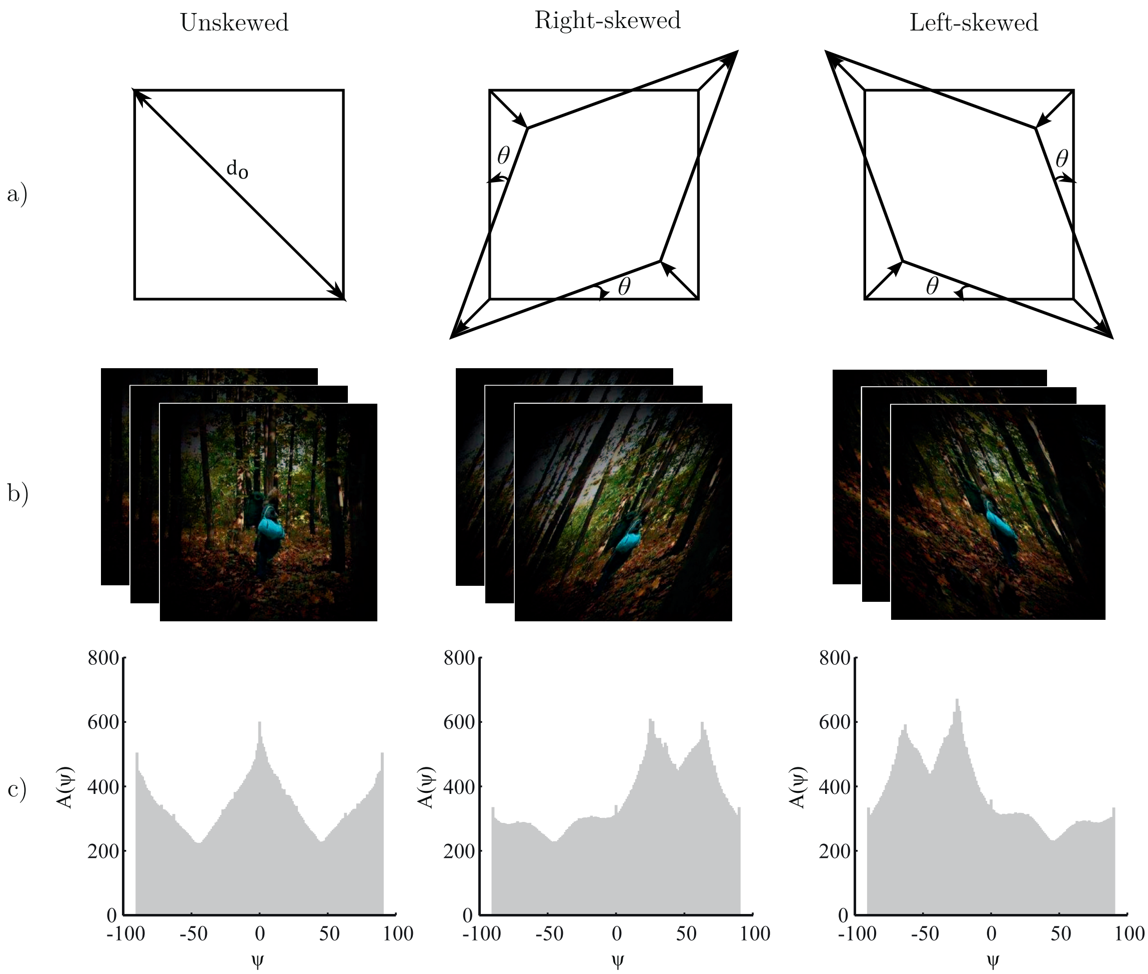

Figure 1. (a) Illustration of skew geometrical distortion. (b) Examples of unskewed ($\theta = 0°$), left skewed ($\theta = 25°$), and right skewed ($\theta = -25°$) adapting image sequences. (c) An example of skew effect on orientation statistics of natural image sequences: amplitude spectrum vs. orientation plot of the average from 22,000 image frames.

discomforts experienced by novice PAL wearers. Observers commonly report vanishing of the visual discomforts after wearing new spectacles continuously for a week or so. However, it is still unknown whether previous extended exposure to the distortions enables the visual system to adapt fast when the distortions are reapplied. To understand the temporal dynamics, it is vital to assess experience-dependent long-term changes of the visual adaptation to such modifications.

Adaptation is a mechanism by which the visual system optimizes visual processing and attains perceptual stability in a continuously changing visual world (Clifford et al., 2007; Smithson & Zaidi, 2004; Webster, 2011; Welch, 1978). Adaptation has been shown in a diversity of attributes, such as adaptation to color (Belmore & Shevell, 2008, 2011; Delahunt, Webster, Ma, & Werner, 2004; Eisner & Enoch, 1982; Neitz, Carroll, Yamauchi, Neitz, & Williams, 2002), contrast (Bao & Engel, 2012; Bao, Fast, Mesik, & Engel, 2013; Kwon, Legge, Fang, Cheong, & He, 2009), distortions and blur (Adams, Banks, & van Ee, 2001; Habtegiorgis, Rifai, Lappe, & Wahl, 2017; Yehezkel, Sagi, Sterkin, Belkin, & Polat, 2010). Adaptation effects are commonly shown as aftereffects that last on a seconds time scale after the adapting features are removed. However, exposure to some changes in the environment does not only induce momentary visual adjustments but also contributes to future visual experience. Experience-dependent long-term facilitation of adaptation can be studied by testing the ability to adapt fast to features that have been adapted in previous sessions. This has been done by a few studies that showed faster re-adaptation to blur after four hours of adaptation on the previous day (Yehezkel et al., 2010) and faster re-adaptation to color after habitual wearing of colored glasses for 14 months (Engel, Wilkins, Mand, Helwig, & Allen, 2016). For such rapid re-adaptations, the visual system might need previous information about the alterations that increase its expectations or minimize its insecurities for the risk of error driven fast adjustments (Todorovic, van Ede, Maris, & de Lange, 2011; Wark, Fairhall, & Rieke, 2009).

