Confidence-dependent Accumulation of Past Decision Variables Biases Perceptual Choice

Anke Braun[1, *], Anne E. Urai[1,2], Tobias H. Donner[1, 2, 3, *]

[1]Department of Neurophysiology and Pathophysiology, University Medical Center Hamburg-Eppendorf, 20246 Hamburg, Germany. [2]Department of Psychology and [3]Amsterdam Brain and Cognition (ABC), University of Amsterdam, 1018 WS Amsterdam, The Netherlands

*Correspondence: a.braun@uke.de, t.donner@uke.de

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Abstract

Perceptual decision-making is biased by previous events, including the history of preceding choices: Observers tend to repeat (or alternate) their choices more often than expected by chance. Here, we find that such sequential choice biases result from the accumulation of action-independent, internal decision variables. Human observers performed different variants of a visual motion discrimination task around psychophysical threshold. First, we decoupled perceptual choices and motor responses on a trial-by-trial basis, to disentangle their relative contributions to sequential biases. The impact of previous choices outweighed the impact of previous motor responses and previous stimuli. Second, observers performed the task in both random and biased environments (containing systematic tendencies towards either repetition or alternation of motion directions) and in the absence of external feedback about the correctness of their choices. Observers adapted their sequential choice biases to the biased environmental statistics, in a way that indicated memory for previous choices and predicted their overall performance. We further found that this adaptation was enhanced by the confidence about the correctness of previous choices, consistent with the idea that decision variables driving choice encode both the categorical choice, as well as the graded confidence associated with it. Thus, our results are consistent with the idea that high-level decision variables, dissociable from both, sensory input and motor output, are accumulated across choices towards biases for upcoming choices. These insights constrain the candidate neural sources of sequential choice biases.

Significance statement:

Studies of perceptual decision-making show that participants' choices are often influenced by the history of their preceding choices. This manifests as a bias to repeat (or alternate) choices more often than expected by chance. We found that such history biases in perceptual choice arise from the accumulation of internal signals referred to as decision variables. These decision variables encode the observers' categorical perceptual choice, they are dissociable from both, sensory input and motor output, and they are modulated by decision confidence. This accumulation of decision variables helps adapt choice behavior to the temporal structure of sensory environments, thus boosting overall performance.

Introduction

Organisms' judgments about their environment do not only depend on the current sensory input, but are systematically biased by the history of preceding choices and stimuli (Fründ et al., 2014). Several studies have found that observers repeat (or alternate) their perceptual choices more often than expected by chance (Fernberger, 1920; Gold et al., 2008; de Lange et al., 2013; Akaishi et al., 2014; Fischer and Whitney, 2014; Abrahamyan et al., 2016; Pape and Siegel, 2016; St. John-Saaltink et al., 2016; Fritsche et al., 2017; Urai et al., 2017). Such sequential biases are ubiquitous across domains of decision-making (Leopold et al., 2002; Allefeld et al., 2013; Padoa-Schioppa, 2013).

One idea holds that sequential choice biases result from accumulation of environmental states across decisions. Computational models postulate that sequential choice biases result from the accumulation of decision-related neural signals (Glaze et al., 2015; Bonaiuto et al., 2016). In that way, observers may update their prior beliefs about the next stimulus and can adapt behavior to their environment (Yu and Cohen, 2009; Glaze et al., 2015). In standard perceptual choice tasks used in the laboratory, stimulus sequences are typically uncorrelated. In this context, sequential biases in observers' choices degrade their performance (Abrahamyan et al., 2016). However, more recent studies introduced perceptual choice tasks with correlated stimulus sequences (Goldfarb et al., 2012; Glaze et al., 2015; Abrahamyan et al., 2016; Kim et al., 2017). Here, sequential biases should improve performance.

Real-life decisions are often associated with uncertainty about their outcome, due to weak evidence and the absence of immediate feedback. Then, decision-makers can only accumulate their own inferences about the state of the environment. These inferences are encoded in the so-called 'decision variable', on which decision-makers base their categorical choices (Bogacz et al., 2006; Gold and Shadlen, 2007). Neural correlates of the decision variable are distributed across many brain regions (Gold and Shadlen, 2007; Siegel et al., 2011; Brody and Hanks, 2016). They are expressed as evolving motor plans (Gold and Shadlen, 2007; Donner et al., 2009; de Lange et al., 2013) as well as in action-independent formats (Bennur and Gold, 2011; Hebart et al., 2012, 2016; O'Connell et al., 2012). Decision variables not only reflect the categorical choice but also the observer's confidence about the correctness of that choice, henceforth referred to as decision confidence (Kiani and Shadlen, 2009; Hebart et al., 2016).

These considerations raise a number of questions. Do sequential biases emerge from the accumulation of decision variables in motor or action-independent formats? Does this accumulation help to adapt sequential biases to the statistical structure of the evidence? Does the strength of such adaptation depend on decision confidence? The latter might be particularly important under conditions, in which no unambiguous external feedback about the true stimulus category is available. Here, we addressed these issues in a visual motion discrimination task widely used in the neurobiology of choice (Gold and Shadlen, 2007). To this end, we systematically modeled human choice behavior under experimental manipulations tailored to address the above questions.

Materials and Methods

We report results from two experiments (referred to as Experiment 1 and 2) quantifying sequential biases during a random dot motion discrimination (up vs. down) task widely used in monkey (Gold and Shadlen, 2007) and human (Donner et al., 2009; de Lange et al., 2013; Kelly and O'Connell, 2013; Hebart et al., 2016) work on perceptual choice. Analyses of behavior irrespective of sequential effects from Experiment 1 were previously published (Tsetsos et al., 2015). Here, we re-analyzed these data to quantify the dependence of choice on previous stimuli, choices, and motor responses. The two experiments aimed at manipulating on different aspects of choice behavior, and thus used different variants of the basic random dot motion task. We used variants of the same statistical approach (Fründ et al., 2014) to model sequential biases in both.

Participants

Six healthy human observers (2 males, mean age: 25; range: 22–29 years) participated in Experiment 1, which was approved by the ethics committee of the Department of Psychology of the University of Amsterdam (reference number 2011-OP-1588). 26 healthy observers (15 female, mean age: 26, range: 20 - 36) participated in Experiment 2, which was approved by the local ethical review board (Ärztekammer Hamburg, reference number PV4714). Four participants were excluded from the data analysis: Three of those did not complete all sessions and one exhibited substantially worse performance than the rest of the group (64 percent correct overall, and 63 percent correct for the

easiest trials (averaged across the three levels with highest motion coherence)). 22 participants remained for the data analysis. All observers gave their written informed consent.

Experimental design

Experiment 1

The following description summarizes the aspects of the experimental design that were most important to current paper; a comprehensive description can be found in our previous paper (Tsetsos et al., 2015). Random dot kinematograms (Figure 1A) were composed of 785 (average) white dots on a black screen. The dots were moving within a circle of 9.1° diameter. A red fixation cross of 0.4° x 0.4° was centered in the middle of the circle. The dot density was 12.07 dots per deg^2. The population of dots was split into “signal dots” and “noise dots”. The signal dots moved either upwards or downwards with a velocity of 2.6°/s. The noise dots changed position randomly from frame to frame. The percentage of signal dots defined the motion coherence, a measure of motion strength. On each trial, three different sequences of dot motion (at the same coherence and direction) were presented in an interleaved fashion, making the effective speed of signal dots 0.87 °/s. Further, one of six different levels of motion coherence, (0.05, 1.26, 3.15, 7.92, 19.91 and 50%) and one of six different viewing durations (150, 300, 600, 1200, 2400, and 4800 ms) were chosen randomly, under the constraint that they occurred equally often within a block of 144 trials. Stimuli were presented on a 22-inch CRT monitor with a resolution of 800 x 600 pixel and a frame rate of 100 Hz at a viewing distance of 68 cm. The participants were instructed to maintain their gaze on the red cross throughout the trial and judge the net motion direction. The motion viewing interval was followed by a variable delay (uniform distribution ranging from 200 to 400 ms), after which the observers had to report their choice by pressing one of two buttons on a computer keyboard, with either the left or the right index finger. Participants received auditory feedback after incorrect responses (a 1000 Hz tone of 100 ms). Perceptual choices (‘up’ vs. ‘down’ motion direction) were decoupled from motor responses (left vs. right button press) by varying their mapping from trial to trial. This mapping was instructed before motion viewing in one condition (‘Pre’ condition) and after motion viewing in the other (‘Post’), by means of a visual cue that mapped each of the two possible net motion directions (presented as arrows) onto the left or right side. This mapping was randomly selected on each trial. Conditions

alternated across blocks. Observer 1-5 participated in both conditions. Participant 6 participated only in the Post condition. We pooled the data from participants 1-5 across both conditions.

