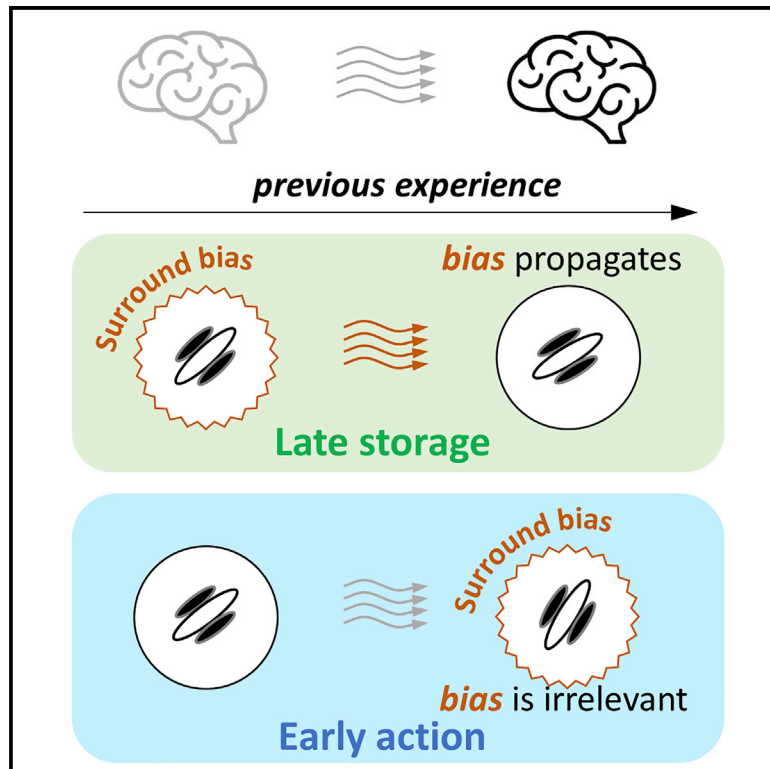


Current Biology

Perceptual history propagates down to early levels of sensory analysis

Graphical Abstract



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In Brief

Perception can be strongly biased by expectations, which are in part shaped by perceptual history. Cicchini et al. demonstrate that the bias is driven by signals from high levels of analysis propagating down to interact at relatively low levels, implicating a recurrent network in sensory analysis.

Highlights

- Perception is heavily biased by perceptual history and expectations
- Perceptual history includes illusory effects driven by spatial context
- This representation propagates back to sensory areas preceding context effects
- The results point to a neural architecture consistent with predictive coding

Report

Perceptual history propagates down to early levels of sensory analysis

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SUMMARY

One function of perceptual systems is to construct and maintain a reliable representation of the environment. A useful strategy intrinsic to modern “Bayesian” theories of perception^{1–6} is to take advantage of the relative stability of the input and use perceptual history (priors) to predict current perception. This strategy is efficient^{1–7} but can lead to stimuli being biased toward perceptual history, clearly revealed in a phenomenon known as serial dependence.^{8–14} However, it is still unclear whether serial dependence biases sensory encoding or only perceptual decisions.^{15,16} We leveraged on the “surround tilt illusion”—where tilted flanking stimuli strongly bias perceived orientation—to measure its influence on the pattern of serial dependence, which is typically maximal for similar orientations of past and present stimuli.^{7,10} Maximal serial dependence for a neutral stimulus preceded by an illusory one occurred when the perceived, not the physical, orientations of the two stimuli matched, suggesting that the priors biasing current perception incorporate the effect of the illusion. However, maximal serial dependence of illusory stimuli induced by neutral stimuli occurred when their physical (not perceived) orientations were matched, suggesting that priors interact with incoming sensory signals before they are biased by flanking stimuli. The evidence suggests that priors are high-level constructs incorporating contextual information, which interact directly with early sensory signals, not with highly processed perceptual representations.

RESULTS

We used a version of the “surround tilt illusion”¹⁷ to unravel the site of action of perceptual priors. In our implementation (Figure 1A), a target grating patch was displayed eccentrically, surrounded by four flanker gratings, all tilted 15° away from the orientation of the target. The flankers biased negatively the perceived orientation of the target by about 15° (Figure 1C). To probe the effects of flanker bias on serial dependence, these illusory stimuli were displayed within sequences interspersed with neutral stimuli (Figure 1B), which were similar targets flanked by non-oriented noise stimuli.

