Build-up of serial dependence in color working memory

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Abstract
Serial dependence, how recent experiences bias our current estimations, has been described experimentally during delayed-estimation of many different visual features, with subjects tending to make estimates biased towards previous ones. It has been proposed that these attractive biases help perception stabilization in the face of correlated natural scene statistics as an adaptive mechanism, although this remains mostly theoretical. Color, which is strongly correlated in natural scenes, has never been studied with regard to its serial dependencies. Here, we found significant serial dependence in 6 out of 7 datasets with behavioral data of humans (total n=111) performing delayed-estimation of color with uncorrelated sequential stimuli. Consistent with a drifting memory model, serial dependence was stronger when referenced relative to previous report, rather than to previous stimulus. In addition, it built up through the experimental session, suggesting metaplastic mechanisms operating at a slower time scale than previously proposed (e.g. short-term synaptic facilitation). Because, in contrast with natural scenes, stimuli were temporally uncorrelated, this build-up casts doubt on serial dependencies being an ongoing adaptation to the stable statistics of the environment.

Introduction
Our perception depends on past experiences [1]. Serial dependence - how our current estimates are biased towards previous ones - has been described experimentally using many different paradigms [2–17]. In particular, paradigms including delayed-estimations of different visual features [2], such as orientation [7,15,17], numerosity [18], location [3,19,20], facial identity [21] or body size [5]. It has been speculated that these ubiquitous attractive biases are a consequence of the world's tendency to be stable, and have the functional role of averaging internal noise [2,6,17,22]. Some have further argued that serial dependence is of adaptive nature, changing its strength depending on the stimuli statistics [2,6,8,17,22]. Color, which is strongly correlated in natural scenes [23], has never been studied with regard to its serial dependencies, possibly due to its strong systematic biases [24–26]. Similar to other perceptual biases for other visual features [27,28], these systematic color biases adapt to stimulus statistics in the course of one experiment [26]. This suggests that typical perceptual bias adaptations occur in time scales of minutes to hours. Slow adaptation of serial dependence, however, has never been characterized. If serial biases are also subject to adaptation with a similar time scale, when exposed to long sessions with uncorrelated stimulus statistics they should decrease or, in case of not being adaptive, they should remain stable. Here, we address serial dependence in delayed-estimation color tasks, controlling for systematic biases and - contrary to our hypothesis - we characterize for the first time a slower dynamics of increasing serial dependence through the experimental session, despite uncorrelated stimulus statistics.

Results

Serial dependence in color working memory

We analysed 7 datasets that are freely available online (see Methods), with a total of n=111 subjects performing variations of the same, delayed estimation of color task (Figure 1a). We found that, across experiments, the subjects' reports were attracted to the previous target color for relative distances between previous and current trial target color of up to 45º in all experiments. Significant serial dependence occurred in all individual datasets for relative distances of up to 45º ($p<0.002$, bootstrap test), except for the dataset collected by Souza et al [29] ($p>0.3$, bootstrap test).