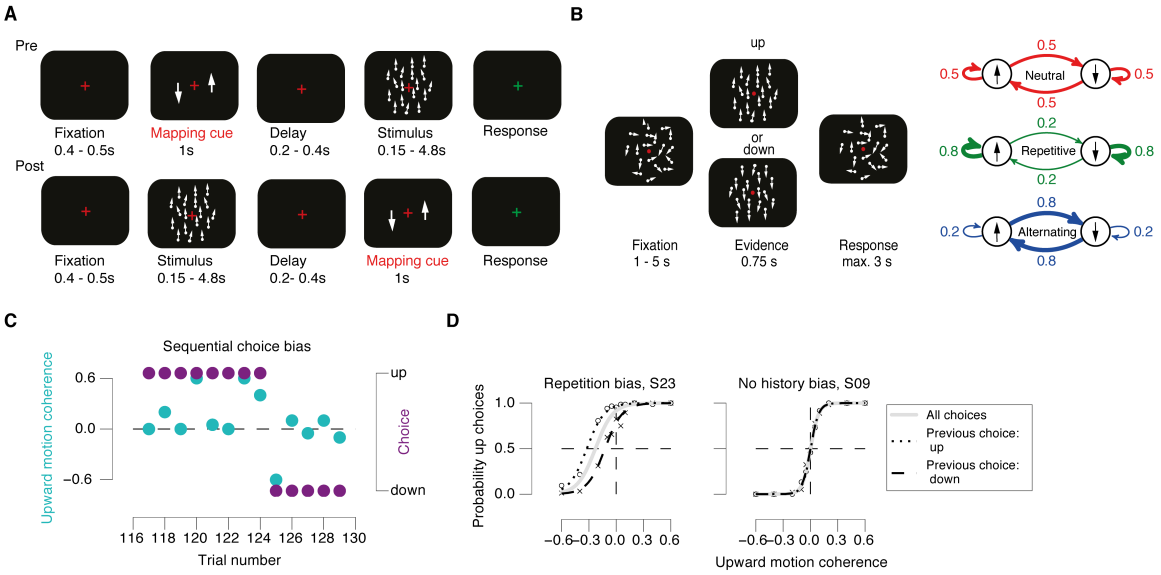

Figure 1. Quantifying sequential choice bias and behavioral task.

(**A**), (**B**) Behavioral task protocols. In all experiments presented here, the net direction and motion coherence of a dynamic random dot pattern varied from trial to trial, and observers were asked to judge the net direction ("up" vs "down"). (**A**) Experiment 1. Random dot motion task with variable decision-response mapping. At the beginning of each trial a red fixation cross was shown for 0.4 – 0.5s. A decision-response cue was shown for 1s before the presentation of the stimulus in the Pre condition and after stimulus presentation in the Post condition. Six different durations of the stimulus presentation ranging from 0.15s to 4.8s were used. In both conditions the presentations of the mapping cue (instructing the mapping between choice and motor response) and of the stimulus were separated by a delay of 0.2 – 0.4s, in which the fixation cross was shown. Participants were instructed to respond after stimulus presentation in the Pre condition and after the presentation of the mapping cue in the Post condition. Auditory feedback was given after incorrect responses. (**B**) Experiment 2. Top: Random dot motion and a red fixation cross were shown throughout the task. Each trial started with a fixation interval of 1-5s. A beep indicated the onset of the decision interval, in which a coherent motion signal of dots moving either upwards or downwards was shown for 0.75s. A second beep indicated the offset of the evidence and the onset of the response interval, which ended as soon as the participant pressed one of two buttons to state their decision or after 3s in case no response was given. Bottom: Three different manipulations of the repetition probability between stimulus directions were used across different sessions, resulting in a Neutral condition (random stimulus sequence with repetition probability of 0.5), a Repetitive condition (stimulus repetition probability of 0.8) and an Alternating condition (stimulus repetition probability of 0.2). (**C**) Local streaks of repeated choices in the face of ambiguous or weak evidence of opposite sign (example observer from Experiment 2). (**D**) Psychometric functions of two example participants from Experiment 2 conditioned on previous choice. Positive values of stimulus intensity correspond to upward motion and negative ones to downward motion. The dotted line referred to previous 'up 'choices (i.e., choice repetitions) and the dashed curve to previous 'down' choices (i.e., choice alternations). Left: Leftward shift from dashed to dotted line, indicating a bias to repeat the previous choice. Middle: Overlap of dashed and dotted curves, indicating absence of sequential bias. Gray line, psychometric function computed based on all trials, irrespective of previous choice.

Experiment 2

To test for the adaptability of sequential choice biases, we manipulated the sequential stimulus statistics between experimental sessions, to make people perform the task in 'Repetitive', 'Neutral' (no sequential dependence), or 'Alternating' environments. Stimuli, task, and procedure for Experiment 2 were identical to Experiment 1, with the following exceptions (Figure 1B). The circle within which the dots were moving had an outer radius of 12° and an inner radius of 2°. The density of dots was 1.7 dots/deg^2 and each dot had a diameter of 0.2°. The dots moved with a velocity of 11.5°/s and each dot had a lifetime of 6 frames. We used the following coherence levels: 0, 5, 10, 20, 40 and 60% (equally many trials per coherence level). A red bulls-eye fixation target (Thaler et al., 2013) at the center of the screen as well as randomly moving dots (0% coherence) were presented throughout each block. The first trial of each block started with a baseline interval of 5 s, with random dot motion. A beep (duration: 50 ms, sine wave at 440 Hz) indicated the onset of the motion-viewing interval with a fixed duration of 0.75 s and variable coherence levels and directions (see above). A second beep indicated the offset of the motion-viewing interval and prompted the observers' response. Observers reported their perceptual choices by pressing one of two keyboard buttons, with the index finger of the left or right hand. After button press (or a response deadline of 3 s), the inter-trial interval started. Inter-trial intervals were uniformly distributed between 1 and 5 s. Observers received auditory feedback during the training sessions, but no feedback during the subsequent six sessions of the main experiment. The motion viewing duration of 0.75 s was selected because a previous human study found little integration of motion information beyond that duration (Tsetsos et al., 2015), similar to what had been observed in monkeys (Kiani et al., 2008). We used a fixed mapping between choices and motor responses, whereby the two possible mappings (right-hand button for up, left-hand for down, or vice versa) were counterbalanced across observers. Experiment 2 consisted of seven sessions per participant (one for training and six main sessions), whereby each session was divided into 10 blocks of 60 trials.

Critically, the transition probabilities (over trials) between the two alternative motion directions (i.e. up vs. down) were manipulated across experimental sessions (Figure 1B, right). Specifically, the probability of a repetition of motion directions (regardless of their identity) was defined as

$$P(stimulus\ repetition) = 1 - P(stimulus\ alternation) = P(stimulus_n = up \mid stimulus_{n-1} = up) = P(stimulus_n = down \mid stimulus_{n-1} = down), \quad \text{eq. 1}$$

whereby *n* indexes trials. This repetition probability was held constant within each session, but varied across the main experimental sessions between the following values: 0.5 in the 'Neutral' condition, 0.8 in the 'Repetitive' condition, and 0.2 in the 'Alternating' condition. The Neutral condition allowed for quantifying observers' intrinsic sequential choice bias, which we used as a baseline for quantifying their adaptation to the biased sequential statistics of the Repetitive and Alternating conditions.

