Individual differences in response precision correlate with adaptation bias

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The internal representation of stimuli is imperfect and subject to bias. Noise introduced at initial encoding and during maintenance degrades the precision of representation. Stimulus estimation is also biased away from recently encountered stimuli, a phenomenon known as adaptation. Within a Bayesian framework, greater biases are predicted to result from poor precision. We tested for this effect in individual difference measures. 202 subjects contributed data through an on-line experiment (https://cfn.upenn.edu/iadapt). During separate face and color blocks, subjects performed three different tasks: an immediate stimulus-match (15 trials), a 5 seconds delayed match (30 trials), and 5 seconds of adaptation followed by a delayed match (30 trials). The stimulus spaces were circular and subjects entered their responses using a color/face wheel. Bias and precision of responses were extracted by fitting a mixture of von Mises distributions to account for random guesses. Two blocks of each measure were obtained, allowing for tests of measure reliability. We found that reliable differences between individuals in precision were as great as those between tasks or materials. The adaptation manipulation induced the expected bias in responses (colors: 7.8°; faces: 5.0°), and the magnitude of this bias reliably and substantially varied between subjects. Across subjects, there was a negative correlation between mean precision and bias (color: $\rho = -0.26$; faces: $\rho = -0.13$). This relationship was replicated in a new experiment with 192 subjects (color: $\rho = -0.22$; faces: $\rho = -0.19$). This result is consistent with a Bayesian observer model, in which individual differences in the precision of perceptual representation influences the magnitude of adaptation bias.

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Introduction

Under conditions of uncertainty, we rely upon prior beliefs about the world to interpret sensory stimuli, giving rise to biases. Perception can be understood as a "best guess" as to what is in the world, and when sensory information is imperfect our best guess relies more heavily on expectations and prior beliefs (von Helmholtz, 1867; Knill and Richards, 1996). Prior knowledge influences perception continuously and automatically, occasionally even leading to perceptual illusions (Bar, 2004; Summerfield and Egner, 2009; Lafer-Sousa et al., 2015). To achieve statistically optimal inference, sensory evidence and prior beliefs can be quantitatively combined using Bayes' rule (Bayes and Price, 1763). Under many circumstances, human perception is consistent with Bayesian observer models (Knill and Richards, 1996; Stocker and Simoncelli, 2006b).

A ubiquitous example of a perceptual bias produced by sensory history is visual adaptation, where estimates are shifted "away" from recently observed stimuli (Levinson and Sekuler, 1976; Clifford, 2002). Visual adaptation has been observed for a variety of stimuli such as line orientation, motion, color, and even complex stimuli such as face identity or gender (Gibson and Radner, 1937; Anstis et al., 1998; Jameson and Hurvich, 1972; Webster et al., 2004; Little et al., 2005). In all cases, stimuli appear to be more different from the adapting stimulus than they actually are, causing illusory perceptual distortions (Eagleman, 2001). While particularly evident in the few seconds following an extended presentation of a stimulus, perception and neural responses are affected by sensory history over a variety of timescales and this process is likely constantly at work in the nervous system (Fischer and Whitney, 2014; Mattar et al., 2016).

An intuitive explanation for visual adaptation within a Bayesian framework is that it affects the prior distribution; i.e., sensory "expectations" are altered after prolonged exposure to a stimulus type. If this is the case, then a greater bias towards this altered prior should be expected when incoming sensory representations are uncertain. For example, adding either internal or external noise to a stimulus to be remembered produces increasingly larger biases towards a stored color prior (Olkkonen et al., 2014). Here, we ask if the fidelity of storing and reproducing sensory percepts (i.e., precision) also influences adaptation biases. Using a web-based visual adaptation experiment with color and face stimuli, we investigated the relationship between variability in response precision and adaptation biases across individuals. We found that the precision and bias are relatively stable measures of an individual, and that biases for color stimuli are correlated with biases for face stimuli. We then investigated the relationship between bias and precision across individuals and found that biases for both materials are larger when precision is lower. These results conform with predictions of Bayesian observer models whereby perception is biased increasingly away from recently observed stimuli when sensory information is uncertain.

Results

We investigated the relationship between variation in precision and adaptation bias across individuals. A total of 530 people recruited through Amazon Mechanical Turk performed an on-line experiment on a website (https://cfn.upenn.edu/iadapt) custom-built for this study. Each subject performed a series of psychophysics experiments on their personal computers and received compensation for their time (Fig. 1a). On each experimental trial, subjects were instructed to report the value of a target stimulus — a color or a face — by clicking and dragging the mouse pointer around a stimulus wheel, allowing a fine adjustment of their responses (Fig. 1b). Wheels were comprised of 360 distinct stimuli varying in hue (colors) or in age and gender (faces; Fig. 1d).

Following a screen contrast adjustment and a web-based version of the Ishihara test for normal color vision (Ishihara, 1960), subjects completed two replications of three experiments for each stimulus class. Each experiment was preceded by a set of written instructions, a mini-quiz containing three questions about the instructions, and a short practice block. Subjects were required to respond correctly to all questions in the quiz and to achieve near-perfect accuracy in the practice blocks (within 5° of the target value in every trial) to proceed to the main experimental trials (Fig. 1a). In the *stimulus-match* experiment (15 trials), designed to obtain a baseline response precision for each subject, subjects were instructed to select a value on the wheel matching the target stimulus, indicated as two colors/faces continuously presented on the left and right sides of the screen, outside of the stimulus wheel (Fig. 1c, top). In the *delayed-match* experiment (30 trials), designed to estimate subject's working memory precision, a target stimulus was presented on the center of the screen for 2.0 s, followed by a 4.0 s delay, after which subjects were to select a value on the wheel matching the target stimulus (Fig. 1c, middle). In the *adaptation* experiment (30 trials), designed to estimate the magnitude of adaptation biases, an adapting stimulus was presented in the center of the screen for 5 seconds followed by brief mask and a target stimulus ±45° away from the adaptor for 100ms, after which subjects were to select a value on the wheel matching the target stimulus (Fig. 1c, bottom). Subjects performed two separate blocks of each experiment in a session, allowing for tests of measure reliability, and the trials within each experiment were sampled uniformly and in random order from the circular space (Fig. 1d). Throughout the entire session, subjects were only allowed to proceed to the next block of the experiment if their accuracy remained above a minimum threshold (see Methods). A total of 328 subjects were either excluded or abandoned the experiment (108 at the color vision test and 202 during the main experimental trials), leaving 202 subjects for the main analyses described in this chapter (Table 1).