The dynamics of adaptation also depend on the statistical distribution of features in the visual stimulus (Wark et al., 2009). Particularly stimuli with higher order statistics, such as natural images (Ruderman & Bialek, 1994), potentially affect the time course of adaptation (Wark et al., 2009). In the daily visual world, the input to the visual system is rapidly changing natural image content. Natural images contain a great variety of visual attributes like spatial frequency, luminance, contrast, orientation, texture, color, or optic flow signals (Betsch, Einhäuser, Körding, & König, 2004; Bex, Dakin, & Mareschal, 2005; Bex & Makous, 2002; Bex, Mareschal, & Dakin, 2007; Bex, Solomon, & Dakin, 2009; Billock, de Guzman, & Kelso, 2001; Dong & Atick, 1995). Adaptation to altered features in a dynamic natural environment might involve coordinated plasticity of several neural populations across multiple cortical areas, e.g., adaptation to skewed dynamic natural images (Habtegiorgis et al., 2017). Due to the hierarchical and interactive nature of the visual system, these coordinated responses might not always be revealed by adaptation of a specific group of neurons to selected stimulus features under controlled experiments (David, Vinje, & Gallant, 2004; Felsen & Dan, 2005; Gallant, Connor, & Van Essen, 1998; Ringach, Hawken, & Shapley, 2002). Since natural image content drives the visual system in its intended mode (Snow, Coen-Cagli, & Schwartz, 2017), visual stimuli that resemble the natural environment are important to comprehensively study the dynamics of the visual system's natural long-term adaptation process.

In the present study, psychophysics was conducted with natural scenes to systematically study the long-term dynamics of adaptation to skew distortion. Immediate visual adjustment after exposure to skewed natural scenes was demonstrated behaviorally in a previous study (Habtegiorgis et al., 2017). To understand the long-term temporal dynamics of the habituation process to distortions of PALs, we examined if fast adaptation to skew distortion can be facilitated in the long term by prior extended adaptation to the distortions. We measured fast adaptation via the amount of perceptual shift after a brief exposure to image skew. Long-term effects were measured by exposing participants to extended skew adaptation and then retesting the fast adaptation several weeks later. The results depicted that 1 hour of extended skew exposure facilitated fast adaptation, even when retested, on average, 57 days later. Thus, extended exposure to image skew facilitates adaptation whose long-term retention might enable fast and efficient re-adaptation when needed.

Materials and methods

Immediate and retained facilitation effects on fast skew adaptation (FA), induced by two extended skew exposure (EE) time scales, were tested. The entire experiment comprised five FA aftereffect measurement sessions and two EE sessions. The five FA aftereffect measurement sessions were: session 1.1, session 1.2, session 2.1, session 2.2, and session 3. The two EE sessions were session EE1 and session EE2.

FA was induced by a brief exposure to skewed natural image sequences. FA aftereffects were then measured in a constant stimulus procedure by the skew magnitude in the test stimuli that subjectively appeared unskewed. During EE sessions, observers watched skewed natural image sequences for extended durations.

Study approval

The study was approved by the Ethics Committee of the Medical Faculty of the Eberhard Karls University of Tübingen and the University Hospital.

Observers

Ten naïve observers, between the ages of 18 to 40, participated in the study with a prior written consent in adherence to the Declaration of Helsinki. All observers took part in all sessions, except one observer who did not participate in session 1.2. All observers had normal or corrected-to-normal vision while taking part in the psychophysical measurements.

Setup

The psychophysical procedure was designed and stimuli were generated in MATLAB (MathWorks, Natick, MA) using the PsychToolbox routines (Brainard, 1997) on an Apple computer (Apple, Inc., Cupertino, CA). The stimuli were displayed on an LCD monitor (Benq Corporation, Costa Mesa, CA) at a screen resolution of $1,920 \times 1,080$ pixels (square pixels, with 0.31 mm pixel pitch) and a screen refresh rate of 60 Hz.

A chin and head rest was used to fix the viewing distance at 57 cm at which the whole screen subtended a visual angle (VA) of 55° horizontally, and 33° vertically (pixel pitch of 0.031° VA). During the experiment, viewing was monocular and stimuli were presented at the center of the screen in an otherwise completely darkened room. During aftereffect measurements, observers' responses were collected using the left and right keys of a keyboard.

Stimuli

The same adapting and test stimuli were used as in our previous adaptation study (Habtegiorgis et al., 2017).

Images were skewed by a shear angle of θ using a geometrical transformation matrix M, in Equation 1 and 2, which remapped the pixel positions of the undistorted image,x and y, to distorted positions, $x_d$and y_d.

$$\begin{pmatrix} x_d \\ y_d \end{pmatrix} = M \times \begin{pmatrix} x \\ y \end{pmatrix} \quad (1)$$

$$M = \begin{pmatrix} 1 & -tan\theta \\ -tan\theta & 1 \end{pmatrix} \quad (2)$$

Natural images were taken from an open source movie (Baumann, 2010). Three image sequences were prepared in this study, containing natural scenes that are unskewed at $\theta = 0°$, right skewed at $\theta = -25°$ and left skewed images $\theta = +25°$. Sharp boundaries were blended by weighting each image with a Hanning window weighting function of the second order (Habtegiorgis et al., 2017; Harris, 1978). Each image subtended $20° \times 20°$ at zero eccentricity. Figure 1 shows an example of scenes from each image sequence. The left and right skewed stimuli were used as adapting stimuli whereas the unskewed image sequence was used as a de-adapting stimuli, as will be explained in the procedure section. The content was similar in the three image sequences. Each image sequence was rendered at a rate of 20 frames per second.