During the training session, the motion direction on each trial was chosen randomly and independently, and all participants started with the 'Neutral' condition in session 1 of the main experiment (which was repeated in session 4). Half of the participants then performed the Repetitive condition in sessions 2 and 5, and the Alternating condition in sessions 3 and 6. For the other half of participants, the order of the Repetitive and Alternating conditions was flipped.

Observers were instructed to maintain stable fixation and perform the motion discrimination task as accurately as possible. They were informed that the sequential statistics of the stimulus identities would change from session to session, but stay constant within each session. Specifically, they were informed that the stimulus sequences could be 'like produced by a coin flip' (Neutral condition), 'more likely repeating than alternating' (Repetitive condition), or 'more likely alternating than repeating' (Alternating condition). Observers were neither informed about the order of these conditions, nor about the exact transition probabilities, nor about the use of this information for their choice behavior.

Modeling sequential choice bias

We used logistic regression (Fründ et al., 2014; Urai et al., 2017) to model observers' sequential choice biases under the different experimental conditions assessed here. The basic approach consisted of adding a linear combination of different components of trial history (which depended on the experiment), as a bias term to a logistic function model of the choice probability. Another variant of this approach estimates the effect of previous choices, contingent on their success or failure (Busse et al., 2011; Abrahamyan et al., 2016). We here used a variant that quantified the relative contributions of previous stimuli, choices, and (for Experiment 1) motor responses. We also assessed the effect of previous correct vs. incorrect choices, by re-combining the weights for previous stimuli and choices

(Fründ et al., 2014), and the modulation of choice weights by reaction time (for Experiment 2).

Standard psychometric function fit

The probability of making one of the two choices $r_t = 1$ ($r_t = 1$ for 'choice up', $r_t = -1$ for 'choice down') on trial t, given the signed stimulus intensity $\tilde{s_t}$ (i.e., motion coherence times direction) was described by:

$$P(r_t = 1|\tilde{s_t}) = \gamma + \left(1 - \gamma - \lambda\right) g(\delta + \alpha\tilde{s_t}). \qquad \text{eq. 2}$$

γ and λ were the lapse rates for the choices $r_t = 1$ and $r_t = -1$, and $g(x) = \frac{1}{1+e^{-x}}$ was the logistic function. The bias term δ, the offset of the psychometric function, described the overall bias for one specific choice. α was the slope of the stimulus-dependent part of the psychometric function, describing perceptual sensitivity.

For visualizing the effect of previous on current choice (Figure 1D), we separated the data from the Neutral condition into two groups, conditioned on the choice from the previous trial, and fitted the psychometric function, i.e. the probability of upward choices, separately for each of the two conditions. Results from two example observers are shown in Figure 1D. The first example observer (left panel) showed a sequential bias towards repeating choices, evident as a rightward shift of the dashed compared to the dotted line. The second observer (right panel) exhibited no sequential choice bias.

Psychometric function fit with history contributions for stimulus and choice

We estimated the contribution of the recent seven stimuli and choices by adding a history-dependent bias term to the argument of the logistic function (Fründ et al., 2014):

$$P(r_t = 1|\tilde{s_t}, \boldsymbol{h_t}) = \gamma + \left(1 - \gamma - \lambda\right) g(\delta(\boldsymbol{h_t}) + \alpha\tilde{s_t}) \qquad \text{eq. 3}$$

$$\delta(\boldsymbol{h_t}) = \delta' + \delta_{\text{hist}}(\boldsymbol{h_t}) = \delta' + \sum_{k=1}^{14} \omega_k h_{kt} \qquad \text{eq. 4}$$

The history bias $\delta_{\text{hist}}(\boldsymbol{h_t}) = \sum_{k=1}^{14} \omega_k h_{kt}$ consisted of the sum of the preceding seven responses r_{t-1} to r_{t-7} and the preceding seven stimulus identities (i.e., motion directions) z_{t-1} to z_{t-7}, each multiplied with a weighting factor ω_k. The vector $\boldsymbol{h}_t$ was written as:

$$\boldsymbol{h}_t = (r_{t-1}, r_{t-2}, r_{t-3}, r_{t-4}, r_{t-5}, r_{t-6}, r_{t-7}, z_{t-1}, z_{t-2}, z_{t-3}, z_{t-4}, z_{t-5}, z_{t-6}, z_{t-7}).$$

All terms in $\boldsymbol{h}_t$ were coded as -1 or 1, with the exception of terms coding for stimuli with zero coherence, which were set to zero. The weighting factors ω_k thus modeled the influence of each of the

seven preceding responses and stimulus identities on the current choice. All weights were estimated with the same procedure as described previously (Fründ et al., 2014; Urai et al., 2017). Specifically, every set of seven past trials was convolved with three orthogonalised, exponentially decaying basis functions (with decay constants 0, 0.5 and 0.25), reducing the number of estimated parameters from 7 to 3 for each history feature. The estimated coefficients were then multiplied with their basis functions, resulting in the full 7-lag kernels shown.

Positive values of ω_k described a bias to repeat the preceding response or stimulus identity at the corresponding lag, and negative values of ω_k described a bias to alternate the preceding response or stimulus identity. Response and stimulus weights added up to the weights for preceding correct responses and the difference between response and stimulus weights resulted in the weights for preceding incorrect responses.

Psychometric function fit with history contributions for stimulus, choice, and motor response

In Experiment 1, perceptual choices and motor responses were decoupled through a mapping that varied from trial to trial. Thus, we could independently estimate the relative contribution of previous choices and motor responses to the current choice bias. We added the last seven choices $c_{t-1}, c_{t-2}, c_{t-3}, c_{t-4}, c_{t-5}, c_{t-6}, c_{t-7}$, each one multiplied with a separate set of history weights ω'_k, to the history bias term $\delta_{\text{hist}}(\boldsymbol{h_t}, \boldsymbol{c_t})$.

$$\delta(\boldsymbol{h_t}, \boldsymbol{c_t}) = \delta' + \delta_{\text{hist}}(\boldsymbol{h_t}, \boldsymbol{c_t}) = \delta' + \sum_{k=1}^{14} \omega_k h_{kt} + \sum_{k=1}^{7} \omega'_k c_{kt} \qquad \text{eq. 5}$$

We performed this analysis in two stages. First, we fitted the psychometric functions separately for each of the six different motion-viewing durations (on the current trial) and compared the resulting weights within each observer. The viewing duration had only negligible impact on the history weights (data not shown), indicating that the history contributions were invariant across viewing durations. Second, we fitted the psychometric functions to the data from all trials irrespective of viewing duration. Group level statistical tests were computed across the six observers, based on the mean weights irrespective of viewing durations. The corresponding weights are presented in Results.

Psychometric function fit with modulation of sequential bias by reaction time

In order to investigate the impact of decision confidence on sequential bias, we added a modulation by

reaction time (Urai et al., 2017). Specifically, we extended the model from equation 3 by a term describing the interaction between previous choices and stimuli with previous reaction times $\sum_{k=1}^{14} \omega'_k h_t rt_{kt}$ and a nuisance covariate $\sum_{k=1}^{7} \omega''_k rt_{kt}$:

$$\delta(\boldsymbol{h_t}, \boldsymbol{rt_t}) = \delta' + \delta_{\text{hist}}(\boldsymbol{h_t}, \boldsymbol{rt_t}) = \delta' + \sum_{k=1}^{14} \omega_k h_{kt} + \omega'_k h_{kt} rt_{kt} + \sum_{k=1}^{7} \omega''_k rt_{kt} \qquad \text{eq. 6}$$

with $rt_{kt} = (rt_{t-1}, rt_{t-2}, rt_{t-3}, rt_{t-4}, rt_{t-5}, rt_{t-6}, rt_{t-7})$ the vector of the log-transformed and then z-scored (within participant), reaction times of the preceding seven trials.