We calculated the error on each trial as the difference between the target value and the response entered ($\varepsilon = \theta_{target} - \theta_{response}$), and we fit the distribution of error values for each subject using a superposition

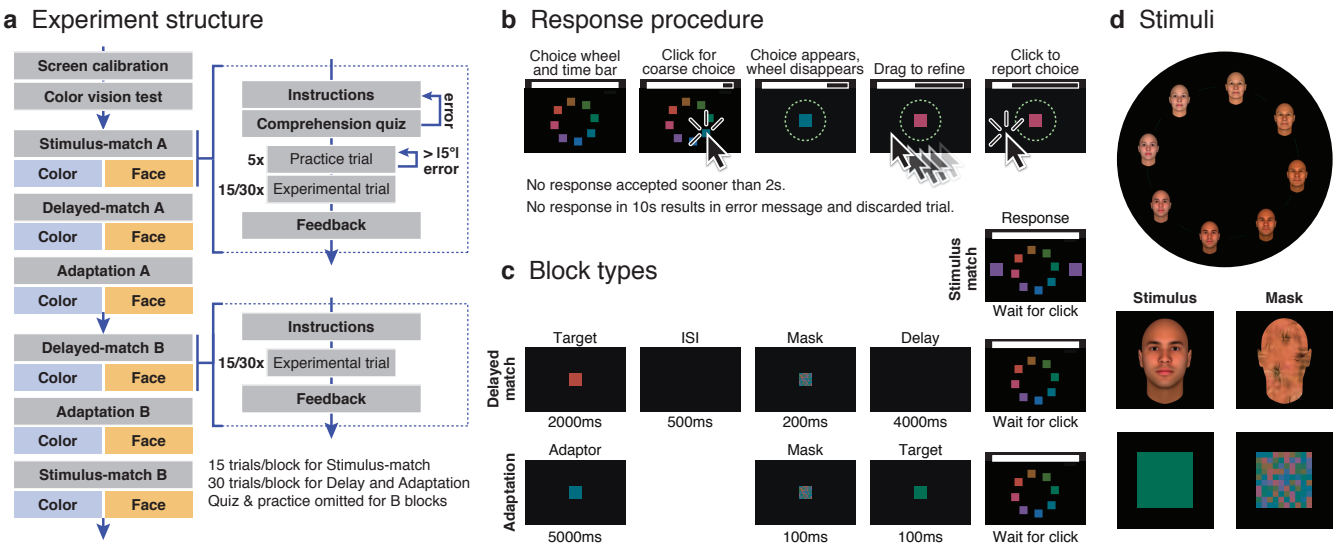

Figure 1: **Experiment setup and methods.** *(a)* Experiment structure. Subjects completed a battery of tests designed to estimate representation precision, precision after a delay, and precision and bias after adaptation. Each subject completed two blocks of each experiment, for both color and face stimuli. Prior to each experiment, subjects were presented with instructions and a comprehension quiz; the first time they performed each block of a given experiment, they also completed 5 practice trials. Each block of the stimulus-match experiment had 15 trials. Each block of the delayed-match and adaptation experiments had 30 trials. *(b)* Response procedure. Subjects were first presented with 8 equally spaced representative stimuli around the wheel. To enter their responses, subjects first performed a coarse selection by clicking on the region of the wheel that approximately matched the target. They then adjusted their selection more precisely by dragging the pointer around the wheel and clicking a second time to confirm their responses. *(c)* Block types. Top: On each trial of the stimulus-match experiment, subjects were instructed to match to a stimulus presented on both sides of the screen; the target stimulus remained on the response screen while the subject made the match. Middle: On each trial of the delayed-match experiment, subjects were instructed to match to a target stimulus following a 4 second interval. Bottom: On each trial of the adaptation experiment, subjects were instructed to match to a target stimulus that was presented after a 5 second adaptation period. *(d)* Stimuli. A circular space with 360 stimuli was used for both color and face stimuli. Color stimuli were generated to vary in hue but not in saturation or luminance (HSL space). Face stimuli varied in age and gender, each forming one axis of the space. Color masks were a checkerboard composed of various stimuli randomly sampled from the color space. The eight stimuli that are snown in the figure and in the response screen are equally spaced examples from the entire set of 360, and were selected at random on each trial. Face masks were created using the steerable pyramids method to match various low-level visual properties (Portilla and Simoncelli, 2000).

Table 1: **Subject enrollment and exclusion in the main experiment.** The total in the cells may not match the total number of subjects due to missing responses from some subjects.

