

Visual priming and serial dependence are mediated by separate mechanisms

Filippo Galluzzi

Institute of Neuroscience, National Research Council,
Pisa, Italy

Centre for Synaptic Neuroscience and Technology,
Italian Institute of Technology, Genova, Italy



Alessandro Benedetto

Department of Translational Research on New
Technologies in Medicine and Surgery, University of Pisa,
Pisa, Italy

Department of Brain and Cognitive Sciences,
University of Rochester, Center for Visual Science,
Rochester, NY, USA



Guido Marco Cicchini

Institute of Neuroscience, National Research Council,
Pisa, Italy



David C. Burr

Department of Neuroscience, Psychology, Pharmacology
and Child Health, University of Florence, Florence, Italy

Institute of Neuroscience, National Research Council,
Pisa, Italy

School of Psychology, University of Sydney, Sydney,
Australia



Perceptual history influences current perception, readily revealed by *visual priming* (the facilitation of responses on repeated presentations of similar stimuli) and by *serial dependence* (systematic biases toward the previous stimuli). We asked whether the two phenomena shared perceptual mechanisms. We modified the standard “priming of pop-out” paradigm to measure both priming and serial dependence concurrently. The stimulus comprised three grating patches, one or two red, and the other green. Participants identified the color singleton (either red or green), and reproduced its orientation. Trial sequences were designed to maximize serial dependence, and long runs of priming color and position. The results showed strong effects of priming, both on reaction times and accuracy, which accumulated steadily over time, as generally reported in the literature. The serial dependence effects were also strong, but did not depend on previous color, nor on the run length. Reaction times measured under various conditions of repetition or change of priming color or position were reliably correlated with imprecision in orientation reproduction, but reliably uncorrelated with magnitude of serial dependence. The results suggest that visual priming and

serial dependence are mediated by different neural mechanisms. We propose that priming affects *sensitivity*, possibly via attention-like mechanisms, whereas serial dependence affects *criteria*, two orthogonal dimensions in the signal detection theory.

Introduction

The world around us appears stable despite large fluctuations in sensory signals, driven by several causes, including eye and body movements, attentional shifts, and internal noise sources. One important factor that may mediate stability is that most of the objects surrounding us change little over time, at least in the short term, so the brain can usefully incorporate recent sensory history into the current perceptual model. Recently, the use of contextual information has been discussed in terms of Bayes theory, where the contextual information based on recent sensory history is referred to as the *prior* (Gregory, 1980; Kersten, Mamassian, & Yuille, 2004; Mamassian, Landy, & Malone, 2002).

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The construction of priors can improve perception efficiency, by using efficient hierarchical generative strategies, such as predictive coding (Friston, 2009; Rao & Ballard, 1999). This approach increases perceptual efficiency, but can bias perception toward the statistics of previous percepts. Thus, perception includes both current sensory input and contextual priors, leading to a phenomenon referred to as *serial dependence*, a type of *serial effect*. Such effects have now been demonstrated for a wide range of stimuli and tasks: orientation judgments (Fischer & Whitney, 2014; Liberman, Zhang, & Whitney, 2016; Manassi, Liberman, Chaney, & Whitney, 2017), numerosity (Cicchini, Anobile, & Burr, 2014; Corbett, Fischer, & Whitney, 2011), expressions and facial gender (Kondo, Takahashi, & Watanabe, 2012; Liberman, Fischer, & Whitney, 2014; Xia, Leib, & Whitney, 2016), and position (Bliss, Sun, & D'Esposito, 2017; Manassi, Liberman, Kosovicheva, Zhang, & Whitney, 2018). Serial effects are modulated by attention (Fischer & Whitney, 2014; John-Saaltink, Kok, Lau, & De Lange, 2016; Makovski & Jiang, 2008) in that attended stimuli undergo stronger serial effects, leading some authors to hypothesize that the more attention allocated the more the influence of the past in defining current perception. In search tasks, it has also been reported that non-target items exert a negative (repulsive) effect on subsequent targets; this effect presumably is found as distractors contribute to search space and indicates that multiple forms of serial dependence can occur in parallel (Rafiei, Chetverikov, Hansmann-Roth, & Kristjansson, 2021; Rafiei, Hansmann-Roth, Whitney, Kristjansson, & Chetverikov, 2021). Interestingly, serial effects are strongest for attributes that rarely change (such as gender), and minimal for attributes that change over time (such as expression), consistent with an implicit belief on the stability of a given attribute (Taubert, Alais, & Burr, 2016).

The effects of perceptual history have been long studied, particularly by a technique known as *priming*, introduced by Lashley (1951). Priming is a phenomenon where exposure to one stimulus influences the response to a subsequent stimulus, without conscious guidance of intention. Priming is an important phenomenon for a range of cognitive studies, from linguistics to social psychology, and particularly in perceptual research (Kristjansson & Campana, 2010). Perhaps the most well-known are priming of “pop-out” studies (Maljkovic & Nakayama, 1994; Maljkovic & Nakayama, 1996; Treisman, 1992), where participants report a specific feature of a “pop-out” stimulus, defined by being the odd-one-out in some attribute, typically color. Observers responded faster to features of a color-defined target when the color was repeated from the previous trial, with the facilitation accumulating over many trials (Maljkovic & Nakayama, 1994). The same effect in simple pop-out search tasks has been observed for several visual features besides color,

including position and orientation (Kristjansson, 2006), shape (Fecteau, 2007; Kristjansson, 2006; Maljkovic & Nakayama, 1994), motion (Campana, Pavan, & Casco, 2008), and size (Huang, Holcombe, & Pashler, 2004). Priming also occurs during conjunction search tasks (Hillstrom, 2000; Kristjansson, Wang, & Nakayama, 2002) with separable effects for target and distractors (Kristjansson & Driver, 2008).

In the current study, we examined the relationship between priming of pop-out and serial effects to determine if they shared common mechanisms. In particular, we hypothesized that priming and serial effects should be similarly affected by feature repetition: decreasing reaction times to consecutive targets with the same feature, and increasing the serial dependence effect. To test this, we devised a paradigm to measure concurrently priming of reaction times and serial bias effects. The results fail to find evidence for a solid relationship between priming of pop-out and serial dependence, and strong evidence to suggest they tap different mechanisms.

Methods

Participants

Sixteen participants (10 women, age = 26.6 ± 2.9), with normal or corrected-to-normal vision, took part in the experiment, and gave informed consent, following the Declaration of Helsinki. The experiments were conducted with the approval of the regional ethics committee. All participants except two of the authors were naïve to the purpose of the experiment.

Apparatus

Observers sat in front of the computer monitor, 60 cm from the screen, in a dimly lit room. The stimuli were generated with PsychoPhysics Toolbox routines for MATLAB (r2021a, The MathWorks) and presented on a gamma calibrated 14-inch IPS monitor spanning 29 degrees \times 16.6 degrees (refresh rate = 60 Hz; 1920 \times 1080 pixels).