In all cases, the parameters $\alpha, \gamma, \lambda, \delta', v$ and the history weights ω_k, ω'_k and ω''_k were determined by maximizing the log-likelihood $L = \sum_t \log P(r_t = 1 | \tilde{s_t}, \boldsymbol{h_t})$ using an expectation maximization algorithm (Fründ et al., 2014).

Statistical analysis

We used t-tests and permutation tests (Efron and Tibshirani, 1986) for all statistical comparisons reported in this paper. In particular, we used the following procedure to test the statistical significance of the history weights as function of previous trials (lags). First, a simple t-test was used to determine if the weights at each lag were significantly different from zero and a paired t-test was used to determine if choice and response weights (Experiment 1), or weights for the two biased conditions (Experiment 2), respectively, were significantly different. Second, false discovery rate correction (Benjamini and Hochberg, 1995) was applied to correct for multiple comparisons across the 7 lags.

The following comparisons were performed using a paired permutation test (N = 10.000 permutations): (i) individual vectors (i.e., vector lengths, and orientations) pointing from the Neutral to each of the two biased conditions; (ii) correlations between individual 'stimulus kernels' from each of the biased conditions and the two 'history templates' (see below); (iii) previous correct versus error weights; and (iv) previous correct versus previous RT*correct weights.

The following correlations were determined using Pearson correlation: (i) correlation between individual previous choice weights and performance; (ii) correlation between the correlation of stimulus kernels with history template and performance.

Lastly, we used Rayleigh's test to assess the clustering of angles in 'adaptation space' (Figure 3B) in both the Repetitive and Alternating conditions, and a Watson-Williams test to assess the difference in mean directions of adaptation between these two conditions (Berens, 2009).

Results

We here use the term 'sequential choice bias' to describe the tendency to repeat, or alternate, previous choices more often than expected by chance. Figure 1C and D illustrate this for example observers from Experiment 2. Figure 1C shows, for one observer, a 'streak' of eight repeats of the same choice, followed by five repeats of the alternative. These streaks occur in the face of trial-to-trial variations of the direction and strength of the random dot motion stimuli. Figure 1D summarizes local choice biases in terms of the psychometric function conditioned on previous choice. The corresponding shifts between the two functions distinguish observers with repetition bias (left panel) and no bias (right). These shifts are only evident under consideration of the sequence of previous choices. Thus, they are distinct from the overall (frequency) bias towards one choice option, irrespective of experimental history (Bogacz et al., 2006; de Lange et al., 2013). The latter are also evident in these observers as leftward (Figure 1D, left) shifts of both psychometric functions.

The current paper pursued two objectives. First, we aimed to disentangle and compare the contribution of decisional and motor signals of sequential biases in perceptual choice. In laboratory tasks, perceptual choice and motor response used for reporting the choice are typically coupled, but can be decoupled with little effect on performance on the current trial (Tsetsos et al., 2015). While there is evidence for either decisional or motor origin of sequential biases (Akaishi et al., 2014; Pape and Siegel, 2016; St. John-Saaltink et al., 2016), their relative contributions have not been quantitatively compared. Second, we aimed to quantify the adaptation of sequential biases to the environment, as a function of varying levels of internal decision confidence, in the absence of external feedback.

Disentangling the impact of previous stimuli, choices, and motor responses

In order to quantitatively compare the relative contribution of previous choices or motor responses on current choice, we reanalyzed data from a previously published study (Tsetsos et al., 2015). In this experiment (Experiment 1), observers performed a random dot motion task under trial-to-trial variations in the mapping between choice and motor response. The direction of motion was chosen randomly and independently on each trial, so that maximizing performance required basing choices solely on the current stimulus and not on its history (i.e., previous stimuli, choices, or motor

responses). We used a logistic regression model (Materials and Methods) to quantify the contribution of those three history effects, as well as of the current sensory evidence, on the current choices.

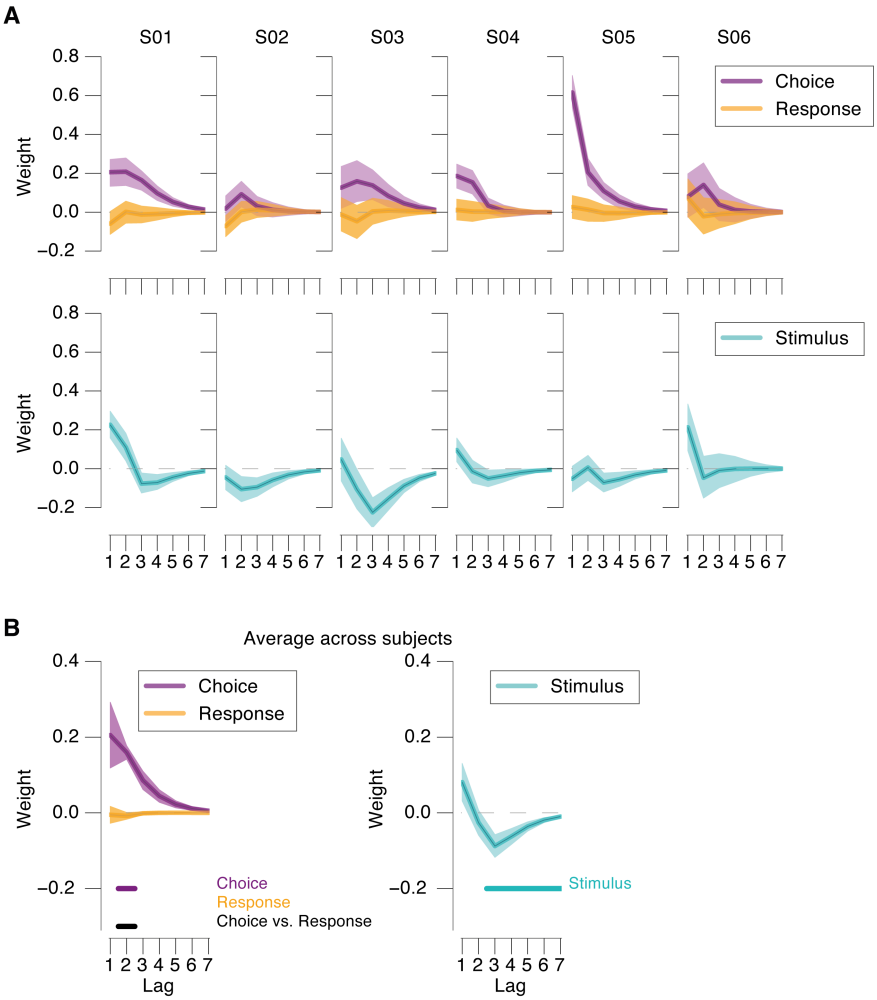

Figure 2. Stronger impact of previous choice than of previous motor response, on current bias

Contributions of previous choices, motor responses and stimuli in Experiment 1. **A)** Mean history contributions as a function of lags. Choice weights (purple), response weights (orange), and stimulus weights (blue; see Materials and Methods). Shading, 95% bootstrap confidence intervals. **B)** As **A**), but averaged across participants. S.e.m. and t-tests are computed across participants, $p < 0.05$ (FDR-corrected t-test) of choice, response and stimulus weights and of the difference between choice and response weights.

Observers showed a significant tendency to repeat their previous choices (indicated by positive choice weights), but not their motor responses (Figure 2A, upper row). In all individual participants, the effect of the previous choice on current choice was positive and stronger than the effect of the previous motor response. The same was true, and statistically significant at lag 2, in the group average (Figure 2B, left column). By contrast, preceding stimuli had negative, and statistically significant, weights at longer lags in the group average (Figure 2B, right; compare panel A, bottom

row, for individual observers). This indicates a long-lasting repulsion of choices from the previous stimulus across a time range of about 35 s.

The analyses presented here collapsed across two different conditions, in which observers were instructed about the required mapping between choice and response either before or after the presentation of the sensory evidence. We also analyzed the data from the two conditions separately and found no difference between them in the group analysis (data not shown). Thus, the predominance of previous choices over motor responses did not depend on observers' knowledge about the required mapping between choice and motor response during decision formation.