Completed:	**Registration**	**Screening**	**Experiment**
Number of subjects	530	422	202
Age: $M \pm SD$	36 ± 12	36 ± 11	35 ± 11
Male/Female	252/277	191/231	92/110
Left/Right-handed	18/508	14/405	3/197

of distributions defined over a circular support ($-180° < \theta < +180°$) (Zhang and Luck, 2008; Bays et al., 2009). This procedure simultaneously estimates the precision of the error distribution (i.e., the inverse of the standard deviation of the corresponding wrapped normal distribution; Jammalamadaka and Sengupta, 2001) and the probability of random guesses (Fig. 2a). In the adaptation experiment, we used the distribution of reflected error values ($-\varepsilon$) from trials where the adaptor was at $+45°$ from the target ($\theta_{adaptor} - \theta_{target} = 45°$), resulting in a distribution of error values where adaptors are effectively all located at $-45°$. In these experiments, the fitting procedure also estimates two additional parameters: the mean of the error distribution (i.e., the bias induced by the paradigm) and the probability that the selected response matches the adaptor stimulus and not the target stimulus (Fig. 2b,c).

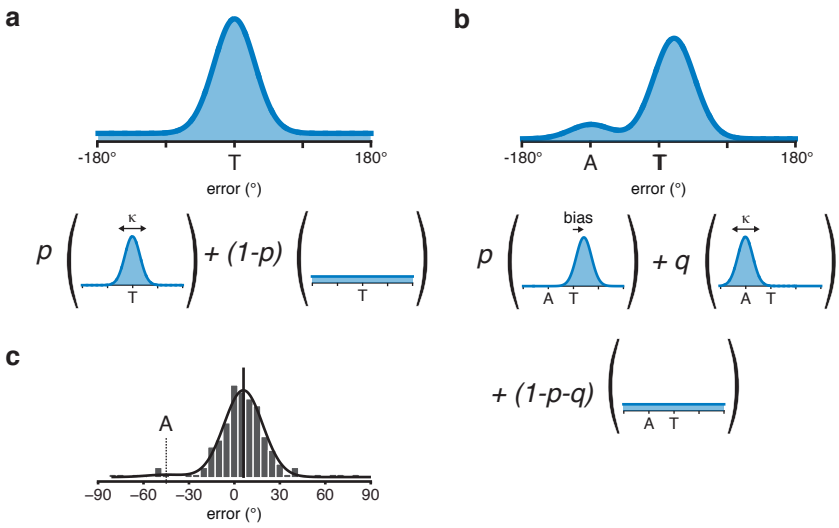

Figure 2: **Mixture model fitting approach.** The distribution of errors were modeled as a superposition of probability distributions to account for different types of responses. *(a)* In the stimulus-match and delayed-match experiments, responses could be concentrated near the target value (von Mises distribution centered at the target value) or fall randomly in any position of the space with equal probability (von Mises distribution with concentration parameter equal to zero). Two parameters were estimated: the concentration parameter of the responses near the target, and the probability of random responses. *(b)* In the adaptation experiment, responses could be concentrated near the target value (von Mises distribution displaced from the target by a fixed amount), concentrated near the adaptor value (a stimulus that the subjects were instructed to ignore, modeled as a von Mises distribution centered at the adaptor value) or fall randomly in any position of the space with equal probability (von Mises distribution with concentration parameter equal to zero). Four parameters were estimated: the magnitude of the displacement of responses near the target (bias), the concentration parameter of the responses near the target, the probability of responses near the adaptor, and the probability of random responses. *(c)* Example of a good fit for a subject in the adaptation experiment. Data are collapsed across both blocks of the adaptation experiment, and indicates the existence of a positive (repulsive) bias in relation to the adaptor.

Table 2: **Parameters from group fit of the adaptation data in the main experiment.**

	Bias	Concentration	P(target)	P(adaptor)	P(random)
Colors	7.8°	10.3	95.1%	2.3%	2.6%
Faces	5.0°	7.0	90.1%	5.2%	4.1%

Adaptation produces a repulsive bias

To confirm the effectiveness of our adaptation paradigm in inducing repulsive biases, we first fit the adaptation data from all subjects combined (12,120 trials per stimulus class) with a mixture of distributions as described. We observed a positive (repulsive) bias of 7.8° and 5.0° for color and face stimuli, respectively. We also estimate that subjects responded randomly in 2.6% and 4.1% of the trials, and that their responses matched the adaptor stimulus in 2.3% and 5.2% of the trials, with the remaining 95.1% and 90.8% concentrating around the target value (Fig. 3). These results confirm that the paradigm induced the typical *repulsive* after-effects, in which subject responses to target stimuli tend to be biased *away* from the preceding, adapting stimulus (Table 2).

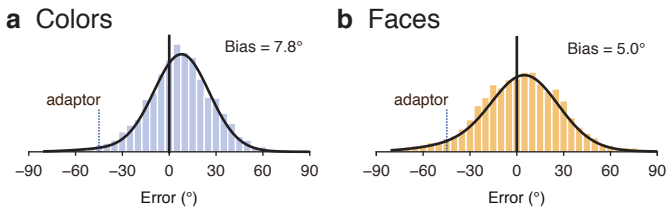

Figure 3: **Estimation of adaptation biases at the population level.** *(a)* Group adaptation results for all color trials. The bars provide the histogram of error (5° bins) in responses across all trials and all subjects in the adaptation experiment that used color stimuli. If subjects reported the color of the target stimulus perfectly, all trials would have zero error. Each trial in the adaptation experiment featured a five second adaptor stimulus, which in this plot has a relative location of −45° and is indicated with the blue dotted line. The black line shows the fit to the data provided by the model shown in Fig. 2b. As can be seen, the peak of the distribution of error responses is shifted to the right of zero, indicating that subjects had a bias ($M = 7.8°$) in reporting the value of the target stimulus. *(b)* Similar results for all face trials. As can be seen, the peak of the distribution of error responses is again shifted to the right of zero, indicating that subjects had a bias ($M = 5.0°$) in reporting the value of the target stimulus.