Figure 1D illustrates the rationale of the experiment. Serial dependence for orientation judgments follows a stereotypical, signature pattern: strong positive assimilation toward the previous stimulus, which increases with orientation difference up to about 15° and then falls off back to zero at about 30°. ^{7,10,16} This is well modeled by assuming that the weight given to the past stimulus is maximal when the orientations of the previous and current stimuli coincide and then falls off within a Gaussian profile (as predicted by ideal observer models).^{7,8} The bias (given by the product of orientation difference and weight) is well fit by the product of a Gaussian and the equality line, approximating the antisymmetric Gaussian derivative functions (δG) shown in

Figure 1D. We examined how the tilt illusion may affect this signature δG . In illusory trials, responses will be biased by the surrounds, causing a vertical shift of the response pattern (blue curves). The curves may also be displaced horizontally, depending on whether maximal serial dependence occurs when physical (blue dashed line) or perceived (blue dotted line) orientations match. Neutral trials following illusory presentations (green curves) should not be shifted vertically but will be displaced horizontally if serial dependence is driven by the *perceived* (green dashed line) rather than physical (green dotted line) orientation of previous trial, which incorporates the antagonistic effect of the surround flankers.

We tested these predictions with a design that interspersed one illusory trial within a quadruplet of trials to create three distinct trial categories: neutral trials preceded by neutral trials (black frame in Figure 1B); neutral trials preceded by illusory trials (green frame); and illusory trials preceded by neutral trials (blue frame). For each category, we plotted the bias (reproduced minus physical orientation) of the current trial as a function of relative orientation of the previous trial (previous minus current physical orientation). Figure 2A shows results for aggregate data (pooled over all participants) for neutral-neutral trials. The bias follows the pattern typically seen with serial dependence:^{7,10} there is strong positive assimilation toward the

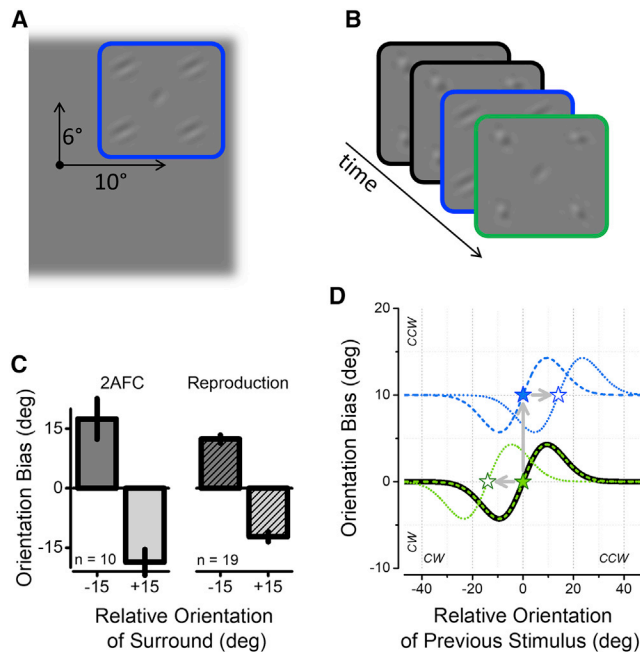


Figure 1. Stimuli and predicted results

(A) The target grating patch was displayed eccentrically to the upper right quadrant (centered at $+10^\circ$, $+6^\circ$), surrounded by four flanker gratings. In illusory trials, the flankers were all tilted 15 clock degrees away from the orientation of the target; for neutral trials, the flankers were non-oriented random noise. Participants reproduced the orientation of the central target grating.

(B) Illustration of the four-trial sequence of stimuli. Each quadruplet started with a neutral trial (target surrounded by noise patches), with target orientation selected randomly. This was followed by another neutral trial, an illusory trial, and then a neutral trial, all differing by a random orientation between $\pm 30^\circ$ from the previous. The black, blue, and green frames color code the type of trial (neutral preceded by neutral, illusory preceded by neutral, and neutral preceded by illusory trial, respectively).

(C) Average orientation bias induced by flanker gratings. The non-hatched bars at left are average measurements from a 2AFC technique (see STAR Methods); hatched bars at right average data from the main experiment, using the reproduction technique. There was no significant difference between the two methods (2AFC mean: 17.4° , -18.7° ; reproduction mean: 13.1° , -12.6° ; two-tailed paired t test on flipped values: $t(9) = 1.76$; $p = 0.11$).