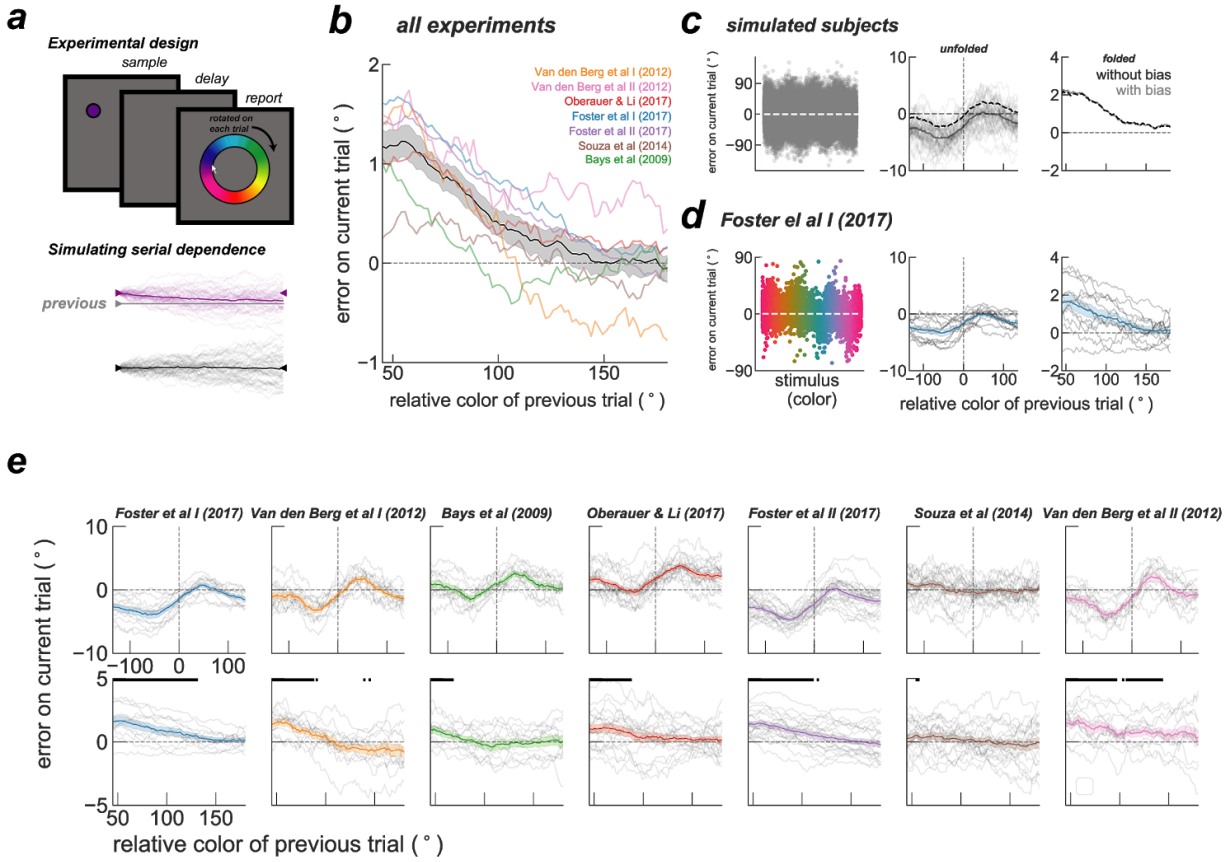

Figure 1. serial dependence in color a) Top, experimental design. All experiments were variations of a delayed-estimation of color task as in [30], differing mostly on set size and number of trials (Table 1). Subjects reported on a color wheel rotated by a random angle in each trial. Bottom, serial dependence was simulated as a drift towards the previous trial trace in a diffusion process. In purple, 50 trials with a stimulus feature (purple triangle) close to previous trial trace (gray) and in black, 50 far trials. Thick lines represent the averages of each condition, which are attracted to previous trial stimulus for trials that are close by. b) Serial bias in the delayed-estimation of color task for all datasets. We found significant serial dependence relative to previous report in all datasets ($p<0.0005$, bootstrap test), except for the dataset collected by Souza et al [29] ($p>0.3$, bootstrap test). c) Left, error to target stimulus reveals systematic biases on simulated trials. Middle, serial dependence calculated separately for trials simulated with and without systematic bias. Right, folded version of serial dependence removes all systematic biases without any additional preprocessing. d), same as c) for trials of Foster et al I [31]. e) Serial dependence in color for each experiment, unfolded at the top and folded at the bottom.

Folding serial bias curve removes systematic biases

Delayed-response reports are subject to systematic biases, which are particularly strong in the case of color [25]. It has been argued that it is necessary to model and remove the systematic bias prior to estimating serial dependence [3,15,20]. Here, we applied a model-free strategy that corrects serial dependence by "folding" the serial bias plot (Figure 1b). We tested this method in surrogate data obtained using a computational modeling approach. We simulated each delay of two consecutive trials as a diffusing memory trace [32] using a simple random walk simulation (see Method for details). On top of independent Gaussian errors responsible for diffusion, we added serial dependence as another source of error that accumulated incrementally at each time step, and two other sources of distortion (see Method for details): 1) systematic biases derived from inhomogeneities of the task space, and 2) systematic rotational biases (e.g. a constant clockwise error [3,7,15]). Figure 1c shows the effect of these systematic biases on serial bias estimation. We simulated n=1000 trials and n=50 subjects with (gray) and without (dashed black) systematic biases. As previously reported [15], we found that systematic biases shift the serial bias function to negative values. This shift precludes the correct identification of attractive and repulsive serial bias regimes, and complicates comparison across subjects. We found that a simple processing of the data allowed for a model-free correction of systematic-bias-induced shifts: we "folded" the serial bias curve by collapsing all negative distances between consecutive targets on positive values, while also inverting for these trials the sign of the behavioral error (*folded error,* see Method). This method effectively removes all systematic biases introduced in simulated trials (Figure 1c, right). For illustration purposes, we show the application of this method in one dataset (Foster et al I [31]) with similar systematic biases (Figure 1d, left), that led to a shifted serial bias function (Figure 1d, middle) and finally a *folded* version, without systematic biases (Figure 1e, right). See Figure 1E and Figure S1 for same analyses on each experimental dataset. Thus, our simulation approach validated the folding approach to correct for systematic biases in serial bias estimations, and allow for across-subject comparisons (Figure 1b).