Individual differences in adaptation bias and representation precision are negatively correlated

We then fit the response bias data for each individual subject. We found that adaptation bias did not significantly differ between blocks (one-way ANOVA: $F(1, 806) = 0.0073$, $p = 0.93$), suggesting that the magnitude of adaptation biases is a stable individual characteristic for the duration of the experiment. For that reason, we collapsed subject data across both blocks of each experiment. We then performed a two-way

analysis of variance to identify the sources of variability in adaptation bias. We observed a significant effect of stimulus class ($F(1, 404) = 87.9$, $p \approx 0$), but this effect explained only 5% of the total variance. We also observed a significant effect of mean subject bias ($F(201, 404) = 3.72$, $p \approx 0$) accounting for 45% of the total variance, an effect greater than the 26% variance attributable to the difference between stimulus type across subjects (subject $\times$ stimulus, $F(201, 404) = 2.14$, $p \approx 0$). Accordingly, we observe that there is a correlation across subjects in their average face and color bias scores (Pearson's $r = 0.22$). The distribution of individual subject bias was well fit with a Gaussian with a mean of 8.0° for colors (95% CI $[0.2°, 18.8°]$) and 5.3° for faces (95% CI $[-4.9°, 17.1°]$). These results are consistent with an individual difference in adaptation bias that is present across face and color stimuli.

We next extracted the width (i.e., precision) of the error distribution for each subject, separately for each block of each experiment. Again, because precision did not significantly differ between blocks (one-way ANOVA: $F(1, 2420) = 0.4$, $p = 0.49$), we collapsed subject data across both blocks of each experiment. We then performed a three-way analysis of variance to identify the sources of variability in response precision. We observed a significant effect of individual variability ($F(201, 1006) = 2.84$, $p \approx 0$), of task type ($F(2, 1006) = 300.0$, $p \approx 0$), and of stimulus class ($F(1, 1006) = 586.6$, $p \approx 0$). Furthermore, we found that subject, task and stimulus all explained about the same variance (21%, 22%, and 21%, respectively). Response precision estimated from *stimulus-match* trials was well correlated with precision estimated from the *adaptation* experiment (color: $r = 0.44$; faces: $r = 0.45$; Fig. 4a,b).

We then asked if subjects with a lower representation precision are more or less prone to adaptation biases. We investigated the statistical relationship between average representation precision and adaptation bias, both estimated from the *adaptation* experiment. We observed that, across subjects, there was a negative correlation between mean precision and bias (Spearman's rank correlation, color: $\rho = -0.26$, 95% CI $[-0.28, -0.25]$; faces: $\rho = -0.13$, 95% CI $[-0.15, -0.12]$; Fig. 4c,d). This suggests that subjects with lower representation precision are subject to larger biases away from the adapting stimulus, in line with predictions from a Bayesian observer model.

Replication experiment

We wished to replicate the observed relationship between representation precision and adaptation bias with more trials per subject. An additional group of 472 people were recruited through Amazon Mechanical Turk. From this set, 89 were excluded or abandoned at the color vision test, and 191 during the main experimental trials, leaving 192 subjects for the replication analyses (Tables 3, 4). Subjects performed a slightly modified version of our experiment: two blocks of the *stimulus-match* experiment (30 trials), two

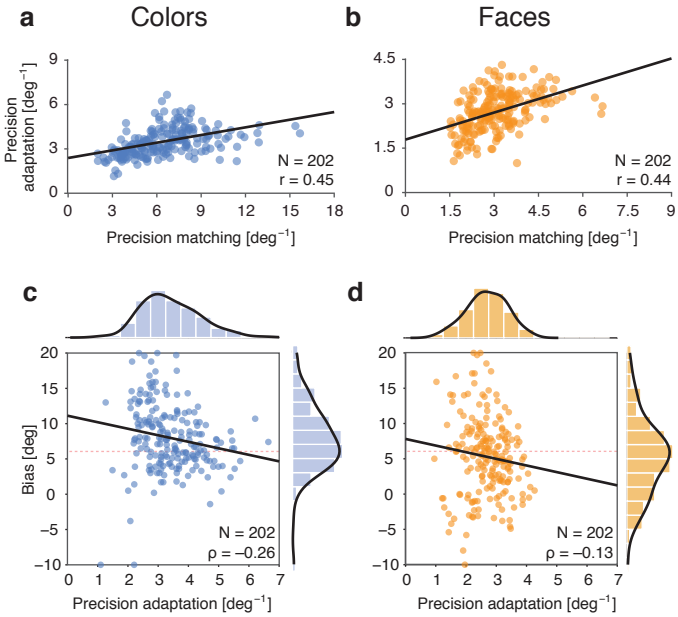

Figure 4: **Individual differences in representation precision are negatively correlated with adaptation bias.** *(a)* We fit data from each subject collapsed across both blocks of the color stimulus-match experiment and across both blocks of the color adaptation experiment, using the mixture model approach described in Fig. 2. The correlation between representation precision in both experiments was $r = 0.45$. *(b)* Similar to (a), for face stimuli. The correlation between representation precision in in the stimulus-match and adaptation experiments was $r = 0.44$. *(c)* We fit data from each subject collapsed across both blocks of the color adaptation experiment, using the mixture model approach described in Fig. 2. The Spearman's rank correlation coefficient between representation precision and adaptation bias was $\rho = 0.26$, 95% CI $[-0.28, -0.25]$. *(d)* Similar to (c), for face stimuli. The Spearman's rank correlation coefficient between representation precision and adaptation bias was $\rho = 0.13$, 95% CI $[-0.15, -0.12]$.