Stimuli and procedure

All trials began with a white fixation cross on the center of the screen on a gray background. Three Gabor stimuli with average luminance matched to the background (space constant with $\sigma = 0.83$ degrees; spatial frequency 1 cycle per degree [cpd]; contrast = 10%; and duration = 300 ms) were shown on the vertices of an equilateral triangle, equidistant (6.14 degrees radial eccentricity) from the fixation cross. Each Gabor was followed by a mask of the same size and average

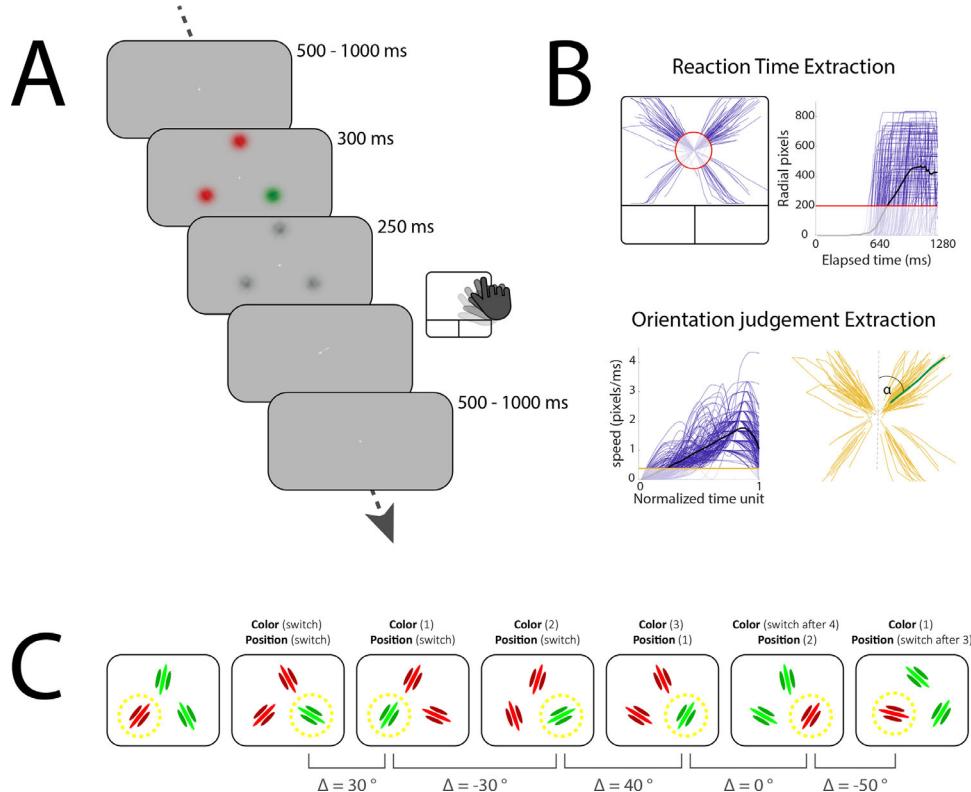


Figure 1. Timeline and stimuli. (A) The typical trial. All trials began with a fixation cross at the center of a gray background, for a random duration between 500 and 1000 ms. This was followed by the stimulus for 300 ms, which comprised three Gabor stimuli (positioned at the vertices of an equilateral triangle, 6.14 degrees radial eccentricity) with average luminance equal to that of the background ($\sigma = 0.83$ degrees, 1 cpd, 10% contrast). The Gabor stimuli were followed by three black and white masks for 250 ms (superimposition of 5 black and white gratings: $\sigma = 0.83$ degrees, random orientations, random phases, 1 cpd, 10% contrast). Participants were instructed to reproduce, as quickly as possible, the orientation of the odd-colored target Gabor by swiping a forefinger to draw a trajectory on the trackpad. After the orientation, reproduction was complete, and a new trial began. (B) Orientation judgments. Reaction times were computed as the difference in time between stimulus onset and the moment in which the drawn trajectory reached a distance threshold, 200 pixels from the screen's center. Orientation judgments were estimated as the circular average of all the orientations within the segments of the trajectory with speeds higher than the 20% of the maximum speed of the whole trajectory. (C) Trial sequences and estimation of serial effects. Randomization of the color of the target with only 25% chance of change tends to lead to sequences of trials where the color of the target is repeated for several consecutive trials. Color maintenance over consecutive trials was set at 75% probability. Gabor orientations were chosen from a bimodal distribution centered at ± 45 degrees in steps of 5 degrees. To measure serial effects, we plotted single-trial reproduction errors (target orientation judgment minus physical orientation) against the relative orientation of the previous target compared to the current one.

luminance of the Gabor (gaussian mask with $\sigma = 0.83^\circ$ vignetting the sum of 5 different black-and-white gratings, random orientations, random phases, 1 cpd, contrast = 10%, and duration = 250 ms). Observers were asked to choose the odd-colored Gabor (either a red target among 2 green distractors or vice versa), and reproduce its orientation by swiping the forefinger of the preferred hand on the trackpad, as quickly as possible (responses faster than 0.2 seconds or slower than 2 seconds were excluded from the analysis). Similar to [Maljkovic and Nakayama \(1994\)](#), unbeknownst to the observer, the target appeared exclusively in one of the two lower positions of the equilateral triangle. The trackpad trajectory was displayed on-screen with visual feedback. Once the participants reported the

perceived orientation, the visual feedback vanished and after a random pause between 500 and 1000 ms, a new trial began (Figure 1A). Gabor orientation was chosen from one of two gaussian distributions centered at ± 45 degrees with $\sigma = 20$ degrees, (in steps of 5 degrees). Stimuli were designed so that the target and distractor stimuli had almost orthogonal orientations (clockwise and counterclockwise or vice versa). This made it possible to uniquely identify whether participants correctly recognized the odd-colored target, and score as correct or in error. By convention, vertical Gabors had orientation zero, and counterclockwise orientations were considered positive. The target color either switched or repeated on each trial with 75% probability of repeating. After a 10-trial training

session, participants performed at least 15 of the 100-trial sessions (each lasting about 4 minutes).

Data analysis

Data analyses were performed for both the aggregate observer and single participants, on reaction times, serial effects, and standard error of the reproduction error. For the aggregate observer, we additionally analyzed the evolution of those indexes along the progression of trial sequences (Figure 1C; i.e. as a function of the number of preceding trials with same/opposite-color target).

Accuracy was assessed confirming that the finger swipe had traced a trajectory in the same quadrant as the stimulus (e.g. if the stimulus was clockwise from vertical a correct response would have been a trajectory crossing the I and III Cartesian quadrants). This criterion enables assessing attentional deployment without the need for an extra task, and relies on the fact that when observers are not paying attention, they risk making a very large error. This approach is perfectly suitable for near oblique stimuli, but less so for near cardinal stimuli, as when the correct response approaches the boundary it is possible that a simple error due to motor planning brings to a response which crosses the boundary. For this reason (and also because we were investigating serial effects which are strongest for oblique stimuli), we excluded from the analysis trials where the target was less than 26 degrees away from the cardinals.