Serial dependence is stronger relative to report, as predicted by simulations

Serial dependence, the impact of the previous trial on the current trial error, is usually calculated relative to the previous stimulus. However, our simulation approach suggested that a better reference should be the previous report: it is a more accurate reflection of the final state of the memory buffer in the previous trial, which sets the trace that induces biases in the forthcoming trial. We validated this intuition using simulations before applying it to the data. Using the same model described above, we simulated serial dependence of n=1000 trials for n=200 subjects under two slightly different conditions: The serial bias component of the model introduced an attraction bias as a function of distance of the diffusing trace to either the previous trial report, or the previous trial stimulus. We then computed serial dependence relative to previous trial report or previous trial stimulus for each of these two conditions. This surrogate model simulations validated our intuition that serial dependence is stronger when estimated based on the true origin of the mechanism that generated them: it is stronger when computed relative to report if the model used the report as a reference for serial dependence (Figure 2a), and stronger when computed relative to stimulus if that was the law used in the model (Figure 2b). We then tested the behavioral data compiled from 7 experiments and we found stronger serial dependence up to relative distances of 45º when computing them relative to the report in the previous trial compared to the stimulus in the previous trial (Figure 2c; $p=0.00014$, bootstrap test for all experiments combined; each with $p<0.015$, except for Souza et al [29], $p=0.44$). See Figure S2 for the same analysis on each experimental dataset. From this analysis we conclude that serial

dependence in delayed estimation of color tasks occurs relative to the previous trial report, rather than to the previous trial stimulus (but see Discussion).

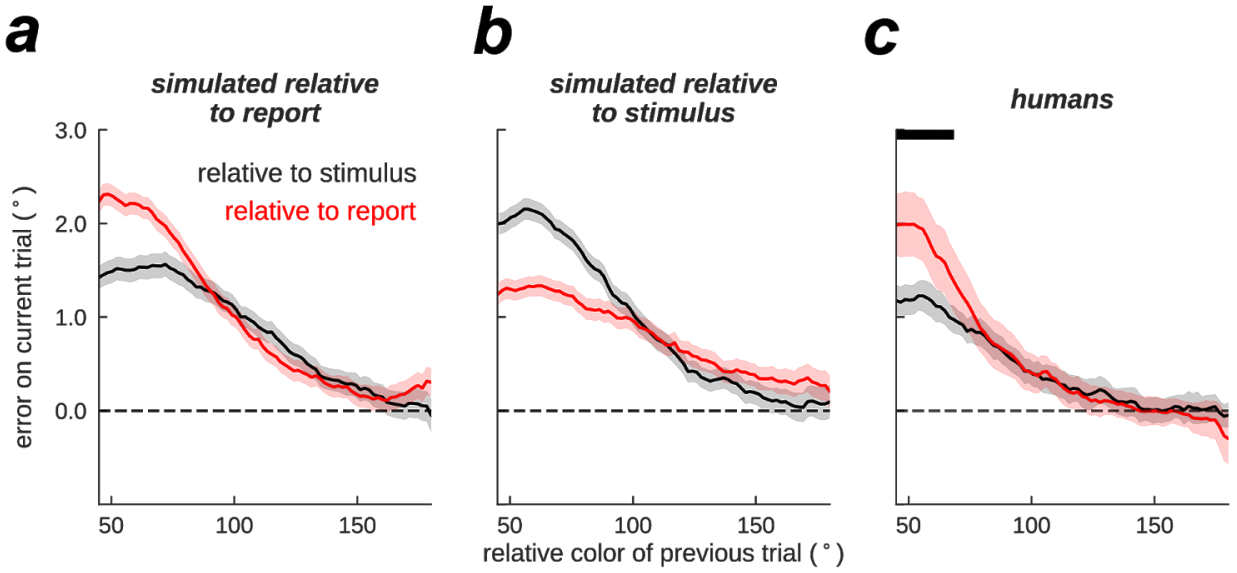

Figure 2. Current trial error depends on previous trial report, rather than on stimulus. Serial dependence calculated relative to previous stimulus (black) or previous report (red) for 3 different cases. a) Model simulations where serial bias depends on the previous trial report, b) Model simulations with serial bias dependent on previous trial stimulus, and c) Data from all experiments (n=7). All error bars are bootstrapped SEM and black bars mark where the two conditions are significantly different ($p<0.05$, paired bootstrap test).