Table 3: **Subject enrollment and exclusion in the replication experiment with colors.** The total in the cells may not match the total number of subjects due to missing responses from some subjects.

Completed:	**Registration**	**Screening**	**Experiment**
Number of subjects	191	149	98
Age: $M \pm SD$	37 ± 12	37 ± 12	39 ± 12
Male/Female	110/81	87/62	60/38
Left/Right-handed	8/176	4/139	0/95

Table 4: **Subject enrollment and exclusion in the replication experiment with faces.** The total in the cells may not match the total number of subjects due to missing responses from some subjects.

Completed:	**Registration**	**Screening**	**Experiment**
Number of subjects	281	234	94
Age: $M \pm SD$	36 ± 12	37 ± 12	37 ± 12
Male/Female	164/117	134/100	48/46
Left/Right-handed	19/262	13/221	3/91

blocks of the *delayed-match* experiment (60 trials), and six blocks of the *adaptation* experiment (180 trials). Each subject performed the experiments for only one of the two stimulus classes (faces: 94 subjects; colors: 98 subjects; Fig. 5a). A slightly more saturated version of the stimuli was used in an attempt to increase overall performance (Fig. 5b,c).

After fitting the data using the same approach as previously (Fig. 2), we analyzed the sources of variability in response precision. In both color and face experiments, experimental block explained essentially no variation in response precision ($F(5, 866) = 1.69$, $p = 0.13$ and $F(5, 839) = 0.81$, $p = 0.54$ in the color and face experiments, respectively). In the color experiment, subject and task explained 27% and 19% of the total variance in precision scores, respectively ($F(96, 866) = 4.94$, $p \approx 0$ and $F(2, 839) = 162.5$, $p \approx 0$). In the face experiment, subject and task explained 40% and 16% of the total variance in precision scores, respectively ($F(93, 839) = 8.36$, $p \approx 0$ and $F(2, 839) = 157.4$, $p \approx 0$). We then analyzed the sources of variability in adaptation bias. In the color experiment, we observed that variability in adaptation bias was explained primarily by subject (44%) and secondarily by block (3%). In the face experiment, variability in adaptation bias was only significantly explained by subject (41%).

To investigate whether the inverse relationship between representation precision and adaptation biases was replicated, we extracted the bias and precision values for each subject, and calculated the correlation between these two quantities. We again observed that, across subjects, there was a negative correlation between mean precision and bias (color $\rho = -0.22$, 95% CI $[-0.25, -0.20]$; faces $\rho = -0.19$, 95% CI $[-0.22, -0.17]$; Fig. 5d,e).

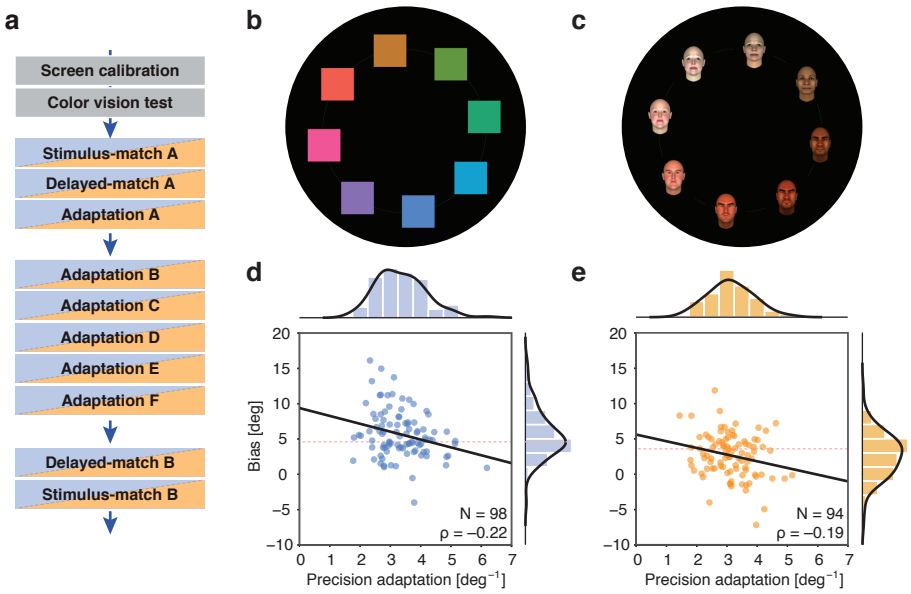

Figure 5: **Relationship between representation precision and adaptation bias in the replication experiment.** *(a)* Replication experiment structure. Subjects completed a battery of tests designed to estimate representation precision, precision after a delay, and precision and bias after adaptation. Each subject completed two blocks of the stimulus-match and the delayed-match experiments, and six blocks of the adaptation experiment, for either colors or faces. Prior to each experiment, subjects were presented with instructions and a comprehension quiz, and in the first time they performed each block of a given experiment, they also completed 5 practice trials. Each block of the stimulus-match experiment comprised 15 trials. Each block of the delayed-match and adaptation experiments comprised 30 trials. *(b)* Color stimuli. A circular space with 360 stimuli was used. Colors were generated to vary in hue but not in saturation or luminance (HSL space), though saturation was higher than in the first experiment. *(c)* Face stimuli. A circular space with 360 stimuli was used. Faces stimuli varied in age and gender, each forming one axis of the space. The extreme points on each axis also varied in identity, to maximize stimulus differences. *(d)* We fit data from each subject collapsed across all blocks of the color adaptation experiment, using the mixture model approach described in Fig. 2. The Spearman's rank correlation coefficient between representation precision and adaptation bias was $\rho = 0.22$, 95% CI $[-0.25, -0.20]$. *(e)* Similar to (d), for face stimuli. The Spearman's rank correlation coefficient between representation precision and adaptation bias was $\rho = 0.19$, 95% CI $[-0.22, -0.17]$.