In sum, previous choices had robust and distinct (in terms of sign and time course) effects on current choice, while motor responses had only a minor impact. This indicates that the commonly observed choice repetition biases are specifically due to previous choices and not the motor responses used to the report them, which has implications for their neural sources (see Discussion). We next investigated the adaptability of sequential choice biases under fixed mapping.

Confidence-dependent adaptation of sequential choice biases to the environment

In laboratory tasks used to study perceptual choice, it is common to generate random sequences of the two alternative stimulus categories. But the states of natural environments, and hence the sensory signals generated by them, often exhibit correlations across time, so that it might be beneficial for decision-makes to adapt their sequential choice biases to that correlation structure (Yu and Cohen, 2009). In Experiment 2, we tested for such adaptation, by systematically manipulating the repetition probabilities between the two possible motion directions across three conditions blocked by experimental session: Repetitive, Alternating, and Neutral (two sessions per condition; see Materials and Methods). Importantly, observers received no external trial-by-trial feedback about the correctness of their choices, which enabled us to also study the impact of decision confidence on the adaptation of their sequential biases to changing environmental statistics.

Also in this experiment, participants exhibited 'intrinsic' sequential patterns in their choice behavior (i.e., in the absence of biased stimulus sequences) during the Neutral condition (Figure 3A). Choice and stimulus weights exhibited a similar temporal profile as the weights observed in previous experiments using standard choice tasks without manipulation of stimulus sequences (e.g., compare

with Figure 2B and Urai et al. 2017 Figure 5C). Choice weights were significantly positive for lag 2 and 3. As in the previous experiment, there was a statistically significant negative impact of previous stimuli on current choice across lags 3-7, indicating long-lasting repulsion of choices from the previous stimulus across a time range of about 30 s.

Adaptation of sequential choice biases to environmental statistics

The manipulation of the sequential statistics of the environment had clear effects on observers' sequential biases (Figure 3B-E). We mapped the individual data into a 'strategy space', defined by previous stimulus weights on the y-axis and previous choice weights on the x-axis (Figure 3B). Absolute x-values larger than absolute y-values indicated a strategy to repeat (in case of positive values) or alternate (for negative values) previous choices independent of their correctness. Whenever stimulus weights were absolutely larger than choice weights, the resulting strategy depended on the accuracy on the previous trial. Positive stimulus weights (upper triangle) referred to repeating choices that were consistent with previously seen stimuli (i.e. repeating previous correct choices and alternating previous incorrect choices), equivalent to a 'win-stay lose-switch strategy'. Conversely, values in the lower triangle indicated a 'win-switch lose-stay strategy'.

Adaptation of observers' choice patterns to biased stimulus sequences predicts that choice and stimulus weights shift in the corresponding direction. Specifically, we expected shifts towards the top right for the Repetitive condition, indicating a bias to repeat the previous choice and stimulus, and towards the bottom left for the Alternating condition, indicating a tendency to alternate previous choice and stimulus (Figure 3B; top right and bottom left corners).

In line with these predictions, participants' weights for both, previous choice and previous stimulus, changed between conditions (Figure 3B; compare dots of different colors). The mean across observers moved from close to zero bias in the Neutral condition (indicated with a black 'x' in Figure 3B) towards more choice (and stimulus) repetition in the Repetitive condition (green arrow in Figure 3B), and towards more choice (and stimulus) alternation in the Alternating condition (blue arrow in Figure 3B), respectively. These shifts in history bias with conditions were statistically significant across the group: The vector angles indicating the shift with respect to Neutral were significantly different from uniform ($p = 0.0002$ in Repetitive and $p = 0.0008$ in the Alternating condition, Rayleigh's test) and the

mean angles of these vectors (i.e., direction of the shift) were significantly different between Repetitive and Alternating conditions ($p = 2.7561*10^{-10}$, Watson-Williams test).

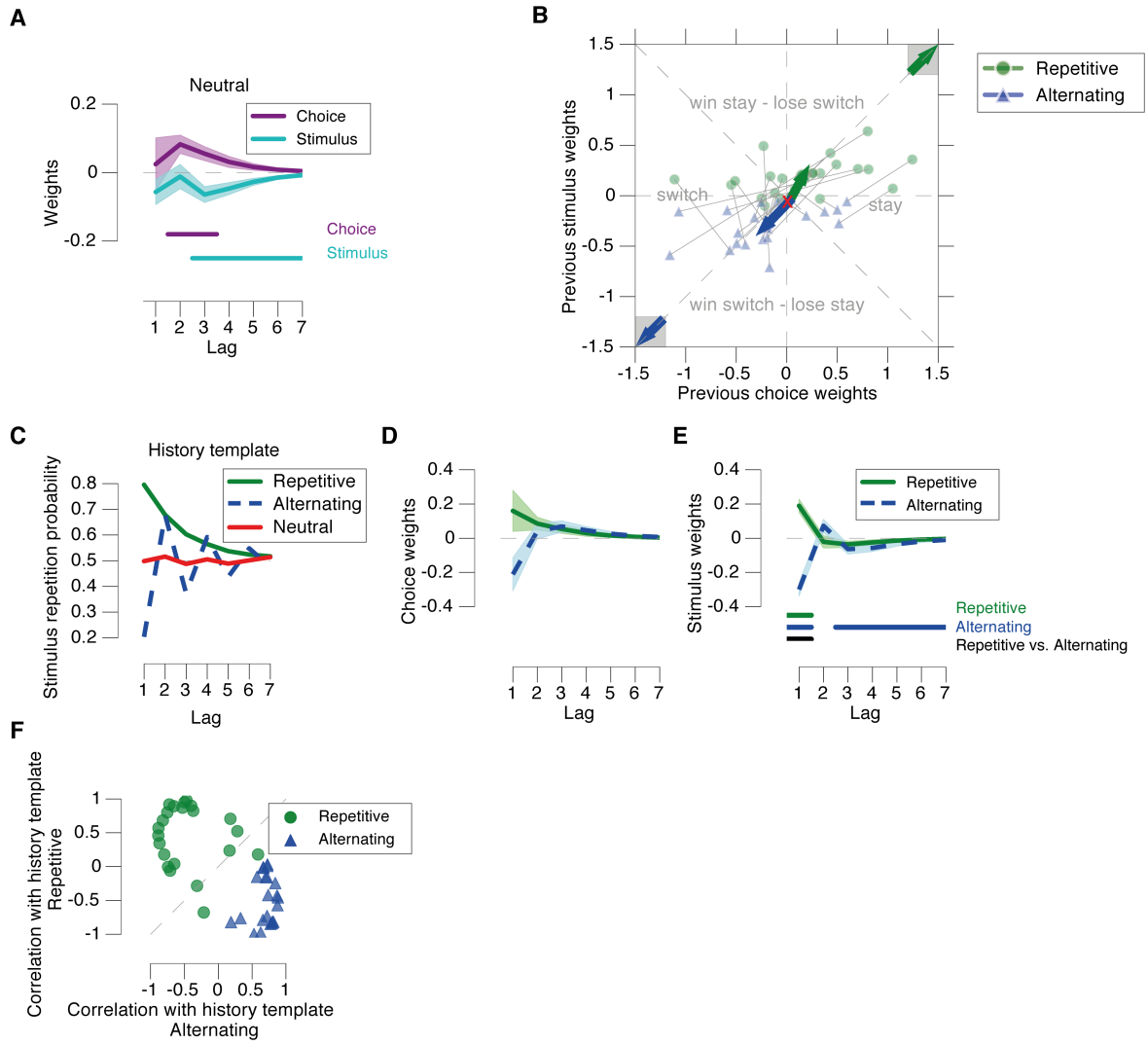

Figure 3. Adaptation of sequential choice biases to environmental statistics.