Reaction time was computed as the time elapsed from the presentation of the stimulus to the moment in which the finger motion over the trackpad reached a distance threshold (200 pixels; Figure 1B, top row). We estimated the orientation reproduced from the finger trajectories from segments with speeds higher than the 20% of the maximum speed. The orientation reproduced was estimated as the circular average of all the orientations within those trajectories (see Figure 1B, bottom row). Trials where reaction times were more than three median absolute deviations from their relative medians were excluded from priming effect analysis.

To measure the serial effects, the single-trial reproduction errors (orientation judgment minus physical orientation) were plotted as a function of the relative orientation of the previous trial with respect to the current trial. Reproduction errors corresponding to orientation changes between ± 35 degrees (77% of trials) were fit with a derivative of Gaussian (DoG) function of the form:

$$DoG = a * x * e^{-\frac{(x-\mu)^2}{\sigma^2}} + b \quad (1)$$

with $\alpha = [-1 \text{ to } 1]$, $b = [-2 \text{ to } 2]$, $\mu = [-2 \text{ to } 2]$, and $\sigma = [15 \text{ to } 25]$. Serial effects values were estimated as the maximum value of the derivative of the DoG,

which captures the maximum weight that the previous orientation can have on the current judgment. The standard deviation of the reproduction errors was calculated for the relative orientations of the current and previous trials. Given that near-cardinal orientations judgments do not inherit much past information to elicit great serial effects (Cicchini, Mikellidou, & Burr, 2018), near-cardinal targets (less than 26 degrees from the cardinal orientations) were excluded from analysis of reproduction errors (33% of total trials). However, they were included in the analysis as predictors for the following response errors.

To exclude blatant errors from the analysis, we excluded trials where either the median absolute deviation from median exceeded three or the raw reproduction error exceeded 30 degrees. Overall, this led to the exclusion of 2% of the trials. Three participants were excluded from the analysis of both serial effects and priming because they reported consistent repulsive serial effects (negative derivative of DoG fit).

When creating the aggregate observer, care was taken not to carry over individual reproduction biases. For this reason, we first estimated the individual biases for those trials where the previous was identical to the current one (this avoids any serial dependence effect) and subtracted this from each observer. Before analysis we also sought to minimize the impact of regression-to-the-mean effect (Cicchini, Arrighi, Cecchetti, Giusti, & Burr, 2012; Hollingworth, 1910; Jazayeri & Shadlen, 2010), as these introduce errors for stimuli far from the mean which can be erroneously ascribed to the stimulus history that leads to those stimuli. To this end, for every orientation of the stimulus, we calculated the average orientation reproduction of that stimulus and discounted it from responses to that orientation. To have an unbiased measure of the reproduction bias free from history effect, we limited the calculation of the average bias only considering trials that had a symmetrical history of orientations (i.e. with equal opportunity of having a clockwise or counterclockwise previous stimulus). An orientation was considered to have a symmetrical history if the relative amount of clockwise and counter-clockwise trials was not below 35% or above 65%.

We investigated the correlation between reaction times and serial effects, either by looking at their values across the entire experiment, or by studying their dynamics within a given sequence of trials.

Statistics

Two-way repeated measures ANOVA were run for both reaction times and serial effects across participants (i.e. for each experimental condition, each participant yielded an average reaction time and serial effect). On the aggregate observer, one-tailed Bayesian correlation analysis (MATLAB package for Bayes statistical