Discussion

We investigated the relationship between individual differences in adaptation bias and response precision for colors and faces. In two cohorts of 202 and 192 subjects recruited through Amazon Mechanical Turk, precision and adaptation bias were found to be stable properties of the observer, with substantial variance in the measurements arising from between-subject differences. Across experiments and materials, we found that greater perceptual bias in an individual was associated with lower response precision.

A notable finding of our study was the substantial individual variation in the magnitude of perceptual adaptation. This measurement was reproducible across blocks within a testing session. As we did not measure across testing sessions, our measurement likely contains a component of state variation as well (although prior studies of individual variation in blur adaptation suggest this component is small; Vera-Diaz et al., 2010). The variation across individuals was roughly twice as large as the variation within subject across stimulus type (face and color). This indicates a stimulus-independent mechanism of variation in adaptation magnitude. We find that individual differences in sensory precision provide one such mechanism.

Our results are consistent with a model in which each subject is a Bayesian observer, each of whom differs in the fidelity with which they represent sensory input. We estimated each subject's precision by measuring response variability. A Bayesian interpretation assumes that response variability in turn reflects (to some degree) individual differences in the precision of sensory encoding. Although quite reproducible, the magnitude of correlation between response precision and adaptation bias was small (accounting for approximately 5% of between-subject variability in adaptation bias). Response precision is therefore an imperfect proxy for sensory precision, or other factors contribute to the substantial between-subject variation in the adaptation effect that is shared across stimulus types.

Consistent with previous theoretical and empirical work (Stocker and Simoncelli, 2006a; Schmack et al., 2016), our results indicate that the sensory prior is adjusted on every trial. This is because the circular stimulus space ensures that any systematic bias produced by non-uniform priors or asymmetric likelihoods on one trial is compensated by an equal and opposing bias on other trials. Instead, the effect of the adapting stimulus is to shift the prior to be centered on the recently viewed stimulus. When combined with a likelihood distribution that is centered at the test value yet asymmetric, the posterior mean contains the observed repulsive bias (Wei and Stocker, 2015).

We recruited subjects through the Amazon Mechanical Turk platform and conducted our experiments using a custom-built website. In addition to allowing a larger sample size, web-based experiments improve subject diversity (Woods et al., 2015). A major challenge of web-based data collection is that subjects may be motivated not to provide a high level of performance, but instead to complete the task as quickly

as possible to obtain payment. To meet this challenge, our on-line test was designed so that it would be completed most rapidly if the subject produced accurate responses. Additional measures to improve data quality included quizzes to ensure comprehension of the instructions and paying proportionally large bonuses for compliant subjects. While the exclusion of subjects with low accuracy limited the range of precision values we could have measured from our population, we regarded this as an acceptable compromise to exclude subjects who made no attempt to achieve the goals of the measurement.

Methods

Participants

A total of 1002 people were recruited through Amazon Mechanical Turk (Tables 1, 3, 4). This research was reviewed and deemed exempt from oversight by the University of Pennsylvania Institutional Review Board, and therefore informed consent was not collected. Information on the home page of the web-based experiment indicated the research nature of the project. No information that could identify participants was collected. All subjects received a fixed minimum compensation of $0.25 for their participation in addition to a performance-based bonus of up to $12.00. The full experiment took approximately 1 hour and 15 minutes for completion, and subjects that reached the end received a bonus of M=$7.68, SD=$0.51).

Stimuli and Materials

The experiment was programmed in Javascript language and hosted on a website which subjects accessed using their own computers (https://cfn.upenn.edu/iadapt). Stimuli consisted of synthetic faces generated with FaceGen Main SDK (Inversions, 2012) and colored squares.

The face set used in the initial experiment varied in age and gender. Two base stimuli were generated by varying the gender of an identity-neutral face from male to female, and another two base stimuli were generated by varying the age of an identity-neutral face from 15 to 65 years old. Based on these four stimuli, a set of 360 faces were generated in a circular space with main axes corresponding to age and gender.

The color set varied in hue with no nominal variation in lightness and saturation. A set of 360 color values were generated in HSL space with L^* held fixed at 25 and saturation equal to 7. This saturation value was determined in pilot experiments as producing stimuli with approximately equal salience to the face stimuli. The set of HSL value were then converted to sRGB space.

For the replication experiment, a new set of face and color stimuli was generated. The face stimuli were again generated based on four stimuli that varied on age (15-65 years old) and gender (male-female), but now also on identity, producing more distinctive faces than the previous set. The color stimuli were again generated in HSL space with L* held fixed at 25, but now with saturation equal to 20 (the maximum value that produced sRGB values within the 0-255 range displayable in regular monitors), producing more distinctive colors than in the initial experiment.

Experimental procedure

Subjects recruited through Mechanical Turk were redirected to the experiment website, where they entered their responses using their mouse and keyboards and, upon completion, received a randomly generated code which they entered again on Mechanical Turk for payment. Each experimental session started with a basic description of the procedures, followed by a demographics questionnaire. Subjects then completed a screen calibration procedure and a color perception test followed by the main experimental blocks.

In the screen calibration procedure, subjects were presented with a set of discrete color gradients, each ranging from black to a distinct, saturated color value. They were then asked to adjust the screen settings and/or the angle of their laptop screen to allow them to simultaneously distinguish between neighboring colors on both ends of the each gradient. In the color perception test, subjects completed eight trials of the Ishihara test, a test for congenital color deficiencies. Subjects proceeded to the main experimental blocks if at least seven responses were correct.