Test stimuli were plaid checkerboards distorted at different skew amplitudes and comprising the same spatial dimension as the images in the adapting stimuli. The plaid checkerboards were prepared by superimposing identical contrast sinusoidal gratings oriented at $-45°$ to the right and $+45°$ to the left (see Figure 2). The dimensions of the plaids' opposite diagonals were defined by the wavelengths of the component gratings in the corresponding directions, i.e., d_{right} and d_{left}, and had the same value $d_o = 1.24$ degrees of VA for a square plaid. Skew was induced by adding or subtracting Δ from the wavelengths the component gratings as in Equation 3. Thus, plaids are skewed to the left when Δ is positive, and to the right when Δ is negative.

$$d_{right} = d_o - \Delta, d_{left} = d_o + \Delta \quad (3)$$

Where, d_{right} and d_{left} are the dimensions of the right and the left diagonals of the plaid and corresponds to the wavelengths of the left and the right oriented component gratings, respectively. Δ, in pixels, is the wavelength variation parameter and defines the amount of the skew. When unskewed, i.e., $\Delta = 0$, the diagonals of the plaid squares have equal dimensions of $d_o = 40$pixels subtending a VA of 1.24°. Non-zero Δ stretches the plaid diagonally and shears the zero-crossings of the squares in the plaid. Positive Δ results in left skewed plaid and negative Δ in right skewed plaid.

The unequal magnification factor in the oblique meridians, induced by either geometrically shearing or varying the diagonal dimensions, was used to quantify the skew amplitude as shown in Equation 4.

$$Skew_{amplitude(\Delta\backslash\theta)}[\%] = \left(1 - \frac{d_{right}}{d_{left}}\right) \times 100 \quad (4)$$

$$Skew_{amplitude(\Delta\backslash\theta)}[\%] = \left(1 - \frac{d_o - \Delta}{d_o + \Delta}\right) \times 100$$
$$= \left(1 - \frac{1 - \tan\theta}{1 + \tan\theta}\right) \times 100 \quad (5)$$

Procedure

All observers were trained on how to respond to the test stimuli and informed about the general measurement procedure.

Fast adaptation (FA) was evaluated five times on three measurement days with different skew EE durations (see Figure 3). On the first day of measurement, FA was tested in session 1.1 and 1.2 respectively before and after EE1. FAs measured in session 1.1 and 1.2 were compared to test immediate facilitation induced by EE1, i.e., 30 min of extended exposure to each adapting image sequence. The second measurement was performed after, on average, 61 $\pm$ 1.3 days wherein FA was again tested in session 2.1 and session 2.2, respectively, before and after EE2. Retained facilitation from EE1 was tested by comparing FA between session 1.2 and 2.1. Moreover, comparison of FA between session 2.1 and 2.2 indicated immediate facilitation induced by EE2, i.e., 1 h of extended exposure to each skewed adapting image sequence. Subsequently, after on average 57 $\pm$ 1 days, a retained facilitation from EE2 was tested by measuring FA in session 3.

In FA measurement sessions, aftereffect was tested after a brief exposure to each skewed adapting stimulus with constant stimulus procedure as illustrated in Figure 4. Ten amplitudes of skew were used for the test stimuli. Observers fixated at the center of the screen. First, the left-skewed adapting stimuli were presented for 1 s followed by inter stimulus interval (ISI) of 0.25 s and another 0.25 s of test stimulus presentation. Then,

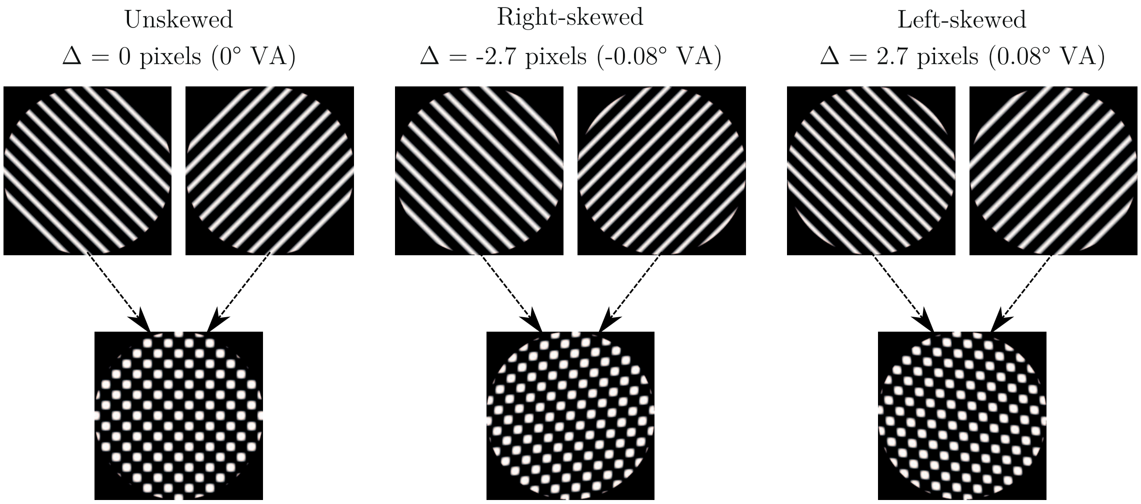

Figure 2. Examples of unskewed (at $\Delta = 0$ *pixels*), left skewed [at $\Delta = 2.7$ *pixels*(0.08 *degrees of VA*)] and right skewed [at $\Delta = -2.7$ *pixels*(-0.08 *degrees of VA*)] plaid checkerboard test stimuli.

observers had to respond whether the test stimulus was skewed to the left or to the right by pressing the left or the right key, respectively, within 1 s of response time (RT). During the ISI and RT, the screen was totally black. Afterward, the unskewed stimuli were presented for 1 s followed by 0.25 ISI. The undistorted stimuli were shown after each distortion FA to minimize a possible adaptation build up due to repeated exposure to the distorted stimuli and also to mimic alterations between distorted and undistorted natural environment that occurs in real world scenarios, e.g., during donning and removing of distortion inducing spectacles. Subsequently, the same steps were followed with the right skewed adapting stimuli, i.e., 1 s of right skew adaptation, 0.25 s ISI, 0.25 s test stimulus presentation, 1 s RT, 1 s de-adaptation and then 0.25 ISI. This cycle was repeated 80 times to collect eight responses per each skew amplitude of the test stimuli. The presentation of the skew amplitude of the test stimuli was in a randomized order.