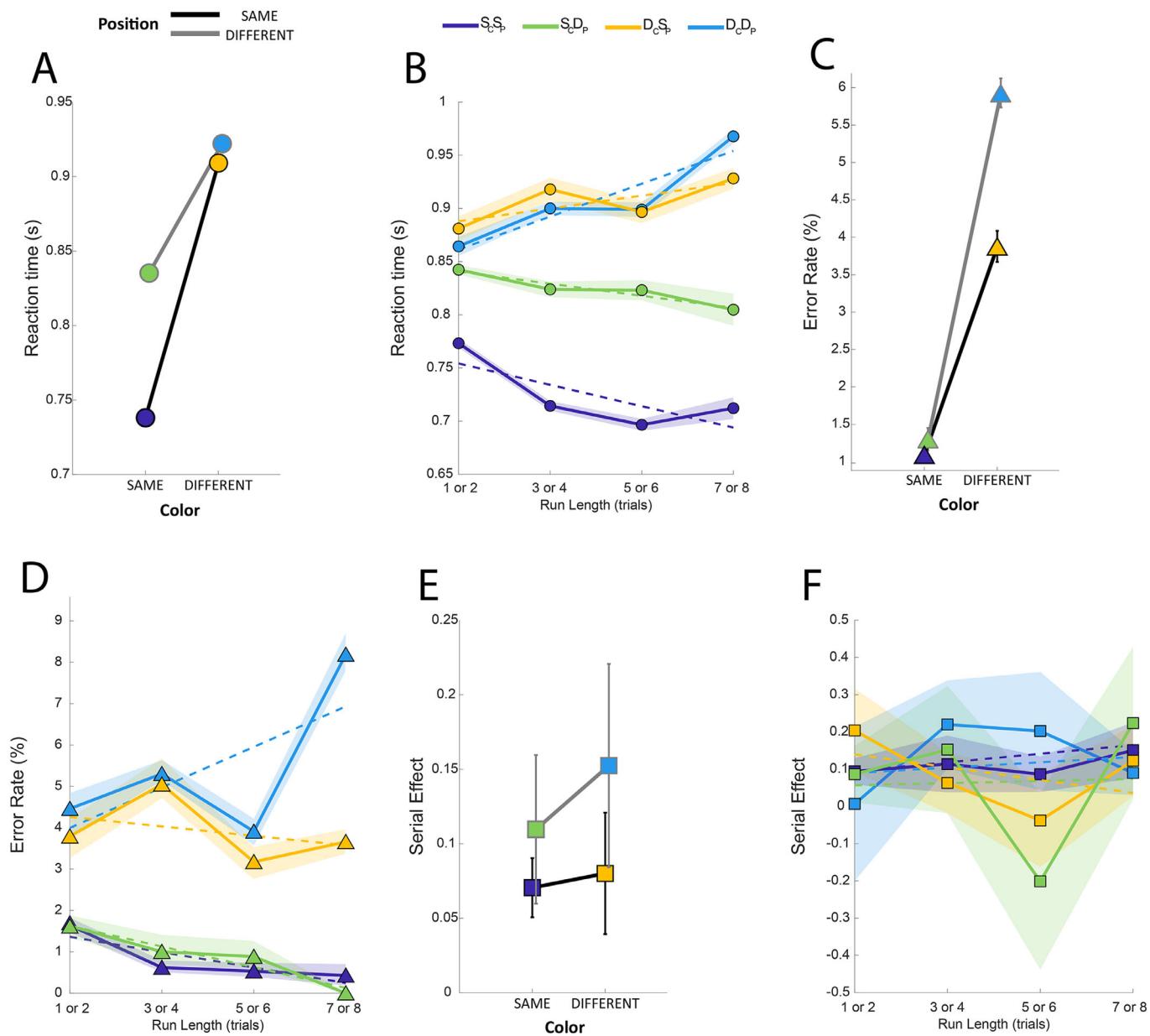


Figure 2. Priming and Serial Dependence effects in different experimental conditions. (A) – Mean reaction times for the aggregate observer for the four conditions. A clear strong effect of color change and a weaker of position change is shown by data and supported by statistics. (B) – Reaction times as a function of run length. The four conditions are color-coded according to the legend in top right (S = same, D = different, and color and position). Trials preceded by a same color target streak show a clear downward trend, increasing the length of the streak (purple and green solid lines, and dashed lines indicate linear regressions). On the contrary, trials preceded by an opposite color target streak display an upward trend of reaction times and a downward trend regarding the accuracy in recognizing the correct target, as the streak increases its length (yellow and light blue solid and dashed lines, respectively). (C) – Aggregate observer mean error rate. Again, there is a strong effect of color and weaker effect of position. (D) – Error rate as a function of run length. Repeated color conditions show a decrease in the percentage of errors with increasing run length indicating greater accuracy (green and purple solid lines and, dashed lines indicate linear regressions). On the other hand, switched color conditions show an increase in error rate with run length (light blue and orange solid and dashed lines, respectively). (E) – Aggregate observer mean serial effect. All four experimental conditions result in serial dependence strengths significantly greater than zero, with a slightly larger effect when position changes. (F) – Serial effects as a function of run length. None of the four experimental conditions shows any upward or downward trend (solid lines indicate real values, and dashed lines display regression lines). In all panels, the shaded areas and error bars indicate standard errors obtained by bootstrapping raw data.

analysis, “*bayesFactor*”) was conducted to quantify the evidence for or against the null hypothesis of correlation. To analyze the correlation between reaction times and serial effects, the Bayes Factor was corrected by Pearson’s correlation *pValue*:

$$bf10_{corr} = 2 * (1 - pValue) * bf10; \quad (2)$$

For the aggregate observer analysis, a bootstrap procedure (1000 simulations, with replacement) was run for both reaction times and serial effects, yielding estimates of measurement variability (Figure 2). For serial effects, the DoG curve parameter σ was bounded between ± 2 of the σ parameter estimated from the original aggregate observer.

Statistical differences for both reaction times and serial effects were calculated with a bootstrap sign-test (2 tail, alpha 0.025), 1000 iterations, sampling with replacement. The average of the 1000 runs was taken as the result of the bootstrap sign-test.

Results

We measured concurrently priming and serial dependence effects in a paradigm where observers selected the odd-colored Gabor patch and reported its orientation, by swiping their forefinger on the trackpad. The experiment follows the paradigm of Maljkovic and Nakayama (1994; Maljkovic & Nakayama, 1996), and results in lower reaction times when the priming color, or position, is repeated across trials. At the same time, the paradigm enables measuring serial effects analyzing the orientation reproduction errors as function of relative orientation of previous and current trials. A positive dependence between previous orientation and current error is a signature of attractive serial effects.

We first separated trials according to the history of the target, leading to four conditions, depending on the repetition of the target color and/or position:

1. Current target shared both color and position with the previous target (S_{CP}).
2. Current target shared only the color of the previous target (S_{Cp}).
3. Current target shared only the position of the previous target (D_{CP}).
4. Current target shared neither color nor position of the previous target (D_{Cp}).

Priming and serial dependence effects

Reaction times for the four conditions are shown in Figure 2A, for the aggregate observer. There is a clear effect, supported by statistics, of reaction times of both color-change and position-change of target (bootstrap

sign-test: $S_{CP} > S_{Cp}, p < 0.001$; $D_{CP} > D_{Cp}, p < 0.05$; $D_{CP} > S_{Cp}, p < 0.001$; $D_{CP} > S_{CP}, p < 0.001$). Reaction times were shorter when either the color or the position was repeated, with the stronger effect (about double) for repetition of color, consistent with previous research (Maljkovic & Nakayama, 1994; Maljkovic & Nakayama, 1996). Two-way repeated measures ANOVA on average reaction times showed significant main effects of the factors “color change” ($F(1,12) = 116, p < 0.001$) and “position change” ($F(1,12) = 31, p < 0.001$). There was also a significant interaction between factors ($F(1,12) = 6.1, p < 0.05$), confirming that color-change had the stronger effect.

To further explore how priming develops over trials, Figure 2B shows reaction times as a function of the number of previous trial targets for the four conditions. When both color and position repeat (S_{CP}), there is the strongest effect, with a clear improvement of reaction times as a function of repetition, at least up to six trials, consistent with previous research (Maljkovic & Nakayama, 1994; Maljkovic & Nakayama, 1996). The slope of the best fitting regression was of 10 ms/repletion. When color repeats, but position changes (S_{Cp}), there is also an improvement over trials, which is to be expected, given that color has the stronger effect on priming, with a slope of 5.4 ms/repletion. In the two conditions where color changes (D_{CP} and D_{Cp}), the effect is reversed, with reaction times increasing steadily with the number of trials (at 15.5 and 6 ms/repletion, respectively), suggesting that the negative effect also accumulates over trials (bootstrap sign test on regression slope: all $p < 0.001$).

Figure 2C reports the error rate (defined as whether the response was in the same angular quadrant) for the four conditions and Figure 2D as a function of number of trials. Errors follow a similar general trend as reaction times, confirming that there is no speed-accuracy tradeoff. The lack of speed-accuracy tradeoff is confirmed by the fact that errors correlate strongly and positively with reaction times ($r = 0.84$, $\log Bf10 = 2.85$).