Subjects then completed 2-6 blocks of each of the following experiments: (i) *stimulus-match*; (ii) *delayed-match*; (iii) *adaptation* (Fig. 1a). Each block consisted of 15-30 trials (∼2-5 minutes) in which subjects were instructed to report the value of a target stimulus – a color or a face – by clicking and moving the mouse cursor around a stimulus wheel (Fig. 1b), allowing a fine adjustment of their responses. Prior to performing each type of experiment for the first time, subjects were presented with detailed instructions, a mini-quiz containing three questions with three alternatives each about the instructions, and five practice trials. If any answer to the quiz was incorrect, subjects were repeatedly presented with the instructions and asked to complete the quiz, until all three answers were simultaneously correct. Similarly, subjects repeated the practice experiment as many times as necessary until all five responses were within 5° of the target. Together, these approaches ensured comprehension of the experiment instructions, and that subjects were able to adequately perform the experiment on their computer.

Experimental blocks were completed in the following order: (1) color stimulus-match; (2) face stimulus-match; (3) color delayed-match; (4) face delayed-match; (5) color adaptation; (6) face adaptation; (7) color delayed-match; (8) face delayed-match; (9) color adaptation; (10) face adaptation; (11) color stimulus-match; (12) face stimulus-match (Fig. 1a). In the replication dataset, blocks (only one stimulus class) were completed in the following order: (1) stimulus-match; (2) delayed-match; (3-8) adaptation; (9) delayed-match; (10) stimulus-match (Fig. 5a).

We calculated subject accuracy on every trial (0%: chance; 100%: perfect) and, at the end of each block, we calculated the average accuracy for that block. The compensation accumulated by subjects increased at the end of each experimental block by an amount proportional to the average accuracy. Subjects were then

presented with their average accuracy in the finished block, the corresponding dollar amount accumulated, and the total compensation accumulated in the experimental session up to that point. If the accuracy on any block ended up below 20%, the session was terminated and subjects were directed back to Amazon Mechanical Turk to receive their payment. Only subjects who maintained accuracy above 20% in all blocks were able to reach the end of the experiment. Those subjects received twice the regular compensation. Out of the 1002 subjects recruited, 197 were excluded for either abandoning or not passing the color perception test, and 411 for not maintaining accuracy above 20% throughout the entire session. Only data from the remaining 394 subjects were included in the analyses described in this paper (Tables 1, 3, 4).

Stimulus-match experiment

Each block consisted of 15 trials, with target values sampled uniformly (24° spacing) from the circular space. On each trial, subjects were presented with a target stimulus on both left and right sides of the black background screen, along with a stimulus wheel containing eight thumbnails with representative stimuli from the circular space (Fig. 1c, Top). The specific thumbnails, their position, and the mapping of stimulus value to screen position, varied randomly on each trial. Subjects were instructed to click once with the cursor positioned on the region of the screen corresponding to the target location. The selected stimulus was then presented in the center of the screen, and subjects were allowed to fine-tune their response by moving the cursor around the stimulus wheel before confirming their selection with a second mouse click (Fig. 1b).

During the fine-tuning phase, the stimulus presented in the center of the screen varied (in steps of 1°), to allow subjects to precisely match their responses to the target stimulus. The second (confirmation) click was registered only if it occurred within 2-10 seconds after the trial onset. If no response was entered for 10 seconds, a dialog box was displayed warning the subject to pay attention and click the OK button to continue. On these trials, an accuracy of 0% was registered (for the purpose of calculating the average block accuracy), though they were not included in the main analyses. Similarly, if responses were more than 90° away from the target, a dialog box was displayed warning the subject to pay attention and click the OK button to continue. These measures ensured that subjects maintained continuous attention throughout the entire block and slowed down subjects who attempted to rush through the experiment without care.

Delayed-match experiment

Each block consisted of 30 trials, with target values sampled uniformly (12° spacing) from the circular space. On each trial, subjects were presented with a target stimulus in the center of the screen for 2000 ms,

followed by a mask stimulus (ISI: 500 ms) at the same location for 200 ms, followed by a 4000 ms interval of a blank screen during which no response was allowed (Fig. 1c, Middle). After this interval, subjects entered their responses using the same procedure described previously (Fig. 1b). The same measures described previously were used to ensure that subjects maintained continuous attention throughout the entire block.

Color masks were checkerboards composed of various colors randomly sampled from within the stimulus set. Face masks were created using the steerable pyramids method, which are modifications of the original face stimuli that retain many low-level visual properties (Portilla and Simoncelli, 2000; Fig. 1d).

Adaptation experiment

Each block consisted of 30 trials, with target values sampled uniformly (12° spacing) from the circular space. On each trial, subjects were presented with an adaptor stimulus in the center of the screen for 5000 ms, immediately followed by a mask stimulus at the same location for 100 ms, by target stimulus for 200 ms (ISI: 50 ms), and by a 100 ms interval of a blank screen during which no response was allowed (Fig. 1c, Bottom). After this interval, subjects entered their responses using the same procedure described previously was used (Fig. 1b). In addition to measures to ensure attention described previously, subjects also received a warning if their responses were within 10° from the adaptor position. In these cases, a dialog box was presented indicating that subjects should ignore the adaptor and report the value of the target, and click the OK button to continue.

Data analysis

We used methods for circular data (Fisher, 1995). We calculated the error on each trial as the angular deviation on the stimulus wheel between the target value and the response entered. We then used maximum likelihood estimation to fit the distribution of error values in the circular space. In both stimulus-match and delayed-match experiments, the distribution of error values was decomposed into two parameters that represent a mixture of a uniform distribution (corresponding to random responses) and a von Mises distribution – the circular analog of the normal distribution on a line – centered on the target value. The parameters fit by this procedure correspond to the probability of guesses, which is inversely related to the height of the uniform distribution, and the precision of responses, which is the inverse of the standard deviation of the von Mises distribution (Fig. 2a).