Data analysis

Two psychometric curves of percentage of leftward responses were computed from the responses collected after left and right skew adaptations in each FA measurement session. Percentage of leftward response as a function of skew amplitude of the test stimuli was fitted with a cumulative Gaussian function using Psignifit 4.0 software (asymptotes set free but assumed to be equal) (Schutt, Harmeling, Macke, & Wichmann, 2016). The skew amplitude that was perceived as undistorted, the point of subjective equality (PSE), was indicated by the skew amplitude at 50% of leftward responses. On each measurement day, observers' PSE was tested before the adaptation sessions to test their unadapted state responses. This unadapted state PSE was subtracted from the PSEs of LSK and RSK FAs. Then, two parameters, i.e., $\sum$PSE and ΔPSE, were computed from the FA PSEs as in Equation 6 and Equation 7. The ΔPSE quantifies the effect size and the $\sum$PSE quantifies the direction bias of alternate LSK

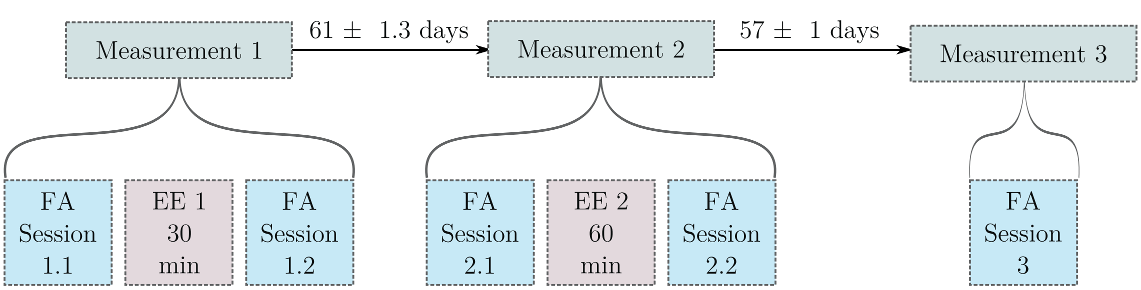

Figure 3. FA measurement paradigm to test long-term fast adaptation dynamics with time and experience. FA was evaluated five times. In session 1.1 and session 1.2, FA was measured before and after 30 min EE to each skew direction. On average, after 61 days, FA was again tested two times in session 2.1 and 2.2 before and after 60 min of skew exposure. After another, on average 57 days, FA was measured in session 3.

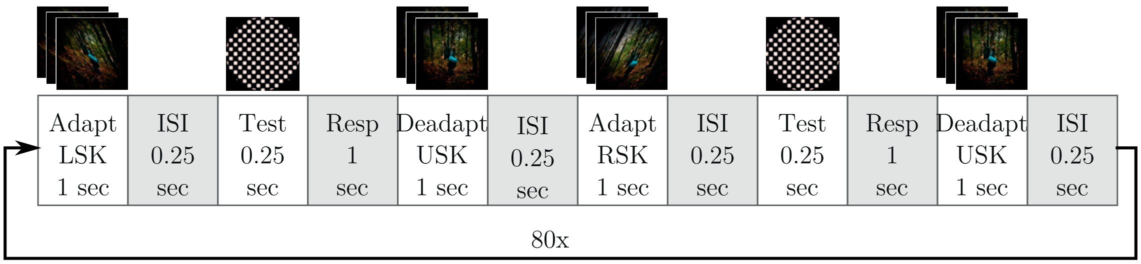

Figure 4. Scheme of FA measurement procedure. Aftereffect was tested alternately to the left skewed stimuli (LSK) and the right skewed stimuli (RSK) with constant stimulus procedure. The unskewed image sequences (USK) were presented after each adaptation as a de-adaptation to minimize a possible adaptation buildup.

and RSK adaptations in FA sessions.

$$\Delta PSE = PSE_{LSK} - PSE_{RSK} \quad (6)$$

$$\sum PSE = PSE_{LSK} + PSE_{RSK} \quad (7)$$

The overall effects were calculated by averaging the ΔPSEs and $\sum$PSEs of all the observers in each session. A paired-sample *t* test was used to evaluate the significance of ΔPSEs and $\sum$PSEs due to the FAs and to compare the parameters between the different sessions.

Results

The overall observers' shift in perception due to the FA in each session is shown in Figure 5a in terms of averagedΔPSE. In all the sessions, the PSE shifted toward the adapting skew direction. A significant positive ΔPSE was obtained in all the sessions, $p < 0.01$. The trend of this shift is the same as the previously shown skew-induced adaptation aftereffects (Habtegiorgis et al., 2017). After exposure to left skewed natural stimuli, observers perceived left skewed checkerboards as unskewed and vice versa after right skew exposure. Comparing the FA magnitude between sessions, the ΔPSEs measured in session 1.1 and session 1.2 were not significantly different from one another. Similarly, the FA measured in session 1.2 and session 2.1 were not different from one another. The 30 min exposure in session 1 thereby did not induce any significant change in the FA dynamics that was retained for, on average, 61 days. However, after 1 h of skew exposure, a significant increase in FA was obtained in session 2.2 relative to previous FA in session 2.1; $p < 0.001$. Thus, there was immediate facilitation due to the 1 h skew exposure. Furthermore, this facilitation was retained for, on average, 57 days, wherein the FA magnitude in session 3 was significantly higher than session 2.1 ($p < 0.01$) and session 1.1 ($p < 0.03$) and not different from session 2.2 ($p > 0.05$). The $\sum$PSE was not significantly different from 0 ($p > 0.05$) in all the sessions. There was also no significant difference of $\sum$PSEs across sessions. Thus, no dicernible direction bias was conceived from any of the FA and EE sessions. In the supplementary materials section, a plot is provided showing the raw PSE_{LSK} and PSE_{RSK} values of individual observers' and overall averages.