Figure 2E shows the average strength of serial dependence for each of the four experimental conditions for the aggregate observer. Positive serial effects occur in all four conditions (bootstrap sign-test = $S_{CP} > 0, p < 0.001$; $S_{Cp} > 0, p < 0.05$; $D_{CP} > 0, p < 0.05$; $D_{Cp} > 0, p < 0.05$) but without significant differences between conditions (bootstrap sign-test, alpha = 0.05, $p > 0.05$). However, the pattern of results is quite different from that of reaction times. There was a small (but significant) effect of position-change (ANOVA = $F(1,9) = 7.35, p < 0.05$), but no significant effect of color change ($F(1,9) = 1.48, p = 0.25$). The interaction was also insignificant ($F(1,9) = 1.45, p = 0.26$). Interestingly, the dependence on position is negative, stronger for when the position changed, at

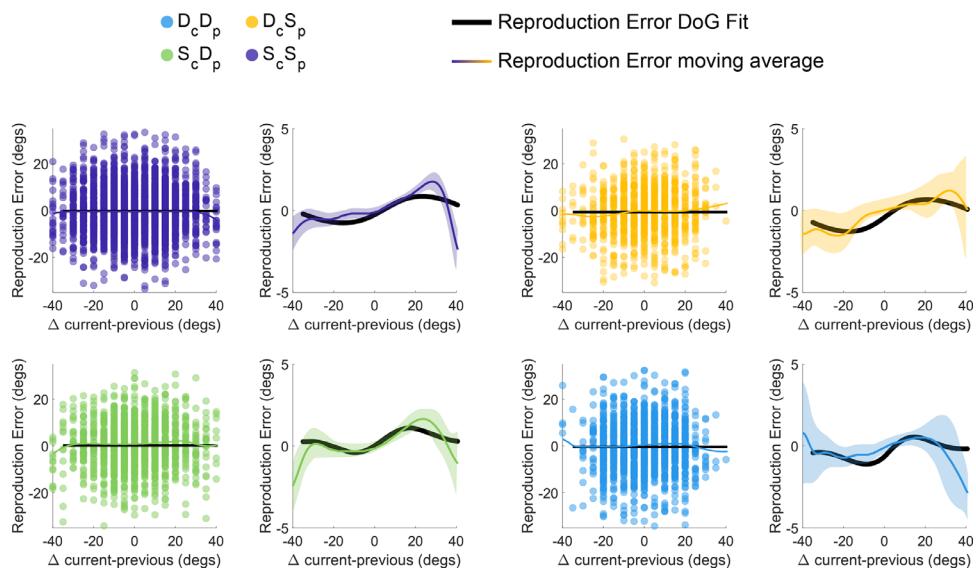


Figure 3. Reproduction errors and serial effects of the four experimental conditions. Scatters show reproduction errors plotted against relative orientation of current and previous trials for the four experimental conditions (S_cS_p , purple; S_cD_p , green; D_cS_p , orange; and D_cD_p , light blue). Magnifications display DoG fits on raw data (black solid line) and Gaussian (resolution = 0.1 degrees, and STD = 5 degrees) moving average curves (colored solid lines, shaded areas indicate ± 1 STD). The standard error of the moving average curves was calculated as the standard deviation of 200 bootstrap repetitions. Serial effects were calculated as the maximum of the slope of the DoG fits.

odds with suggestions that serial dependence is spatially selective (Collins, 2019; Fischer & Whitney, 2014).

As with reaction times, we studied the dependence of serial effects on run length (the number of preceding trials with a given attribute in relation to the current trial; Figure 2F). Unlike the effect on reaction times, no condition shows any significant effect of run length (bootstrap sign test on regression slope: all $p > 0.11$). Repeated exposure to the same position and/or color does not increase (or decrease) the magnitude of serial dependence.

Figure 3 displays raw reproduction errors from which the data of Figures 2E and F were derived, together with Gaussian moving averages and DoG fits of the four experimental conditions. Inspection of the DoG fits confirms the pattern of the data of Figure 2.

Relationship between priming and serial effects

We further explored the relationship between the evolution of priming and serial effects over trial sequences. Figure 4A plots reaction times against serial effects for variable consecutive trials of the same or opposite color or position. The two measures are clearly uncorrelated ($r = -0.006$, $\log Bf10 = -0.72$). We also investigated the possibility of correlation after removing the mean effects from each condition. Figure 4B shows there is again substantive evidence that the two measures do not correlate with each other ($r = -0.06$, $\log Bf10 = -0.64$). This reinforces the results

of Figure 4A, by avoiding any disruption of the correlation caused by the different average effects of the different experimental conditions, decoupling the evolution of measures within a given trial sequence and the experiment.

We further examined the relationship between the effect of priming on reaction times, defined as the difference between the average reaction time of the switched-color trials (D_cS_p and D_cD_p) and the repeated-color trials (S_cS_p and S_cD_p), and overall serial effects for the 16 single subjects (Figure 4C). Again, there was substantial evidence for no correlation between priming and serial effects ($r = -0.06$, $\log Bf10 = -0.72$). To confirm our measurement, we performed an additional analysis on the relationship between priming and serial effect in three aggregate participants, comprising groups characterized by high, low, or medium priming effect. All the three aggregate participants have positive serial effects ($p < 0.001$; Figure 4D), which do not correlate with their respective priming effects (slope > 0 on 55.3% of reiterations).

Relationship between priming effect and orientation reproduction precision

The results so far show a lack of correlation between priming and serial dependence effects. We then investigated if the priming effect could be related to the precision in reproducing a measure of perceptual