In the adaptation experiment, the distribution of error values was decomposed into four parameters that represent a mixture of a uniform distribution (corresponding to random responses), a von Mises distribution centered on the adaptor value (corresponding to responses where the subject mistakenly attempts to report

the value of the adaptor), and a von Mises distribution with equal concentration parameter centered *near* the target value. The parameters fit by this procedure correspond to the probability of guesses, the precision of responses, which is the inverse of the standard deviation of the von Mises distributions, and the bias, which is the mean of the von Mises distribution centered near the target value (Fig. 2a).

References

Anstis, S., Verstraten, F. A., and Mather, G. (1998). The motion aftereffect. *Trends in cognitive sciences*, 2(3):111–117.

Bar, M. (2004). Visual objects in context. *Nature Reviews Neuroscience*, 5(8):617–629.

Bayes, M. and Price, M. (1763). An essay towards solving a problem in the doctrine of chances. by the late rev. mr. bayes, frs communicated by mr. price, in a letter to john canton, amfrs. *Philosophical Transactions (1683-1775)*, pages 370–418.

Bays, P. M., Catalao, R. F., and Husain, M. (2009). The precision of visual working memory is set by allocation of a shared resource. *Journal of vision*, 9(10):7–7.

Clifford, C. W. (2002). Perceptual adaptation: motion parallels orientation. *Trends in cognitive sciences*, 6(3):136–143.

Eagleman, D. M. (2001). Visual illusions and neurobiology. *Nature Reviews Neuroscience*, 2(12):920–926.

Fischer, J. and Whitney, D. (2014). Serial dependence in visual perception. *Nature neuroscience*, 17(5):738.

Fisher, N. I. (1995). *Statistical analysis of circular data*. Cambridge University Press.

Gibson, J. J. and Radner, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. i. quantitative studies. *Journal of Experimental Psychology*, 20(5):453.

Inversions, S. (2012). Facegen. *Singular Inversions*.

Ishihara, S. (1960). *Tests for colour-blindness*. Kanehara Shuppan Company.

Jameson, D. and Hurvich, L. M. (1972). Color adaptation: Sensitivity, contrast, after-images. In *Visual psychophysics*, pages 568–581. Springer.

Jammalamadaka, S. R. and Sengupta, A. (2001). *Topics in circular statistics*, volume 5. World Scientific.

Knill, D. C. and Richards, W. (1996). *Perception as Bayesian inference*. Cambridge University Press.

Lafer-Sousa, R., Hermann, K. L., and Conway, B. R. (2015). Striking individual differences in color perception uncovered by the dress photograph. *Current Biology*, 25(13):R545–R546.

Levinson, E. and Sekuler, R. (1976). Adaptation alters perceived direction of motion. *Vision research*, 16(7):779IN7–781.

Little, A. C., DeBruine, L. M., and Jones, B. C. (2005). Sex-contingent face after-effects suggest distinct neural populations code male and female faces. *Proceedings of the Royal Society of London B: Biological Sciences*, 272(1578):2283–2287.

Mattar, M. G., Kahn, D. A., Thompson-Schill, S. L., and Aguirre, G. K. (2016). Varying timescales of stimulus integration unite neural adaptation and prototype formation. *Current Biology*.

Olkkonen, M., McCarthy, P. F., and Allred, S. R. (2014). The central tendency bias in color perception: Effects of internal and external noise. *Journal of vision*, 14(11):5–5.

Portilla, J. and Simoncelli, E. P. (2000). A parametric texture model based on joint statistics of complex wavelet coefficients. *International journal of computer vision*, 40(1):49–70.

Schmack, K., Weilnhammer, V., Heinzle, J., Stephan, K. E., and Sterzer, P. (2016). Learning what to see in a changing world. *Frontiers in human neuroscience*, 10:263.

Stocker, A. and Simoncelli, E. P. (2006a). Sensory adaptation within a bayesian framework for perception. *Advances in neural information processing systems*, 18:1289.

Stocker, A. A. and Simoncelli, E. P. (2006b). Noise characteristics and prior expectations in human visual speed perception. *Nature neuroscience*, 9(4):578–585.

Summerfield, C. and Egner, T. (2009). Expectation (and attention) in visual cognition. *Trends in cognitive sciences*, 13(9):403–409.

Vera-Diaz, F. A., Woods, R. L., and Peli, E. (2010). Shape and individual variability of the blur adaptation curve. *Vision Research*, 50(15):1452–1461.

von Helmholtz, H. (1867). Treatise on physiological optics vol. iii.

Webster, M. A., Kaping, D., Mizokami, Y., and Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, 428(6982):557–561.

Wei, X.-X. and Stocker, A. A. (2015). A bayesian observer model constrained by efficient coding can explain'anti-bayesian'percepts. *Nature neuroscience*, 18(10):1509–1517.

Woods, A. T., Velasco, C., Levitan, C. A., Wan, X., and Spence, C. (2015). Conducting perception research over the internet: a tutorial review. *PeerJ*, 3:e1058.

Zhang, W. and Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, 453(7192):233–235.

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Conceptualization, M.G.M., G.K.A., and S.L.T.-S.; Methodology, M.G.M. and G.K.A.; Software and Formal Analysis, M.G.M., M.C., and M.Z.; Visualization, M.G.M. and G.K.A.; Supervision, G.K.A. and S.L.T.-S.; Writing – Original Draft, M.G.M. and G.K.A.; Writing – Review Editing, M.G.M., G.K.A., and S.L.T.-S.; Funding Acquisition, G.K.A. and S.L.T.-S.

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