The corresponding long-term change in the psychometric curves of all observers' responses collected in session 1.1, session 2.1, and session 3 is shown in Figure 5b. To ease the realization of the amount of shift in responses in the different sessions, the curves from each session are calibrated in the x-axis by the PSE measured after the RSK adaptation. Thus, in each session, the amount of the perceptual shift after the alternate skew exposures is indicated by position of the LSK adaptation PSE relative to a common point 0. The FA induced shift in the psychometric curves was increasing depending on amount of previous skew experience. The psychometric curves clearly show a larger shift of perception in session 3 than in session 2.1 relative to the baseline measurement in session 1.1.

In sum, after a brief exposure to skewed natural scenes, FA was observed. Furthermore, 1 h of exposure to image skew induces facilitation in the FA dynamics, which can be retained for over a month.

Discussion

In this study, experience-dependent and long-term retained facilitation of skew adaptation was presented. Visual adaptation to geometrical skew distortion was induced in response to distorted natural image sequences. The adaptation aftereffect was tested via a skew identification in a simple geometrical pattern; specifically a checkerboard. In line with previous finding, oppositely skewed dynamic natural image sequences led to adaptation aftereffects in opposite directions (Habtegiorgis et al., 2017). Facilitated fast adaptation was obtained after 1 h of extended exposure

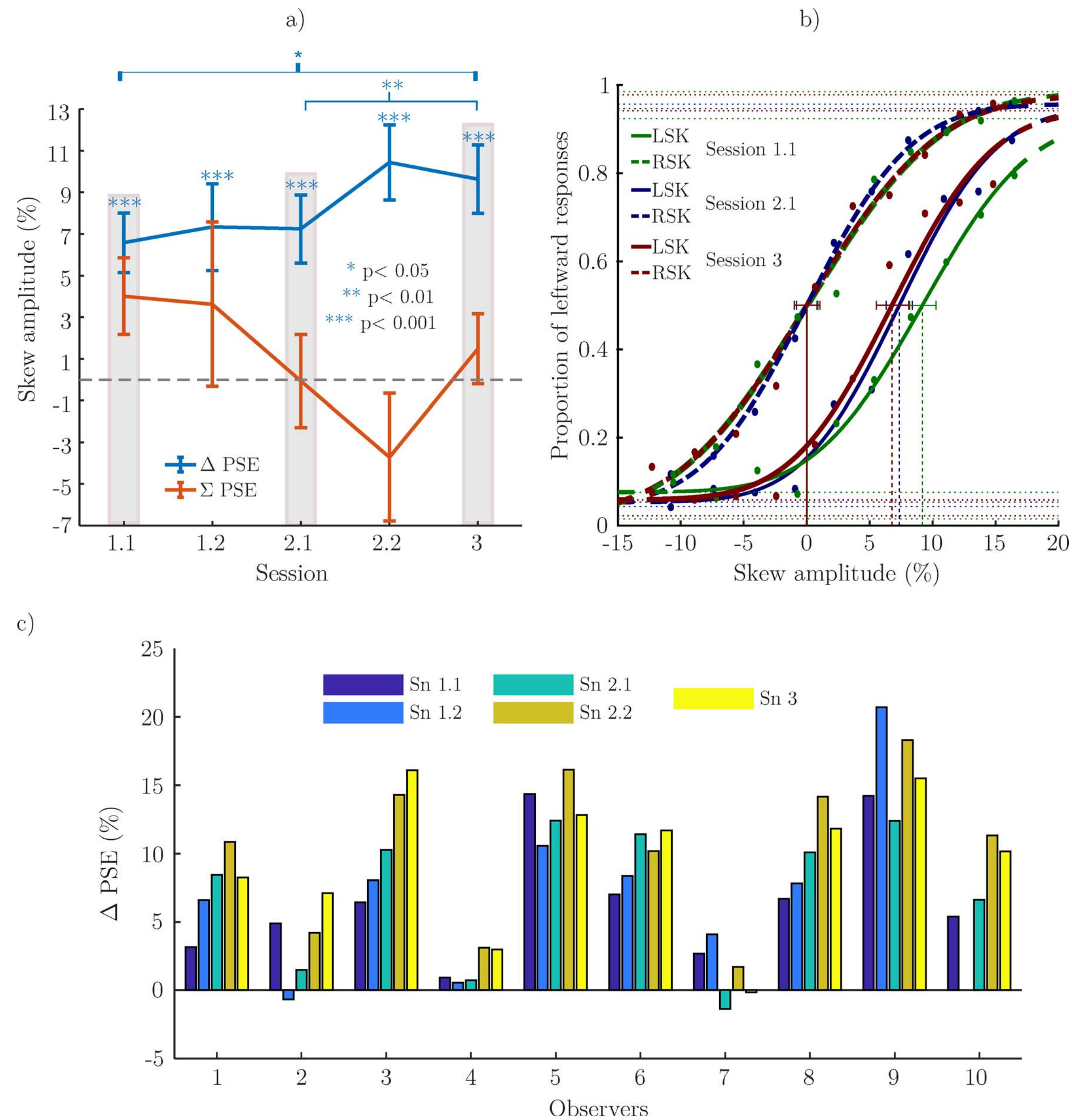

Figure 5. Time and experience dependent FA dynamics. FA is estimated by the ΔPSE after alternate brief exposure to left and right skewed natural image sequences. (a) The overall FA in the five sessions: the averaged ΔPSEs and $\sum$PSEs from all the observers. The connecting line illustrates the trend of the ΔPSEs and $\sum$PSEs across the sessions. The error bars around the average represent the standard errors. The transparent bars show the data used to illustrate the long-term retention effect considered in Figure 5b. (b) Long-term changes in the FA psychometric curves of all the observers' responses: measured at first day in session 1.1 (red), after 61 $\pm$ 1.3 days in session 2.1 (blue) and after another 57 $\pm$ 1 days in session 3 (green). For each session, the curves are calibrated in the x-axis to the RSK adaptation PSE. The Gaussian fitted function and the confidence intervals at PSE are shown by the broken lines for the RSK adaptation aftereffects and in solid lines for the LSK adaptation aftereffects. (c) The individual observer's ΔPSEs in the five sessions.

to the skewed natural stimuli. A long-term retained facilitation was demonstrated after, on average, 57 days during which there was no skew exposure.