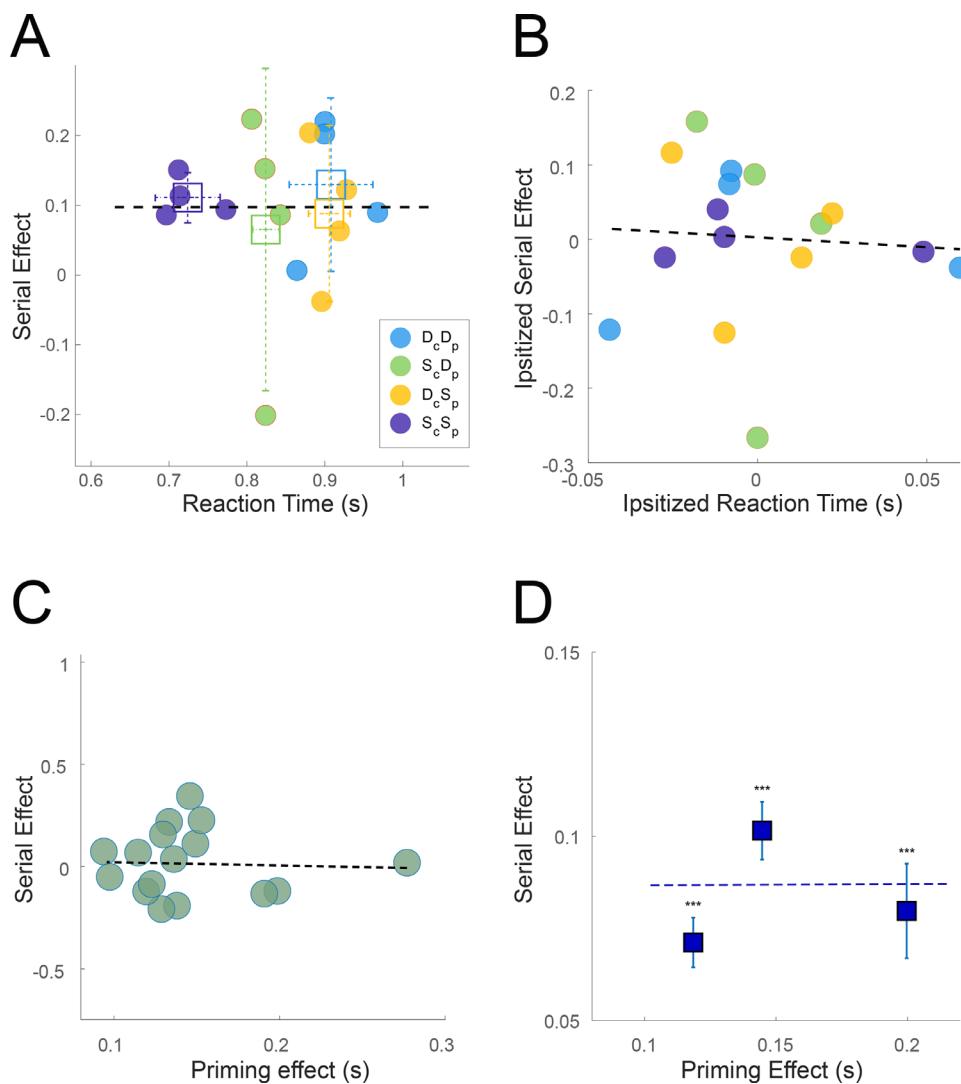


Figure 4. Priming and serial effects correlation. **(A)** - Reaction times versus serial effects for the four experimental conditions. Color-coded circles plot magnitude of serial effects against reaction times of the aggregate observer for the different conditions and run length (position within a sequence, same as the x-axis of Figures 2B, 2D, 2F), with average values shown by open squares. There is clear evidence of no correlation (black dashed line, $r = -0.006$, $\log Bf10 = -0.72$). **(B)** Same data as A with the mean effects subtracted, separately for the four experimental conditions. Again, there is strong evidence for lack of correlation between the two measures (black dashed line, $r = -0.06$, $\log Bf10 = -0.64$). **(C)** – Priming versus overall Serial effect for single subjects. Priming effect (difference between the average reaction time of the switched-color trials and the repeated-color trials) versus overall serial effects (over all experimental conditions) of all the 16 single participants tested. There is evidence of no correlation between priming and serial effects (black dashed line, $r = -0.06$, $\log Bf10 = -0.72$). **(D)** – Priming versus overall serial effect for differently primed aggregate subjects. Priming effect versus overall serial effects of the three aggregate participants comprising participants with low, high, or medium priming effect. There is evidence of no correlation between priming and serial effects (blue dashed line, slope > 0 on 55.3% of reiterations).

performance. However, measures of accuracy and precision did correlate with reaction times. Figure 5A plots errors against reaction times for the various run-length conditions (see data from Figure 2). The two measured errors correlate strongly and positively with each other ($r = 0.84$, $\log Bf10 = 2.85$), as previously observed. Figure 5B plots average standard deviation, which is a measure of imprecision (rather than

inaccuracy) against reaction times, for the four different conditions, and for various run-lengths of the same or opposite targets. Again, there is substantive evidence that the two measures positively correlate with each other ($r = 0.62$, $\log Bf10 = 0.71$), consistent with no speed-accuracy trade-off, even with this novel measure of performance. However, when we subtracted from the trials the mean effects of their condition, leaving only

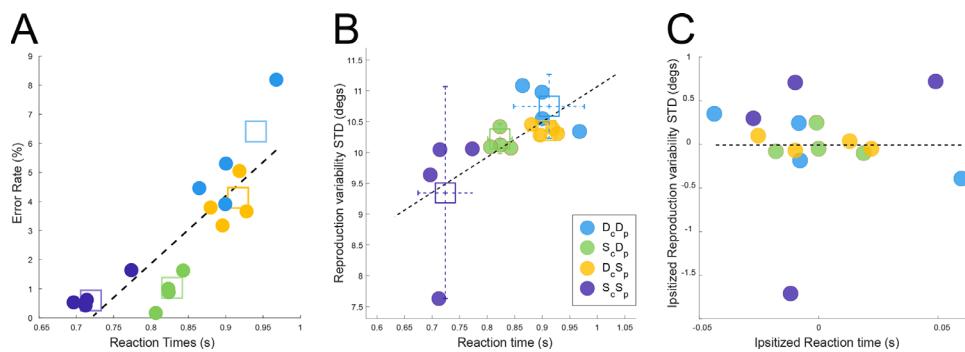


Figure 5. Reproduction errors plotted against reaction times for the four experimental conditions. (A) – Correlation between reaction times and error rate, for the data of Figure 2 (the squares illustrate average values, and the circles illustrate the values as a function of the run length). (B) Standard deviations of reproduction (a measure of imprecision) plotted against reaction times for the four experimental conditions, with average values shown as squares, and different run lengths shown by filled circles. There is clear evidence of positive correlation between the two measures (black dashed line, $r = 0.62$, $\log Bf10 = 0.71$), consistent with no speed-accuracy tradeoff, at least over different conditions. (C) Same data as B with the mean effects of the four experimental conditions subtracted out. Here, there is strong evidence for lack of correlation between the two measures (black dashed line, $r = -0.01$, $\log Bf10 = -0.74$), suggesting that the lack of speed-accuracy tradeoff is inherent in the different judgments made under different experimental conditions.

the variability induced by run-length, the correlation disappeared (Figure 5C; $r = -0.01$, $\log Bf10 = -0.74$). This suggests that the variability in reaction times caused by run length does not covary with reproduction precision.

Discussion

The aim of this study was to test whether visual priming and serial dependence share common mechanisms. Using a paradigm similar to that pioneered by Maljkovic and Nakayama (1994; Maljkovic & Nakayama, 1996) we were able to demonstrate robust priming for pop-out and serial dependence within the same experiment: there was considerable speeding of responses for repeated color and spatial position, with positive and negative effects accumulating over trials; and reproduction of orientation was systematically biased toward that of the previous trial. However, the conditions that led to an increase in priming of pop-out did not lead to greater serial dependence effects. Repetition of the same feature, particularly color, speeded reaction times considerably, with the effects accumulating over many trials. However, repetition had little effect on serial dependence: indeed, repetition of position slightly decreased the magnitude of serial dependence, and repetition of color had no significant effect. Similarly, there was no measurable effect of run length on serial dependence. There was no correlation between reaction times and strength of serial dependence in the various conditions of feature repetition, and substantial Bayesian evidence in favor

of lack of correlation. That the effects do not covary with the experimental manipulations strongly implies that they are mediated by different neural mechanisms.

Weaker serial dependence for targets in the same position may seem to contradict findings of a spatial tuning of the serial effect. However, all experiments which reported tuning have estimated a window larger than 10 degrees (Collins, 2019; Fischer & Whitney, 2014), whereas, here, the two positions for the target are only 6.14 degrees apart. Why is the effect actually weaker? One possibility is that, because priming improves precision (see Figure 5; Sigurdardottir, Kristjansson, & Driver, 2008) and precise stimuli display less serial dependence (Cicchini, Mikellidou, & Burr, 2018), the priming itself drives this decrease of serial dependence.