Color serial dependence builds up in the course of an experimental session

Serial dependence, some argue, reflects the world's tendency to be stable [2,6,22]. The reasoning is that because similar stimuli usually elicit similar behavior, the brain would incorporate mechanisms to exploit these patterns [22]. Along these lines, a recent study has shown that systematic biases in color working memory change in the course of an experimental session to adapt to stimuli statistics [26], arguing that systematic biases seen in delayed-estimation of color reflect real-world statistics. If similar adaptive plasticity operated for serial dependence in the time scale of the experimental session, we would expect to see a reduction of serial biases as one is exposed to a sequence of uncorrelated stimuli. To our knowledge, the stability of serial dependence within an experimental session is yet to be characterized. To address this question, we divided each session in two halves and computed serial dependence relative to the previous trial report for each subject and experiment in each of these two halves (Figure S3). When averaging all experiments together, we found that, contrary to our hypothesis, there was stronger serial dependence in the second half than in the first half of the experimental session (Figure 3a). To further characterize this serial dependence build-up, we used the folded error on each trial as a scalar measuring the evolution of serial dependence in the course of the session (see Methods). Figure 3b illustrates this analysis using a sliding window of 150 trials for the Foster et al I dataset [31], showing a clear increase of serial dependence as the session progressed. To test this effect across subjects and experiments, we obtained the regression slope of the folded error as a function of trial number (Figure 3b). We computed this slope for each subject and for all experiments (Figure 3c). The data shows that although the serial dependence build-up was weak and only significant for one dataset (Foster et al I [31], $p=2e-06$, bootstrap test), it was significantly positive when considering the mean slope of all 7 datasets ($p=0.008$, bootstrap test). Together,

these results show that serial dependence is not stable on the time scale of one experimental session, as previously assumed, and it also discards a mechanism that adapts to stimulus statistics. Instead, our result suggests the involvement of slowly accumulating plastic mechanisms in serial dependence of color delayed-estimations.