Previous studies have shown similar long-term effects in perceptual learning, depending on particular tasks and stimuli (Ball & Sekuler, 1987; Fahle, 2002; Fiorentini & Berardi, 1981; Gibson, 1970; Karni & Sagi, 1991; Redding, Rossetti, & Wallace, 2005; Sagi & Tanne, 1994). However, in the paradigm followed in the present study, no feedback was given regarding a mistake or a correct response given by the observers. Thus, there was no opportunity of task-related perceptual learning during aftereffect measurement. Therefore, extended exposure to skew geometric distortions in an hour time scale, induced visual adaptation and distortion information were retained long term and facilitated future adaptations.

Adaptation is a mechanism that happens at several time scales. Adaptation to changes that occur frequently in the natural world is rapid to allow the visual system to operate in a wide range of conditions, such as to continuously varying luminance, contrast, color, and orientation. Adaptation to rare and subtle alterations, on the other hand, is rather slow, e.g., in adaptation to changes by wearing new glasses. It is commonly known that the visual system starts to adapt quicker after repeated exposure to these subtle changes. Experience-dependent facilitation of adaptation to color and blur features demonstrated these dynamics (Engel et al., 2016; Yehezkel et al., 2010). Observers who wore colored glasses for 14 months exhibited faster adaptation to color changes than control groups. Four hours of extended exposure to blur also induced facilitation, which was retained for a day. These results suggested that prior experience to recurrent alterations allows the visual system to adapt fast. Our study reveals a novel long-term plasticity of the visual system to geometrical distortion. We found long-term facilitatory effects after 1 h of skew exposure. Exposure duration of 1 h is rather short compared to the other facilitation studies (Engel et al., 2016; Yehezkel et al., 2010). Moreover, the retention duration of this facilitation, i.e., on average for 57 days, was longer than previous long-term retention reports (Yehezkel et al., 2010). Long-term effects of this form have not been reported so far and would thus point to a long-retained learning component in adaptation.

We tested the long-term facilitation of skew adaptation sequentially for two time scales of extended exposure; first for 30 min and then for 1 h. An immediate and retained facilitation effect was found almost 2 months after the 1 h of exposure but not after the 30 min of exposure. The exposure time thereby has an effect on the facilitation. The 30 min of exposure might not have accumulated enough information about the skew to induce long-term facilitation. The long-term facilitated re-adaptations after 1 h skew exposure in our study could have had two possible origins. The first possibility is that the 1 h of exposure was enough per se to induce the retained facilitation. Second, some information might have been retained for 2 months after the prior 30 min exposure, which was not enough to facilitate the adaptation but subsequently adds to the 1 h exposure and contributes to the facilitation.

The facilitation of visual adaptation with extended exposure to the image skew might be governed by an inference process similar to the recently demonstrated effect of repeated donning and removing of color filters (Engel et al., 2016; Grzywacz & de Juan, 2003; Kording, Tenenbaum, & Shadmehr, 2007; Wark et al., 2009). In inference theory, the visual system adjusts its response to infer the environment under the Bayesian decision-making framework, the parameters of which could be affected by previous stimulus history. Thus, according to the inference model of adaptation, previously acquired distortion information possibly increases the prior probability of the distorted scenes to recur or their likelihood, which determines their detectability. If distorted scenes are recurrent, it would also be costly to the visual system to adapt slowly every time the distortions are reapplied. Moreover, to minimize the risk of error-driven fluctuations in neural responses, optimum perceptual adjustments to some subtle or rare environmental alterations, like our skew distortions, might be rather slow (Todorovic et al., 2011; Wark et al., 2009). However, extended exposure to the distortions could accumulate enough evidence about the distortions outweighing the risk of fast readjustments when the distortions reappear again. Accordingly, with past experience with the distortions, the visual system might have learned to re-adapt fast.

Physiologically, synaptic changes between neurons are one of the possible underling mechanisms for stimulus dependent sensory response changes, like adaptation (Castellucci, Pinsker, Kupfermann, & Kandel, 1970; Thompson & Spencer, 1966). Studies have suggested that short-term adjustments operate upon presynaptic terminals through a reduction of effective neurotransmitter release (Hawkins, Kandel, & Siegelbaum, 1993) while long-term adjustments are possibly associated to structural changes in presynaptic terminals (Tetzlaff, Kolodziejski, Markelic, & Worgotter, 2012; Wang, 1993). Exposure to a skewed natural environment affects multiple levels in the visual hierarchy (Habtegiorgis et al., 2017). In line with the aforementioned studies, we suggest that the observed long-term facilitation of visual adaptation to image skew possibly constitutes long-term synaptic changes in the intracortical circuitry that encode features altered by the image skew, e.g., orientation, magnification or optic flow direction.

Habituation to progressive lenses might consist of oculomotor and visual components. Skew adaptation, although it simplifies the visual input, has been shown to mirror a variety of properties of the visual component of the habituation process. The current manuscript shows long-term retention of skew adaptation, as it occurs in a habituated progressive lens wearer. In contrast to skew adaptation in the present study, progressive lenses show a complex pattern of distortions. Skew produced by PALs is in opposite directions on the left and right side of the lens resulting in a different skew for each gaze direction. Parts of this complex adaptation are carried by a spatiotopic adaptation mechanism, retaining adaptation at a definite spatial location across saccades, and a retinotopic mechanism, which has to adapt to specific distortions for different gaze directions (Habtegiorgis, Rifai, & Wahl, 2018). During habituation, fast adaptation is needed in these mechanisms, e.g., to a skewed and unskewed environment during donning and removing of spectacles and to opposite skews during gazing through the opposite parts of PALs specifically in the retinotopic mechanism. Thus, the FA paradigm followed in the present study can be used as a valuable tool to systematically explore the ability of these mechanisms to handle habituation to complex distortions of PALs.