(**A**) Stimulus and choice weights for the Neutral condition. (**B**) Impact of previous stimuli and choices on current choice in Experiment 2. Weight for immediately preceding trial (i.e. lag 1). Dots, single observers, arrows changes of group mean weights from Neutral (black crosses) during Repetitive and Alternating conditions, respectively. Green and blue arrows and underlying grey areas in upper right and lower left in the left panels indicate direction and range of expected effects (see main text for explanation). (**C**) Stimulus repetition probabilities for the Repetitive, Alternating and Neutral conditions. In the Repetitive condition, repetition of the motion direction from two trials back could occur due to a sequence of two repetitions or due to a sequence of two alternations resulting in a probability of 0.8 x 0.8 + 0.2 x 0.2 = 0.68, and so on for further lags. Likewise, for the Alternating condition the probability of repetition of the same direction oscillated around 0.5 as a function of lags, but again with decreasing deviations from 0.5. (**D**) Choice weights as functions of lags in Repetitive and Alternating conditions. (**E**). As (D), but for stimulus weights. Shaded areas, s.e.m.; bars, $p < 0.05$ (FDR-corrected t-test) across participants. **(F)** Correlation of stimulus kernels with history template in the Repetitive vs. in the Alternating condition.

The changes of history biases between conditions were not simply 'inherited from' the correlations evident in the stimulus sequences. We simulated the performance of synthetic observers, which were constructed individually for each participant, such as to yield the same perceptual sensitivity as that participant (within each of the three conditions), but without any memory for the preceding stimulus and choice sequence. As expected, the choice and stimulus weights obtained for these models varied slightly between models and lags (due to statistical fluctuations for finite amounts of data), but consistently approached zero for increasing numbers of simulated choices (data not shown). Thus, the deviations from zero of the experimentally measured weights reflected an active adjustment in observers' sequential biases to the statistics of the environment.

Bias adaptation tracks environmental statistics and predicts performance

The statistical structure of both biased conditions implied characteristic, and distinct, time courses of the probability of stimulus repetition as a function of lag (Figure 3C). The repetition probability was most different from 0.5 for lag 1 and approached 0.5 for larger lags in both conditions. But the Repetitive condition exhibited a monotonic decay towards 0.5, whereas the Alternating condition exhibited a damped oscillation around 0.5 (Figure 3C). In what follows, we refer to these two time courses characterizing the statistical structure of the environment as 'history templates'.

Adaptation to the structure of environment predicted that participants' history weights as a function of lag should exhibit similar profiles. We refer to the latter time courses as 'history kernels'. Indeed, the history kernels for previous choices and stimuli showed similarly decaying profiles (Figure 3D, E). The adaptation effect was pronounced, and statistically significant, for the stimulus kernels for lag 1 and tracked the shape of the history templates beyond that lag (Figure 3E). We quantified the similarity between the entire history templates and participants' stimulus kernels by means of temporal correlation (Figure 3F). For the Alternating condition, the correlations should be regarded as lower bound of the true similarity between history kernels and history template because the estimation of the former through three independent basis functions precluded sign reversals from lag 4 onwards (see Materials and Methods). The stimulus kernels of both conditions, Repetitive and Alternating, were significantly correlated with their corresponding history template (kernel for Repetitive to template for Repetitive: $p = 5*10^{-4}$; kernel for Alternating to template for Alternating: $p < 10^{-4}$). Furthermore stimulus

kernels of both conditions were more similar to their corresponding history template (i.e., kernel for Repetitive to template for Repetitive) than to the non-corresponding history template (Repetitive: $p < 10^{-4}$; Alternating: $p < 10^{-4}$; permutation tests; Figure 3F). Thus, participants adapted their history biases to the statistical structure of their environments with a time course matched to the time course of the task statistics.

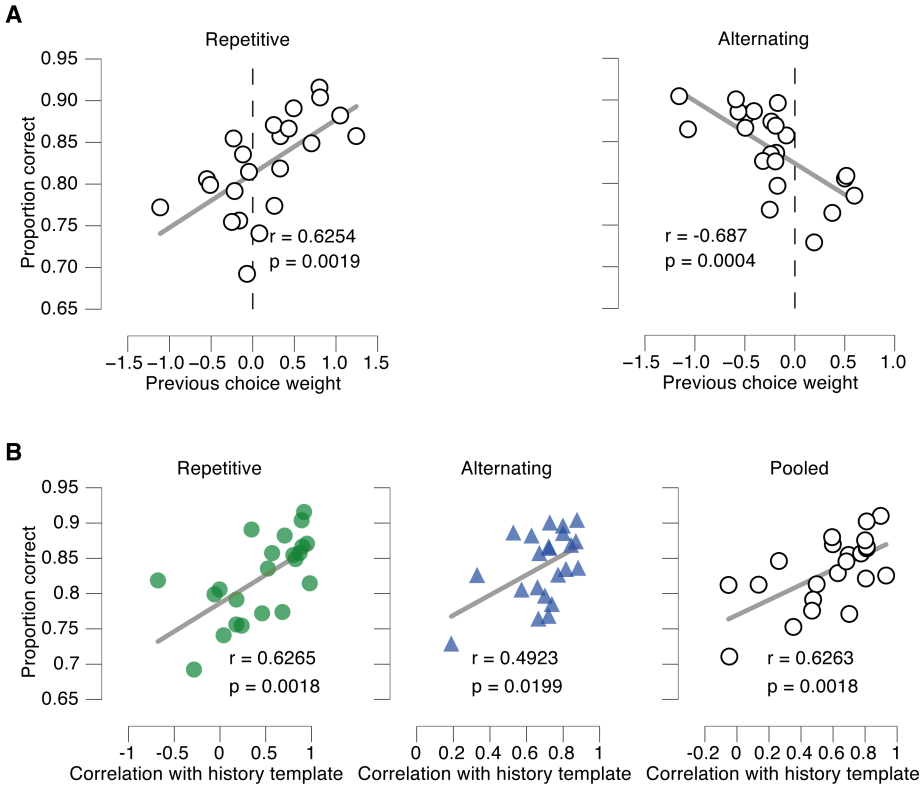

Figure 4. Correlation between adaptation and proportion of correct trials.

Assessing the benefit of adaptation of sequential bias for overall performance. (**A**) Left, correlation between previous choice weight and the proportion of correct choices in the Repetitive condition. Right as left panel, but for Alternating condition. R and p: Pearson correlation coefficient and p-value. **(B)** Left, correlation between correlation of stimulus kernels with history template and the proportion of correct choices in the Repetitive condition. Middle as left panel, but for Alternating condition. Right pooled across Repetitive and Alternating conditions. R and p: Pearson correlation coefficient and p-value.

While the bias adaptation was highly consistent across participants, individuals differed in the extent to which they shifted their history biases between conditions. These individual differences were strongly predictive of participants' overall task performance (Figure 4). Choice weights were significantly correlated with performance, for both the Repetitive (Figure 4A, left) and Alternating (Figure 4A, right) conditions, but with opposite sign, reflecting the opposite directions of the adaptation of choice weights in the two conditions. An analogous effect was evident for the similarity of their

stimulus kernels to the history templates of the two conditions: Those participants with a larger similarity to the history templates also performed best, in both Repetitive and Alternating conditions (Figure 4B, left and middle) and averaged across both biased conditions (Figure 4B, right). Thus, the more strongly observers adapted their choice biases to the biased stimulus sequences, the more successful they were on the task.

Our results supported the idea that participants accumulated signals from the past previous trials into biases for the current choice. This helped adapt their behavior to the statistics of their sensory environment, improving performance. Our interpretation is in line with current models of sequential effects, which postulate an active accumulation (with leaky memory) for previous stimuli and choices into their biases for upcoming choices (Yu and Cohen, 2009; Glaze et al., 2015; Meyniel et al., 2016). Our final series of analyses, presented next, revealed that this accumulation was modulated by trial-to-trial variations in decision confidence.