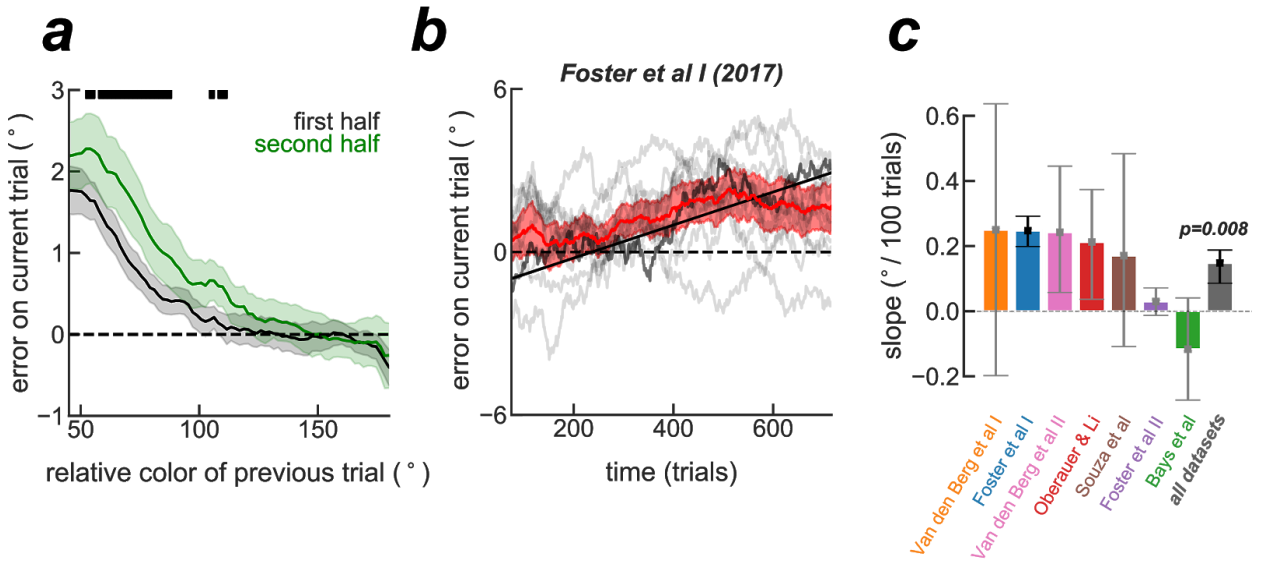

Figure 3. Serial bias builds up during a session. a) Serial biases computed using first half (black) and second half (green) of the trials for each session averaged over all experiments (n=7) show a significant increase in serial dependence through the session**.** b) Serial dependence computed with a sliding window of 150 trials for Foster et al I [31]. Gray lines are serial dependence calculated for each subject and in red their grand mean. Shaded red area is 95% confidence interval of the mean. Highlighted in black is one subject and the straight black line is a linear fit to her data (p=0.015). For each subject, we computed the slope of serial dependence over the course of the session (without averaging). c) Average slopes for each experiment. Black bars on top are p<0.05, paired bootstrap test. Unless stated otherwise, error-bars are bootstrapped standard error of the mean.

Discussion

We provide the first evidence of serial dependence in color working memory. Serial dependence had been characterized with great detail for other visual features [2], and in particular in spatial working memory [3,19,20]. Several common features of color and spatial working memory suggest that serial dependence could also be similar in color: simultaneously memorized stimuli interfere attractively when presented at close distances [33,34], and memory precision decreases with memory period duration [3,35,36]. These commonalities are in contrast with the differences of neural representations. While spatial representations consolidate early in the visual pathway [37], complex transformations in color representations occur as color information travels from the photoreceptors in the retina, to visual cortex, and into association cortex [38]. The fact that serial dependence is similar for color and spatial working memory thus suggests that it depends on inter-trial interferences that occur at processing stages with representational maps equally distant from the corresponding perceptual map, and this points at higher color processing stages. A candidate region for this is the inferotemporal (IT) cortex, where continuous neuronal representations of color of circular shape on the two perceptual cardinal axes (yellowish-bluish and greenish-reddish axis) have been found [39,40].

The analogy of color and angular location neural representations motivated us to simulate color working memory similarly to spatial working memory of angular locations [41]. We simulated the angular memory trace in the memory period as a diffusion process [32] with a drift toward the previous trial memory trace that introduces serial dependence [42]. We used this model test the concerns about the impact of systematic biases in the estimation of serial dependence. This is a general concern that has been raised for other visual features [3,15,19,20], but in the case of color it may be particularly important for the marked perceptual systematic biases that have been reported [25]. We therefore incorporated strong systematic biases in the reports of our model simulations, we tested the impact on the estimation of serial dependence and we developed new analysis strategies to address this. One typical strategy for systematic bias removal is to low-pass filter the responses as a function of stimulus feature [3,15,19,20]. This approach depends on parameters that are often subjectively decided (e.g. size of sliding window). In addition, removing systematic biases incorrectly, for example when subjects do not have systematic biases, can introduce extra biases in otherwise clean data (Figure S4). We showed that by folding the serial dependence function, one can reduce the impact of systematic biases on serial dependence without adding biases in unbiased data and without specifying arbitrary parameter values. We therefore conclude that this analysis allows a more robust estimation of serial dependence in behavioral studies.

The nature of serial dependence is a topic of debate [2], with some arguing for a main perceptual component and others supporting a working memory basis. A main argument for working memory origins is that the current trial delay duration, and not the previous trial delay duration, has an impact on the strength of serial dependence [3,7,20]. These effects are readily explained in a bump-attractor working memory model, where the interfering effect of the previous trial is enhanced when the bump is allowed to evolve longer under its influence in the delay [42]. We tested another prediction of this model and we found that serial biases computed relative to previous report, instead of relative to previous stimulus, revealed stronger attractive biases. Our model explains this based on accumulating diffusion of the memory trace during the previous delay. Alternatively, a perceptual explanation could also be formulated: any given stimulus could be perceived differently in different trials, and the behavioral report could describe more accurately the perceived color than the color presented nominally. This would also result in stronger serial dependence for report than for stimulus reference. These two alternatives could be tested in experiments that vary delay durations. The working-memory hypothesis predicts that increasing previous delay durations should increase the difference between serial dependence curves computed relative to report and stimulus. Instead, the perceptual hypothesis predicts that this difference is fixed and will not change with increasing delay durations.