Distortion of the environment is a daily visual constraint in spectacle lens wearers. These modifications can be challenging in day-to-day living, e.g., when mobility is affected by distortion-induced spatial disorientation (Johnson, Buckley, Scally, & Elliott, 2007). Proper and fast habituation is therefore essential to optical modifications. Here, we showed long-term facilitation of adaptation to skew geometrical distortions with ecologically valid stimuli. The reported adaptation dynamics could be one of the possible mechanisms to compensate for skew distortions commonly occurring in spectacles (Meister & Fisher, 2008). Our approach provides a new insight to address the habituation process to PALs.

To summarize, with extended exposure to skew geometric distortions in an hour time scale, adaptation can be facilitated in the long term, enabling fast visual adjustments whenever the distortions are reapplied.

Keywords: spatial distortions, *visual adaptation*, *natural vision*, *long-term retention*, *plasticity*

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References

Adams, W. J., Banks, M. S., & van Ee, R. (2001). Adaptation to three-dimensional distortions in human vision. *Nature Neuroscience*, *4*(11), 1063–1064.

Ball, K., & Sekuler, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research*, *27*(6), 953–965.

Bao, M., & Engel, S. A. (2012). Distinct mechanism for long-term contrast adaptation. *Proceedings of the National Academy of Sciences, USA*, *109*(15), 5898–5903.

Bao, M., Fast, E., Mesik, J., & Engel, S. (2013). Distinct mechanisms control contrast adaptation over different timescales. *Journal of Vision*, *13*(10): 14, 1–11, https://doi.org/10.1167/13.10.14. [PubMed] [Article]

Barbero, S., & Portilla, J. (2015). Geometrical interpretation of dioptric blurring and magnification in ophthalmic lenses. *Optics Express*, *23*(10), 13185–13199.

Baumann, T. (Director). (2010). Valkaama. Retrieved from: http://www.valkaama.com

Belmore, S. C., & Shevell, S. K. (2008). Very-long-term chromatic adaptation: Test of gain theory and a new method. *Visual Neuroscience*, *25*(03), 411–414.

Belmore, S. C., & Shevell, S. K. (2011). Very-long-term and short-term chromatic adaptation: Are their influences cumulative? *Vision Research*, *51*(3), 362–366.

Betsch, B. Y., Einhäuser, W., Körding, K. P., & König, P. (2004). The world from a cat's perspective–statistics of natural videos. *Biological Cybernetics*, *90*(1), 41–50.

Bex, P. J., Dakin, S. C., & Mareschal, I. (2005). Critical band masking in optic flow. *Network: Computation in Neural Systems*, *16*(2-3), 261–284.

Bex, P. J., & Makous, W. (2002). Spatial frequency, phase, and the contrast of natural images. *Journal of the Optical Society of America A*, *19*(6), 1096–1106.

Bex, P. J., Mareschal, I., & Dakin, S. C. (2007). Contrast gain control in natural scenes. *Journal of Vision*, *7*(11):12, 1–12, https://doi.org/10.1167/7.11.12. [PubMed] [Article]

Bex, P. J., Solomon, S. G., & Dakin, S. C. (2009). Contrast sensitivity in natural scenes depends on edge as well as spatial frequency structure. *Journal of Vision*, *9*(10):1, 1–19, https://doi.org/10.1167/9.10.1. [PubMed] [Article]

Billock, V. A., de Guzman, G. C., & Kelso, J. A. S. (2001). Fractal time and 1/f spectra in dynamic images and human vision. *Physica D: Nonlinear Phenomena*, *148*(1), 136–146.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436.

Castellucci, V., Pinsker, H., Kupfermann, I., & Kandel, E. R. (1970, March 27). Neuronal mechanisms of habituation and dishabituation of the gill-withdrawal reflex in Aplysia. *Science*, *167*(3926), 1745–1748.

Clifford, C. W. G., Webster, M. A., Stanley, G. B., Stocker, A. A., Kohn, A., Sharpee, T. O., & Schwartz, O. (2007). Visual adaptation: Neural, psychological and computational aspects. *Vision Research*, *47*(25), 3125–3131.

David, S. V., Vinje, W. E., & Gallant, J. L. (2004). Natural stimulus statistics alter the receptive field structure of v1 neurons. *The Journal of Neuroscience*, *24*(31), 6991–7006.

Delahunt, P. B., Webster, M. A., Ma, L., & Werner, J. S. (2004). Long-term renormalization of chromatic mechanisms following cataract surgery. *Visual Neuroscience*, *21*(03), 301–307.

Dong, D. W., & Atick, J. J. (1995). Statistics of natural time-varying images. *Network: Computation in Neural Systems*, *6*(3), 345–358.

Eisner, A., & Enoch, J. M. (1982). Some effects of 1 week's monocular exposure to long-wavelength stimuli. *Perception & Psychophysics*, *31*(2), 169–174.

Engel, S. A., Wilkins, A. J., Mand, S., Helwig, N. E., & Allen, P. M. (2016). Habitual wearers of colored lenses adapt more rapidly to the color changes the lenses produce. *Vision Research*, *125*, 41–48.

Fahle, M. (2002). Perceptual learning: Gain without pain? *Nature Neuroscience*, *5*(10).

Fannin, T. E., & Grosvenor, T. (2013). *Clinical optics*. Oxford, UK: Butterworth-Heinemann.

Felsen, G., & Dan, Y. (2005). A natural approach to studying vision. *Nature Neuroscience*, *8*(12), 1643–1646.

Fiorentini, A., & Berardi, N. (1981). Learning in grating waveform discrimination: Specificity for orientation and spatial frequency. *Vision Research*, *21*(7), 1149–1158.

Gallant, J. L., Connor, C. E., & Van Essen, D. C. (1998). Neural activity in areas V1, V2 and V4 during free viewing of natural scenes compared to controlled viewing. *Neuroreport*, *9*(9), 2153–2158.

Gibson, E. J. (1970). Principles of perceptual learning and development. *Science*, *168*, 958–959.