Modulation of sequential bias adaptation by decision confidence

Previous accounts of sequential effects in behavior postulate the accumulation of binary external variables, such as stimulus repetitions (Yu and Cohen, 2009; Meyniel et al., 2016), performance feedback (Abrahamyan et al., 2016), or reward (Sugrue, 2004). Our experimental conditions precluded any of the above: Observers performed under generally high uncertainty about the actual stimulus identities, and they did not receive external feedback about choice outcomes. We reasoned that, under these conditions, observers may have accumulated internal signals related to the decision process. Specifically, they might have accumulated the decision variable underlying choice (Glaze et al., 2015), neural representations of which not only encode the categorical choice, but also the graded confidence associated with that choice (Kepecs et al., 2008; Kiani and Shadlen, 2009; Hebart et al., 2016). Consequently, the impact of previous choices on current bias should be modulated by the confidence associated with previous choices. We here use the term ‘decision confidence’ in a statistical sense, to refer to the observer’s internal estimate of the posterior probability of having made a correct choice, given the evidence (Kepecs et al., 2008; Pouget et al., 2016; Sanders et al., 2016; Urai et al., 2017). This operational definition of confidence is agnostic about the link to subjective confidence reports (but see Sanders et al, 2016). It is formalized by a model based on signal detection

theory (Kepecs et al., 2008; Sanders et al., 2016; Urai et al., 2017), the key features of which are reproduced in Figure 5A. We here used two proxies for decision confidence that were consistent with this model: accuracy (Figure 5B) and reaction time (Figure 5D).

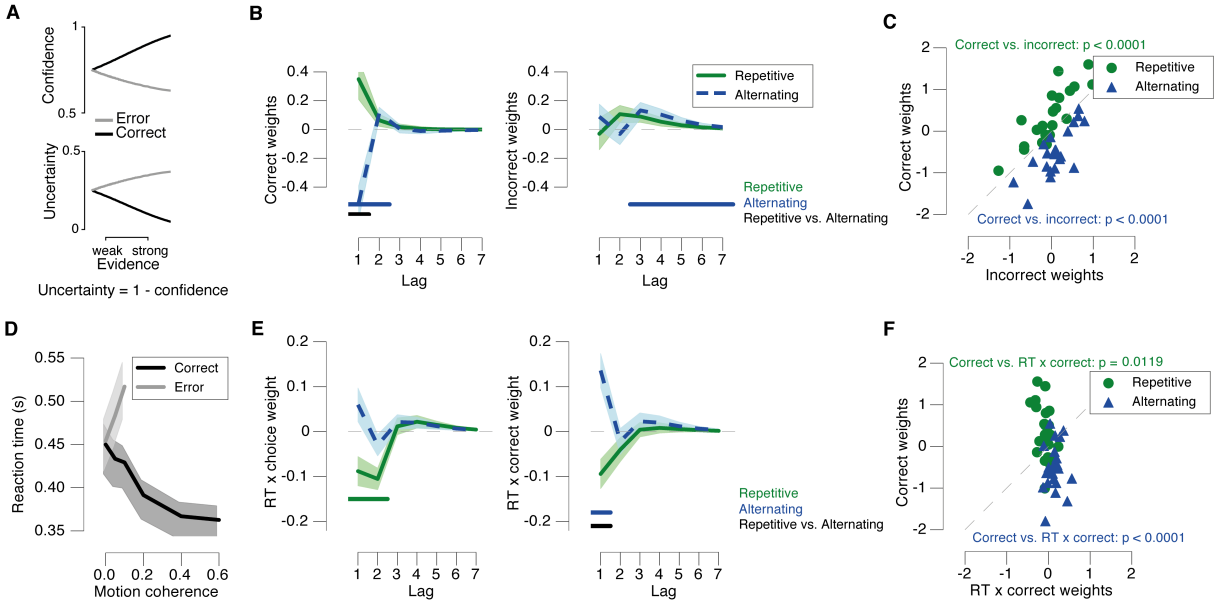

Figure 5. Modulation of adaptation by decision confidence.

(**A**) Scaling of a model-based confidence and uncertainty with evidence strength in correct and error trials. Adapted from (Urai et al., 2017) under a CC-BY 4.0 license. (**B**) Left, weights of correct preceding choices as function of lags. Right, weights of incorrect choices as function of lags. Shaded areas, s.e.m.; bars, $p < 0.05$ (FDR-corrected t-test). (**C**) comparison between correct and incorrect weights for previous trial (lag 1). (**D**) Reaction time as a function of motion coherence, sorted by correctness, collapsed across Repetitive and Alternating condition. (**E**) Left, multiplicative modulation of the weights of previous choice by reaction time (RT). Right, modulation of the weights of previous correct choices by RT. (**F**) Comparison between previous correct and previous RT x correct weights.

The model shows that correct choices are overall associated with higher confidence (Figure 5A, top). To assess the effects of the correctness of previous choices on current bias, we recombined the response and stimulus weights for the previous trials into weights for correct and incorrect choices (Materials and Methods). As expected, the impact of previous choices on current bias was larger when these choices were correct (Figure 5B). In both biased conditions, participants' weights for previous correct choices deviated from zero at lag 1 and then decayed for further lags (Figure 5B, left), an effect not evident for previous incorrect choices (Figure 5B, right). At lag 1, the weights were significantly larger for correct than incorrect previous choices in the Repetitive condition, and the other way around

for the Alternating condition (Figure 5C). This pattern of results was consistent with the idea that the accumulation of evidence across choices was boosted by decision confidence.

In the present data, the scaling of reaction times with the absolute strength of sensory evidence (i.e., motion coherence) for correct and incorrect choices also replicated a characteristic signature of decision uncertainty (i.e., the complement of confidence) from previous studies (Sanders et al., 2016; Urai et al., 2017): reaction times (i.e., uncertainty) decreased with evidence strength for correct choices, but increased for error choices (Figure 5D, compare to Figure 5A). Correspondingly, linear regression revealed opposite-signed relationship between motion coherence and reaction times, separately for correct (β = -0.150, s.e.m. = 0.027, p = 0.005) and error trials (β = 0.628, s.e.m. = 0.025, p = 0.025). This pattern of evidence- and accuracy-dependent changes in reaction time is consistent with the model of decision confidence (Kepecs et al., 2008), as well as with previous psychophysical data (Sanders et al., 2016; Urai et al., 2017).

To assess the modulatory effect of reaction times on sequential choice bias, we built on an extension of our statistical model by multiplicative (interaction) terms, which quantified the degree to which the impact of previous choices on current bias was modulated by previous reaction times (see *Psychometric function fit with modulation of sequential bias by reaction time* in Materials and Methods for details). Longer reaction times (i.e. lower decision confidence) reduced the impact of the previous choices on the current bias (Figure 5E). Specifically, the interaction weights in the Repetitive condition were significantly negative at lag 1 and 2, indicating a confidence-linked reduction of the choice repetition bias in that condition (Figure 5E, left). Conversely, in the Alternating condition the interaction weight for the previous choice was positive, indicating a (albeit not significant) reduction of the choice alternation bias (Figure 5E, left).

This modulatory effect of reaction time on the impact of previous choices on current bias was also evident when assessed for previous correct choices in isolation: here the previous interaction weight was statistically significant (Figure 5E, right), for the Alternating condition and significantly larger than the corresponding interaction weight from the Repetitive condition. As expected for a negative modulatory effect of previous decision uncertainty on current choice bias, most weights of the interaction terms (RT x correct) had opposite sign to those of the weights for the corresponding (i.e. correct) previous choices (compare Figure 5E, right and 5B, left). At lag 1, the interaction weights were

consistently (and statistically significantly) smaller than the main effect weights for (correct) choices in the Repetitive condition, and the other way around in the Alternating condition (Figure 5F). Thus, even for correct choices only, the varying uncertainty (indexed by reaction time) associated with these choices counteracted their impact on current choice.

Taken together, two independent proxies of decision confidence, choice accuracy and reaction time, both supported the conclusion that decision confidence modulated (boosted) the adaption of sequential choice bias to the statistical structure of the environment.