Theoretical models have proposed that short-term subthreshold mechanisms in inter-trial intervals underlie serial dependence in delayed-estimation of location [42–44]. In this class of models, neural activity in previous trial's mnemonic representations engage plasticity mechanisms that leave a selective trace in the network's synapses. This trace interferes with neural activations in the next trial by biasing the neural representation of the new stimulus towards the previous memorized location. These dynamics explain most experimental findings of serial dependence in spatial working memory [42], and our simplified modeling approach is consistent with this mechanistic substrate [42]. However, our finding that attractive serial biases build up in the course of an experimental session is not explained by these models. Indeed, the short-term synaptic plasticity mechanisms invoked so far operate in time scales of a few

seconds, much shorter than the time scale of the experimental session. Our results reveal that additional mechanisms, accumulating in a time scale of 10's of minutes or hours, are also responsible for the instantiation of serial dependencies in delayed-estimation of color tasks. Possible mechanisms are changes in plasticity efficacy itself (i.e. "metaplasticity"), modulating synaptic release probability over the experimental session. We tentatively speculate that habit-related endocannabinoid modulation of synaptic release [43,45] could mediate serial dependence build-up as a non-adaptive result of task habituation.

The build-up of serial dependencies during an experimental session has further implications for how we interpret their functional role. If serial dependence was an adaptation to exploit the world's tendency to remain stable [22], and this adaptation could occur in the time scale of hour fractions (as recently shown for systematic biases in delayed-estimation of color tasks [26]), memorizing a sequence of uncorrelated stimuli should decrease serial dependence in the course of an experimental session. Alternatively, if hard-wired mechanisms underlie serial dependence, we wouldn't expect any change. Instead, our results show that serial dependence builds up, suggesting that it does not respond to an active adaptation to the statistics of visual stimuli in the environment (at least in the time scale of hours) but instead may reflect a plasticity mechanism driven by repeated selective neuronal activations in the circuit.

Methods

Participants and design

We analysed 7 datasets that are freely available online (Table 1), with a total of n=111 subjects performing variations of the same, delayed estimation of color task (Figure 1a). We will briefly describe the general experiment and Table 1 summarizes the specifics of each task, for detailed descriptions please refer to the original studies [29,31,46–48]. On each trial, a set of colored stimuli (varying from 1 to 8 stimuli) were briefly shown. After a delay period of roughly 1 second (see Table 1 for details), during which stimuli were no longer visible, subjects had to report the target color of a cued location. These color reports correspond to angles (i.e. degrees) on a color wheel rotated by a random amount on every trial, to avoid a spatial memory strategy.

Serial dependence analysis

As in previous studies (e.g. [17]), serial dependence was measured by calculating the mean error as a function of distance between current and previous target (or report). Positive (negative) errors for positive (negative) distances are interpreted as attraction towards the previous target while negative (positive) errors for positive (negative) distances as repulsion. Most of the studies, except for Foster et al [31], where multi-item working memory. On trials with more than one stimulus, we use the target stimulus as reference. The reason why we didn't compute serial dependence to other non-target stimuli, was because experiments were designed constraining minimal distances between stimuli, causing stimuli distance correlations that could confound our analyses.

Folded errors. We corrected for the effect of systematic biases in color estimation [25] by computing a folded version of typical plot (e.g. [17], see Discussion) as follows. We computed "folded" error (multiplied by the sign of the target-to-target distance) as a function of absolute distance between targets.

Serial dependence (SD) build-up. SD build-up was measured by splitting each session's trials in two equal consecutive halves (first and second) and computing serial dependence separately. SD build-up was also measured by using the whole session data. For the whole session data analyses, we computed the folded error on each trial (by multiplying each error with the sign of the target to previous target/report distance, see above). For each session, we fitted a regression slope of folded error against trial number and averaged across sessions, keeping one slope per subject and experiment.