Grzywacz, N. M., & de Juan, J. (2003). Sensory adaptation as Kalman filtering: Theory and illustration with contrast adaptation. *Network: Computation in Neural Systems*, *14*(3), 465–482.

Habtegiorgis, S. W., Rifai, K., Lappe, M., & Wahl, S. (2017). Adaptation to skew distortions of natural scenes and retinal specificity of its aftereffects. *Frontiers in Psychology*, *8*, 1158, https://doi.org/10.3389/fpsyg.2017.01158.

Habtegiorgis, S. W., Rifai, K., & Wahl, S. (2018). Transsaccadic transfer of distortion adaptation in a natural environment. *Journal of Vision*, *18*(1):13, 1–10, https://doi.org/10.1167/18.1.13. [PubMed] [Article]

Harris, F. J. (1978). On the use of windows for harmonic analysis with the discrete Fourier transform. *Proceedings of the IEEE*, *66*(1), 51–83.

Hawkins, R. D., Kandel, E. R., & Siegelbaum, S. A. (1993). Learning to modulate transmitter release: Themes and variations in synaptic plasticity. *Annual Review of Neuroscience*, *16*(1), 625–665.

Johnson, L., Buckley, J. G., Scally, A. J., & Elliott, D. B. (2007). Multifocal spectacles increase variability in toe clearance and risk of tripping in the elderly. *Investigative Ophthalmology and Visual Science*, *48*(4), 1466–1471, https://doi.org/10.1167/iovs.06-0586.

Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences, USA*, *88*(11), 4966–4970.

Kording, K. P., Tenenbaum, J. B., & Shadmehr, R. (2007). The dynamics of memory as a consequence of optimal adaptation to a changing body. *Nature Neuroscience*, *10*(6), 779–786.

Kwon, M., Legge, G. E., Fang, F., Cheong, A. M. Y., & He, S. (2009). Adaptive changes in visual cortex following prolonged contrast reduction. *Journal of Vision*, *9*(2):20, 1–16, https://doi.org/10.1167/9.2.20. [PubMed] [Article]

Meister, D. J., & Fisher, S. W. (2008). Progress in the spectacle correction of presbyopia. Part 1: Design and development of progressive lenses. *Clinical and Experimental Optometry*, *91*(3), 240–250.

Neitz, J., Carroll, J., Yamauchi, Y., Neitz, M., & Williams, D. R. (2002). Color perception is mediated by a plastic neural mechanism that is adjustable in adults. *Neuron*, *35*(4), 783–792.

Redding, G. M., Rossetti, Y., & Wallace, B. (2005). Applications of prism adaptation: A tutorial in theory and method. *Neuroscience & Biobehavioral Reviews*, *29*(3), 431–444.

Ringach, D. L., Hawken, M. J., & Shapley, R. (2002). Receptive field structure of neurons in monkey primary visual cortex revealed by stimulation with natural image sequences. *Journal of Vision*, *2*(1):2, 12–24, https://doi.org/10.1167/2.1.2. [PubMed] [Article]

Ruderman, D. L., & Bialek, W. (1994). Statistics of natural images: Scaling in the woods. *Physical Review Letters*, *73*(6), 814–814.

Sagi, D., & Tanne, D. (1994). Perceptual learning: Learning to see. *Current Opinion in Neurobiology*, *4*(2), 195–199.

Schutt, H. H., Harmeling, S., Macke, J. H., & Wichmann, F. A. (2016). Painfree and accurate Bayesian estimation of psychometric functions for (potentially) overdispersed data. *Vision Research*, *122*, 105–123, https://doi.org/10.1016/j.visres.2016.02.002.

Smithson, H., & Zaidi, Q. (2004). Colour constancy in context: Roles for local adaptation and levels of reference. *Journal of Vision*, *4*(9):3, 693–710, https://doi.org/10.1167/4.9.3. [PubMed] [Article]

Snow, M., Coen-Cagli, R., & Schwartz, O. (2017). Adaptation in the visual cortex: A case for probing neuronal populations with natural stimuli. *F1000Research, 6*.

Tetzlaff, C., Kolodziejski, C., Markelic, I., & Worgotter, F. (2012). Time scales of memory, learning, and plasticity. *Biological Cybernetics*, *106*(11-12), 715–726, https://doi.org/10.1007/s00422-012-0529-z.

Thompson, R. F., & Spencer, W. A. (1966). Habituation: A model phenomenon for the study of neuronal substrates of behavior. *Psychological Review*, *73*(1), 16.

Todorovic, A., van Ede, F., Maris, E., & de Lange, F. P. (2011). Prior expectation mediates neural adaptation to repeated sounds in the auditory cortex: An MEG study. *The Journal of Neuroscience*, *31*(25), 9118–9123.

Vlaskamp, B. N. S., Filippini, H. R., & Banks, M. S. (2009). Image-size differences worsen stereopsis independent of eye position. *Journal of Vision*, *9*(2): 17, 1–13, https://doi.org/10.1167/9.2.17. [PubMed] [Article]

Wang, D. (1993). A neural model of synaptic plasticity underlying short-term and long-term habituation. *Adaptive Behavior*, *2*(2), 111–129.

Wark, B., Fairhall, A., & Rieke, F. (2009). Timescales of inference in visual adaptation. *Neuron*, *61*(5), 750–761.

Webster, M. A. (2011). Adaptation and visual coding. *Journal of Vision*, *11*(5):3, 1–23, https://doi.org/10.1167/11.5.3. [PubMed] [Article]

Welch, R. B. (1969). Adaptation to prism-displaced vision: The importance of target-pointing. *Perception & Psychophysics*, *5*(5), 305–309.

Welch, R. B. (1978). *Perceptual modification: Adapting to altered sensory environments*: New York, NY: Academic Press.

Yehezkel, O., Sagi, D., Sterkin, A., Belkin, M., & Polat, U. (2010). Learning to adapt: Dynamics of readaptation to geometrical distortions. *Vision Research*, *50*(16), 1550–1558.