The total lack of correlation between the two effects was far from foregone. Both priming of pop-out and serial dependence tap some form of memory of perceptual history, which affects performance of the current trial. What mechanisms may serve the two paradigms, and in what key respects may they differ? Priming results in improved performance – revealed either in reaction times, accuracy or precision – whereas serial dependence results in systematic biases towards the previous targets. In Signal Detection Theory terms, priming increases sensitivity whereas serial dependence changes criteria. It seems reasonable that sensitivity and criteria, two orthogonal measures, tap different neural mechanisms, which have different properties. For example, increase of sensitivity by priming could tap attention-like mechanisms, keeping attention focused on a particular feature (color or position), with a disengagement cost when the feature changes.

Changes in criteria, or bias, on the other hand, are well modeled within the Bayesian framework by weighted combination of present and past information, similar to the processes that occur in combining information from different senses. That reaction times correlated well with the precision of reproduction (see [Figure 5](#)) rather than with the bias (see [Figure 4](#)) is consistent with the idea that different measures of sensitivity share the same mechanism, even when using quite different paradigms.

Recent theoretical ([Friston, Bastos, Pinotsis, & Litvak, 2015](#)) and experimental work has strongly implicated neural oscillations as a putative mechanism for transmitting contextual information over time, both for vision and audition. The frequency of context-dependent oscillations varies considerably. Broadly speaking, theta frequencies (4–8 Hz) seem to be associated with changes in sensitivity, and alpha/beta (8–18 Hz) with changes in criterium. Y. [Huang, Chen, and Luo \(2015\)](#) demonstrated theta oscillations associated with visual priming, suggesting the effect of priming is conveyed over time in an alternating theta-band rhythm. In addition, sensitivity for contrast detection ([Landau & Fries, 2012](#)) and discrimination ([Tomassini, Spinelli, Jacono, Sandini, & Morrone, 2015](#)) are modulated at a similar theta frequency. On the other hand, criteria for audiovisual temporal order judgment ([Benedetto, Burr, & Morrone, 2018](#)), and for judging the gender of the faces ([Bell, Burr, Crookes, & Morrone, 2020](#)) are oscillated within the alpha/beta range. In both the visual and auditory domains, different frequencies of oscillations for sensitivity and criteria have been demonstrated within the same experiment ([Benedetto & Morrone, 2019; Ho, Burr, Alais, & Morrone, 2022; Ho, Leung, Burr, Alais, & Morrone, 2017](#)). Sensitivity oscillated in the theta range, and criterion in the alpha range. Crucially, alpha oscillations have been recently linked to predictive coding mechanisms ([Alamia & VanRullen, 2019](#)) and to serial dependence effects ([Ho, Burr, Alais, & Morrone, 2019; Ho et al., 2022](#)).

Pupillometry studies also implicate multiple mechanisms in priming. Using the [Maljkovic and Nakayama \(1994\)](#) paradigm, [Pomè, Binda, Cicchini, and Burr \(2020\)](#) showed that switching the priming color was associated with an increase in pupil size. However, the increase in size did not accumulate over trials, like the reaction time advantage. Furthermore, the magnitude of the pupil dilation depended on personality traits, specifically “autistic-like traits,” whereas the reaction time advantage did not, all implicating multiple mechanisms in priming. Similarly, although serial dependence effects on face identity and gender are very robust ([Liberman et al., 2014; Taubert et al., 2016](#)), there appears to be no evidence for priming effects for facial recognition ([Ariga & Kawahara, 2004](#)).

Priming is one of the most venerable phenomena in perception, going back at least to [Lashley \(1951\)](#), and is

manifested over a whole range of areas, from linguistics to perception ([Bargh, 2014](#)). Serial dependence has been more recently described and studied intensely over the past 8 years. Given that priming is such a general phenomenon, it is tempting to suppose that the recently described serial dependence reflects yet another version of it, revealed by a different paradigm. However, the results of the current experiment suggest that this is not the case, but that they are two distinct processes. We suggest that a useful distinction is to consider priming to affect sensitivity (in Signal Detection terms), probably related to deployment and disengagement of attention mechanisms, whereas serial dependence reflects changes in criteria, resulting from integration with perceptual expectations. The two processes could be mediated, at least in part, by neural mechanisms, priming in the theta range ([Huang et al., 2015](#)), serial dependence in the alpha range ([Ho et al., 2019](#)).

Keywords: visual priming, serial dependence, sequential effects, priming of pop-out

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Corresponding author: Filippo Galluzzi.

Email: filippo.galluzzi@iit.it.

Address: IIT - Center for Synaptic Neuroscience and Technology, Padiglione IST-NORD, Largo Rosanna Benzi, 10, 16132 Genova GE, Italy.

References

- Alamia, A., & VanRullen, R. (2019). Alpha oscillations and traveling waves: Signatures of predictive coding? *PLoS Biol.*, 17(10), e3000487.
- Ariga, A., & Kawahara, J. (2004). The perceptual and cognitive distractor-previewing effect. *Journal of Vision*, 4(10), 891–903.
- Bargh, J. A. (2014). The historical origins of priming as the preparation of behavioral responses: Unconscious carryover and contextual influences of real-world importance. *Social Cognition*, 32(Supplement), 209–224.
- Bell, J., Burr, D. C., Crookes, K., & Morrone, M. C. (2020). Perceptual Oscillations in Gender Classification of Faces, Contingent on Stimulus History. *iScience*, 23(10), 101573.
- Benedetto, A., Burr, D. C., & Morrone, M. C. (2018). Perceptual Oscillation of Audiovisual Time