Discussion

Sequential biases are a long-known, pervasive phenomenon in perceptual choice (Fernberger, 1920; Fründ et al., 2014), which likely reflect the interplay of multiple factors. Here, we systematically quantified the contributions of a number of important candidate factors: preceding choices versus motor responses, the sequential statistics of the sensory evidence, and decision confidence in the absence of external feedback. We showed that the contribution of previous choices to sequential biases dominated over the contribution of previous motor responses. We further found that, in the absence of explicit feedback about choice outcome, observers could still adapt their sequential choice biases to biased (repetitive or alternating) sequences of sensory evidence. The strength of this adaptation was modulated by observers' confidence about their previous choices (with stronger adaptation after more certain choices), as indicated by previous choice accuracy and reaction time. Finally, we established that the adaptation of sequential bias was beneficial, improving the observer's overall performance. Our report provides a comprehensive characterization of these various different history contributions, within a common statistical modeling framework. Further, our current approach also identified novel effects, in particular the confidence dependent adaptation of sequential choice biases. This yielded a number of new insights into the computations underlying sequential biases in perceptual choice, with direct implications for their neural bases.

Multiple factors contributing to history biases in perceptual choice

Our analyses revealed that the contributions of previous stimuli, perceptual choices, and motor responses were dissociable in terms of their strength, sign, and time course (as function of previous trials). For two experiments, we found that previous stimuli exerted weak, but consistently repulsive

biases on current choice, across a long timescale (significant several tens of seconds into the past). The fact that these long-lasting, repulsive effects of previous stimuli on current choice were present in both, Experiment 1 and 2, indicate that they are irrespective of the presence of trial-by-trial feedback. Analogous results have been obtained fine discrimination tasks (Fischer and Whitney, 2014; Fritsche et al., 2017). These repulsive effects may reflect the impact of bottom-up sensory adaptation mechanisms (Kohn, 2007) on sensory-guided behavior.

The dominant and consistent bias in uncorrelated stimulus sequences (irrespective of the presence of trial-by-trial feedback, compare Figures 2 and 3A) was to repeat the preceding one or two choices. Similar observations have been made in a number of previous studies of perceptual choice (de Lange et al., 2013; Akaishi et al., 2014; St. John-Saaltink et al., 2016; Fritsche et al., 2017; Urai et al., 2017). Importantly, we here established that this repetition bias was due to the previous perceptual choices, rather than motor responses.

Two recent studies similarly decoupled perceptual choice and motor response (Akaishi et al., 2014; Pape and Siegel, 2016). One of them showed that a bias to alternate response hands from trial to trial systematically contributed to sequential effects, due to activity dynamics within motor cortex (Pape and Siegel, 2016). Effector-selective beta-band activity in motor cortex is suppressed during decision formation (Donner et al., 2009; O'Connell et al., 2012; de Lange et al., 2013), followed by a rebound. The stronger this 'beta-rebound', the stronger the tendency to alternate response hands (Pape and Siegel, 2016). This motor response alternation bias was superimposed onto a choice repetition bias in their study, but they did not compare the magnitude and time course of these two effects directly. Here, we performed such a direct comparison across seven previous trials. While the lack of a robust response alternation bias in all but one participant (S02) in our sample does not rule out the alternation effect, our comparison revealed that the contribution of previous choices to current bias was more consistent across observers, significantly stronger, and more prolonged in time (most robust for a lag of two trials).

This predominance of the impact previous choices over previous motor responses is consistent with the results from Akaishi et al (2014), who also focused on the contribution of the immediately preceding trial. This predominance implies that sequential biases in perceptual decision-making are governed by neural signals encoding choice in an action-independent format. Such signals exist in

associative brain regions, such as posterior parietal or prefrontal cortex (Bennur and Gold, 2011; Hebart et al., 2012, 2016), which also exhibit the short-term memory dynamics necessary for the persistence of biases in the decision-making machinery (Wang, 2002; Bonaiuto et al., 2016; Morcos and Harvey, 2016). Under the assumption that the same principle holds when the mapping between choices and motor responses is fixed, the adaptation of sequential biases to the different environmental statistics observed in our second experiment were also dominated by action-independent decision variables, rather than by motor signals.

Previous evidence for adaptable history biases

Another recent study also revealed adaptable history biases in perceptual choice (Abrahamyan et al., 2016), However, different from us, Abrahamyan et al (2016) provided unambiguous external feedback about the outcome of each choice, and their manipulation of the stimulus sequence depended on the participants' success or failure. Consequently, the process adapting history biases likely depended on the combination of choices and their outcome. By contrast, in our task, participants remained uncertain about their choice outcomes, and could only base their history biases on internal signals (see below). Thus, the adaptation effects in their and our study likely resulted from different mechanisms, and our current results complement those from Abrahamyan et al (2016). Indeed, a direct comparison of sequential effects in saccadic choice tasks with and without feedback points to an important influence of feedback on the profile of stimulus-dependent history biases (Kim et al., 2017)

Computational basis of adaptable sequential biases

The main novel contribution of the present study is the identification of a confidence-dependent adaptation of sequential choice biases. This adaptation likely reflected the ongoing accumulation of internal (likely action-independent) decision variables across trials, in line with recent computational models (Glaze et al., 2015; Bonaiuto et al., 2016). This idea is related to earlier proposals on the origins of sequential effects in cognition and choice behavior (Yu and Cohen, 2009; Meyniel et al., 2016), which however postulate the accumulation of external observables rather than internal signals. Integration of information over time is a widely established concept in current models of perceptual choice (Bogacz et al., 2006; Gold and Shadlen, 2007; Ratcliff and McKoon, 2008; Wang, 2008; Ossmy

et al., 2013), but, in these models, refers to within-trial accumulation of incoming sensory evidence across hundreds of milliseconds. The notion of accumulation of rewards across trials is widely established in the theory of reinforcement learning and value-guided choice, but there it critically depends on the experience of choice outcomes (i.e., rewards) and spans time scales of tens of seconds or even longer (Montague, 1999; Sugrue, 2004; Glimcher, 2011).

Our interpretation assumes an accumulation mechanism with timescales situated in between these two classes of models, which operates on internal decision variables that may, in turn, be computed through within-trial accumulation of sensory evidence. This 'higher-order' across-trial accumulation has been described by recent belief updating models for perceptual choice in changing environments (Glaze et al., 2015; Doyeon Kim et al., 2017). It will be important to explore such mechanisms with biophysical models of inter-choice neural dynamics (Bonaiuto et al., 2016), as well as recordings of neural activity during similar tasks as the ones used here.

The framework outlined above also provides a natural interpretation of the modulatory effect of decision confidence on the adaptation of sequential choice biases that we observed. Representations of decision variables in the brain do not only reflect categorical choices, but also the graded certainty about these choices (Kepecs et al., 2008; Kiani and Shadlen, 2009; Hebart et al., 2016). In the face of noisy sensory evidence and in the absence of single-trial feedback, such internal decision variables are a good proxy for the state of the environment available to the decision-maker. Uncertain choices are based on a smaller decision variable, they are likely to be incorrect and accompanied by slow responses (Sanders et al., 2016). Consequently, accumulation of internal decision variables predicts that incorrect choices, or choices with long reaction time, have little impact on sequential choice bias. Accumulation of confidence-dependent decision variables into biases for upcoming choice may also account for the confidence-dependent (as measured by reaction times) modulation of 'intrinsic' sequential choice biases measured under conditions of random stimulus sequences (Urai et al., 2017). In sum, one possibility is that the 'confidence-weighting' of the impact of previous choices on current bias observed here and in (Urai et al., 2017) may directly result from the accumulation of graded decision variables.

Conclusion

We conclude that, in the absence of certainty about stimulus identities and choice outcome, the brain accumulates confidence-dependent (and likely action-independent) decision variables towards choice biases in a way that promotes adaptation to correlated environments. Our findings also put strong constraints on the candidate neural sources of sequential choice biases, setting the stage for future neurophysiological work into the underlying mechanisms.

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