Dataset	***Set size***	***Subjects***	***Trials***	***Delay***	***Observations***
Experiment 1 of Oberauer & Li (2017) [46]	1-8	19	400 x 2	1 s	Stimuli: colored squares of 1.25º at viewing distance of 50cm. 360 different colors on a color wheel: CIE L,a,b = (70,20,30).
Experiment 1 (I) of Foster et al (2017) [31]	1	12	~960	1.2 s	Stimuli: circle, 1.6º diameter, centered at 3.8º at viewing distance of 100cm. 360 colors. Color wheel in Figure 1
Experiment 2a (II) of Foster et al (2017) [31]	1	21	~960	1.15 s	Stimuli as I, plus: During presentation, a distractor with different shape and color was present at another location.
Experiment 1 (I) of Van den Berg et al (2012) [48]	1-8	13	288 x 3	1 s	Stimuli: circle, 2º diameter, centered at 4.5º at viewing distance of 60cm. 180 different colors on a color wheel: CIE 1979, L,a,b = (70,10,10).
Experiment 3 (II) of Van den Berg et al (2012) [48]	1-8	13	288 x 3	1 s	Same as I, but report done by scrolling through all possible colors (drawn uniformly and independently from the wheel).
Experiment 2 of Souza et al (2014) [29]	1-8	21	496 x 2	1 s	Stimuli: circles of 1.1 cm diameter at 5.5cm from fixation. 360 different colors samples from hue dimension of HSL (saturation=1, lightness=.5). Condition 1: color wheel present during delay Condition 2: Last 1 sec of - sec delay was location cued.
Bays et al (2009) [47]	1-8 (in blocks)	12	600	0.9 s	Stimuli: 2x2º patches at viewing distance of 57cm. 180 different colors samples from CIE L,a,b=(70,20,38). Presentation duration varied: 0.1, 0.5, or 2 s in a block design. This could potentially confound build-up analysis.

Table S1. Experimental details of each dataset. With the exception of Foster et al I & II [31], all datasets have a varying set size of 1-8.

Simulating consecutive trials

We simulated the memory trace in trial *k* as a random walk, θ_t^k (t=0..T, with T the duration of the delay period). Each random walk (Eq. 1) started at its corresponding stimulus location, θ_0^k. On top of independent Gaussian errors ξ_t responsible for diffusion (controlled by the parameter *σ=0.006* deg), we added serial dependence as one more source of error that accumulated incrementally at each time step. This increment was obtained from a derivative-of-Gaussian (DoG) function of the distance between the instantaneous memory trace and the previous trial's stimulus or report (i.e. starting or ending location of the previous trial simulated trace θ_t^{k-1}, with t=0 or t=T, respectively) (Eq. 2, [7,15,17,21]) The DoG curve was defined by parameters *a = 0.09* deg, c = $\sqrt{2e}$, and *w=0.007* deg^{-1} (Eq. 2), similar to [15].

Equation 1. $\theta_t^k = \theta_{t-1}^k + \sigma \cdot \xi_t - DoG(\theta_{t-1}^k, \theta_{t'}^{k-1})$, with *t'*=0 or *t'*=*T*

Equation 2. $DoG(\theta, \theta') = a \cdot w \cdot c(\theta - \theta') \cdot e^{-((\theta-\theta')w)^2}$

The *response* in each simulated trial was then derived from the last point of the memory trace θ_T^k , by applying two sources of distortion: 1) systematic biases derived from inhomogeneities of the perceptual space were simulated as $\theta_T^k - 0.2 \cdot cos(4 \cdot \theta_0^k)$, with constants chosen to fit the data by visual inspection (Fig. 2c,d, left); 2) systematic rotational biases (e.g. a constant clockwise error [3,7,15]) were simulated by adding a constant arbitrary angle $\theta_T^k + 1.4^\circ$

Statistical tests

We applied two kinds of bootstrap hypothesis testing: two-sided paired test and two-sided one-sample test [49]. For paired testing, we computed the difference between the paired samples from the two distributions, computed its mean θ and proceeded as in one-sample test. For one-sample testing we computed n=10,000 synthetic distributions of the same size as the data, by sampling with repetition from the original distribution. From each of this synthetic distributions we computed their means $\widehat{\theta}$, and subtracted the real mean $\widehat{\theta} - \theta$. We finally computed one-sided p-value as how many $\widehat{\theta} - \theta$ were bigger (or smaller) than the real mean θ. To compute two-sided tests we multiplied this p-value by 2.

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Author contributions

JB and AC designed the study, JB and AC analysed the data and JB and AC wrote the manuscript.

Competing interests

The authors declare no competing interests.

Data availability

Each dataset is available from the original publications [29,31,46–48] and all code used for the analyses will be available at https://github.com/patra/serial_color after publication.

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