- Simultaneity. *eNeuro*, 5(3), ENEURO.0047-18.2018.
- Benedetto, A., & Morrone, M. C. (2019). Visual sensitivity and bias oscillate phase-locked to saccadic eye movements. *Journal of Vision*, 19(14), 15.
- Bliss, D. P., Sun, J. J., & D'Esposito, M. (2017). Serial dependence is absent at the time of perception but increases in visual working memory. *Scientific Reports*, 7(1), 1–13.
- Campana, G., Pavan, A., & Casco, C. (2008). Priming of first- and second-order motion: mechanisms and neural substrates. *Neuropsychologia*, 46(2), 393–398.
- Cicchini, G. M., Anobile, G., & Burr, D. C. (2014). Compressive mapping of number to space reflects dynamic encoding mechanisms, not static logarithmic transform. *Proceedings of the National Academy of Sciences*, 111(21), 7867–7872.
- Cicchini, G. M., Arrighi, R., Cecchetti, L., Giusti, M., & Burr, D. C. (2012). Optimal encoding of interval timing in expert percussionists. *Journal of Neuroscience*, 32(3), 1056–1060.
- Cicchini, G. M., Mikellidou, K., & Burr, D. C. (2018). The functional role of serial dependence. *Proceedings. Biological Sciences*, 285(1890), 20181722.
- Collins, T. (2019). The perceptual continuity field is retinotopic. *Scientific Reports*, 9(1), 1–6.
- Corbett, J. E., Fischer, J., & Whitney, D. (2011). Facilitating stable representations: serial dependence in vision. *PLoS One*, 6(1), e16701.
- Fecteau, J. H. (2007). Priming of pop-out depends upon the current goals of observers. *Journal of Vision*, 7(6), 1.
- Fischer, J., & Whitney, D. (2014). Serial dependence in visual perception. *Nature Neuroscience*, 17(5), 738–743.
- Friston, K. J. (2009). The free-energy principle: a rough guide to the brain? *Trends in Cognitive Sciences*, 13(7), 293–301.
- Friston, K. J., Bastos, A. M., Pinotsis, D., & Litvak, V. (2015). LFP and oscillations—what do they tell us? *Current Opinion in Neurobiology*, 31, 1–6.
- Gregory, R. L. (1980). Perceptions as hypotheses. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 290(1038), 181–197.
- Hillstrom, A. P. (2000). Repetition effects in visual search. *Perception & Psychophysics*, 62(4), 800–817.
- Ho, H. T., Burr, D. C., Alais, D., & Morrone, M. C. (2019). Auditory Perceptual History Is Propagated through Alpha Oscillations. *Current Biology : CB*, 29(24), 4208–4217.e4203.
- Ho, H. T., Burr, D. C., Alais, D., & Morrone, M. C. (2022). Propagation and update of auditory perceptual priors through alpha and theta rhythms. *European Journal of Neuroscience*, 55(11–12), 3083–3099.
- Ho, H. T., Leung, J., Burr, D. C., Alais, D., & Morrone, M. C. (2017). Auditory sensitivity and decision criteria oscillate at different frequencies separately for the two ears. *Current Biology*, 27(23), 3643–3649.e3643.
- Hollingworth, H. L. (1910). The central tendency of judgment. *The Journal of Philosophy, Psychology and Scientific Methods*, 7(17), 461–469.
- Huang, L., Holcombe, A. O., & Pashler, H. (2004). Repetition priming in visual search: Episodic retrieval, not feature priming. *Memory & Cognition*, 32(1), 12–20.
- Huang, Y., Chen, L., & Luo, H. (2015). Behavioral oscillation in priming: competing perceptual predictions conveyed in alternating theta-band rhythms. *Journal of Neuroscience*, 35(6), 2830–2837.
- Jazayeri, M., & Shadlen, M. N. (2010). Temporal context calibrates interval timing. *Nature Neuroscience*, 13(8), 1020–1026.
- John-Saaltink, E. S., Kok, P., Lau, H. C., & De Lange, F. P. (2016). Serial dependence in perceptual decisions is reflected in activity patterns in primary visual cortex. *Journal of Neuroscience*, 36(23), 6186–6192.
- Kersten, D., Mamassian, P., & Yuille, A. (2004). Object perception as Bayesian inference. *Annual Review of Psychology*, 55, 271–304.
- Kondo, A., Takahashi, K., & Watanabe, K. (2012). Sequential effects in face-attractiveness judgment. *Perception*, 41(1), 43–49.
- Kristjansson, A. (2006). Simultaneous priming along multiple feature dimensions in a visual search task. *Vision Research*, 46(16), 2554–2570.
- Kristjansson, A., & Campana, G. (2010). Where perception meets memory: a review of repetition priming in visual search tasks. *Attention, Perception & Psychophysics*, 72(1), 5–18.
- Kristjansson, A., & Driver, J. (2008). Priming in visual search: separating the effects of target repetition, distractor repetition and role-reversal. *Vision Research*, 48(10), 1217–1232.
- Kristjansson, A., Wang, D., & Nakayama, K. (2002). The role of priming in conjunctive visual search. *Cognition*, 85(1), 37–52.
- Landau, A. N., & Fries, P. (2012). Attention samples stimuli rhythmically. *Current Biology : CB*, 22(11), 1000–1004.

- Lashley, K. S. (1951). *The problem of serial order in behavior* (Vol. 21). Oxford, United Kingdom: Bobbs-Merrill.
- Liberman, A., Fischer, J., & Whitney, D. (2014). Serial dependence in the perception of faces. *Current Biology: CB*, 24(21), 2569–2574.
- Liberman, A., Zhang, K., & Whitney, D. (2016). Serial dependence promotes object stability during occlusion. *Journal of Vision*, 16(15), 16.
- Makovski, T., & Jiang, Y. V. (2008). Proactive interference from items previously stored in visual working memory. *Memory Cognition*, 36(1), 43–52.
- Maljkovic, V., & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory Cognition*, 22(6), 657–672.
- Maljkovic, V., & Nakayama, K. (1996). Priming of pop-out: II. The role of position. *Percept & Psychophysics*, 58(7), 977–991.
- Mamassian, P., Landy, M., & Maloney, L. T. (2002). Bayesian modelling of visual perception. *Probabilistic Models of the Brain*, 13, 36.
- Manassi, M., Liberman, A., Chaney, W., & Whitney, D. (2017). The perceived stability of scenes: serial dependence in ensemble representations. *Scientific Reports*, 7(1), 1971.
- Manassi, M., Liberman, A., Kosovicheva, A., Zhang, K., & Whitney, D. (2018). Serial dependence in position occurs at the time of perception. *Psychonomic Bulletin & Review*, 25(6), 2245–2253.
- Pomè, A., Binda, P., Cicchini, G. M., & Burr, D. C. (2020). Pupillometry correlates of visual priming, and their dependency on autistic traits. *Journal of Vision*, 20(3), 3.
- Rafiei, M., Chetverikov, A., Hansmann-Roth, S., & Kristjansson, A. (2021). You see what you look for: Targets and distractors in visual search can cause opposing serial dependencies. *Journal of Vision*, 21(10), 3.
- Rafiei, M., Hansmann-Roth, S., Whitney, D., Kristjansson, A., & Chetverikov, A. (2021). Optimizing perception: Attended and ignored stimuli create opposing perceptual biases. *Attention, Perception & Psychophysics*, 83(3), 1230–1239.
- Rao, R. P., & Ballard, D. H. (1999). Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, 2(1), 79–87.
- Sigurdardottir, H. M., Kristjansson, A., & Driver, J. (2008). Repetition streaks increase perceptual sensitivity in visual search of brief displays. *Visual Cognition*, 16(5), 643–658.
- Taubert, J., Alais, D., & Burr, D. (2016). Different coding strategies for the perception of stable and changeable facial attributes. *Scientific Reports*, 6(1), 32239.
- Tomassini, A., Spinelli, D., Jacono, M., Sandini, G., & Morrone, M. C. (2015). Rhythmic oscillations of visual contrast sensitivity synchronized with action. *Journal of Neuroscience*, 35(18), 7019–7029.
- Treisman, A. (1992). Perceiving and re-perceiving objects. *The American Psychologist*, 47(7), 862–875.
- Xia, Y., Leib, A. Y., & Whitney, D. (2016). Serial dependence in the perception of attractiveness. *Journal of Vision*, 16(15), 28.