(D) Illustration of the "signature" of serial dependence for orientation judgments, well modeled by a derivative of Gaussian (δG) function, for an exemplar case in which the illusory trial contained flankers with a negative CW tilt (inducing a positive CCW bias, illustrated here as a $+10^\circ$ displacement). The bias comprises both the repulsive effects of the surround flankers and the serial dependence of the previous trial. If the current trial is an illusory one (blue lines), the surround illusion should cause the template curve to shift vertically. Orthogonal horizontal shifts could also occur, if the illusory orientation was incorporated within the prior (dotted blue). Neutral trials following illusory trials should not be shifted vertically but may be shifted horizontally by the illusory bias of the previous trial (dotted green curve). The stars, here and Figure 2, correspond to the center of the curve.

previous stimulus, rising to a maximum for differences around 15° and then falling off for larger differences.

Figure 2B shows results for neutral trials preceded by illusory trials, separately for clockwise (CW) and counterclockwise (CCW) flankers (dark and light green, respectively). If serial dependence were driven by the physical orientation of the

previous target grating, both conditions should align horizontally, with the centers of the fitted curves both near zero, like the neutral-neutral data; if driven by the perceived orientation of the previous grating, however, the curves should shift horizontally against the illusion to offset its effect. The data show that perceived orientation drove serial dependence. The curve fitting trials preceded by CW flankers (causing a positive CCW illusion) is clearly displaced in the negative direction, although that for trials preceded by CCW flankers is shifted in the positive direction. The magnitudes of the shifts are, respectively, $-11.2^\circ \pm 3.7^\circ$ and $+8.2^\circ \pm 3.7^\circ$ (mean and SEM), similar to the shifts created by the surround illusion (-12.6° and $+13.1^\circ$, respectively).

Figure 2C shows the results for the complementary class of trials, where the current trial was illusory (with oriented flankers) and the previous trial was neutral. As expected, the flankers heavily biased the orientation of the current trials, causing a large vertical displacement of the data (note the break in the ordinate). However, this bias did not change the horizontal pattern of serial dependence. For both conditions, the centers of the fitted δG functions are near zero, consistent with serial dependence acting on physical rather than perceived orientation, before the orientation is influenced by the surrounding flankers. The centers of the curves are at $+1.5^\circ \pm 3.4^\circ$ and $+3.3^\circ \pm 3^\circ$ and for CW and CCW flankers, respectively (blue and navy blue), both statistically indistinguishable from 0° . The data are not consistent with an interaction after the surround illusion takes effect, which predicts that the curves be centered on the dashed vertical lines ($+12.6^\circ$ and -13.1°).

We complemented this aggregate analysis with an analysis of individual participants, using the same procedure as that for the aggregate data. For the two illusory conditions, we fitted the δG curve to the serial dependence data (like Figures 2B and 2C for aggregate data) and then plotted the centers of the curve fits against the average bias induced by the slanted flankers for that participant and condition.

Figure 3A shows results for neutral trials preceded by illusory trials. There is a clear negative correlation in the data (slope = -0.70 ± 0.11 ; $r = -0.71$; $p < 10^{-5}$; $\text{BF}_{10} > 10^4$), showing that the centers of the fitted serial dependence curves are strongly related to, and almost equal (and opposite) to, the average bias in the previous trials. The dashed lines show the predictions if serial dependence was anchored with physical or perceived orientation (0° and -45° slope, respectively). We calculated the Bayes factor as the ratio of the likelihoods of following each of these lines (see STAR Methods): $\text{BF}_{10} > 10^4$, definitive evidence for the alternate hypothesis, that the center of the model is closer to the perceived than physical orientation of the preceding stimulus.

Figure 3B plots the other interesting condition: illusory trials preceded by neutral stimuli, again plotted against average bias induced by slanted flankers. Here, the results are quite different. There is no clear dependency on bias magnitude, with slope of linear fit equal to 0.09 ± 0.15 ($r = 0.11$; $p > 0.5$; $\text{BF}_{10} = 0.24$). Again, we tested the predictions of the models, that the serial dependence should follow either the physical or perceived orientation of the preceding stimulus. In this case, the data follow the physical orientation prediction. The relative likelihoods yield $\text{BF}_{10} < 10^{-4}$, definitive evidence in favor of the null hypothesis (physical orientation).

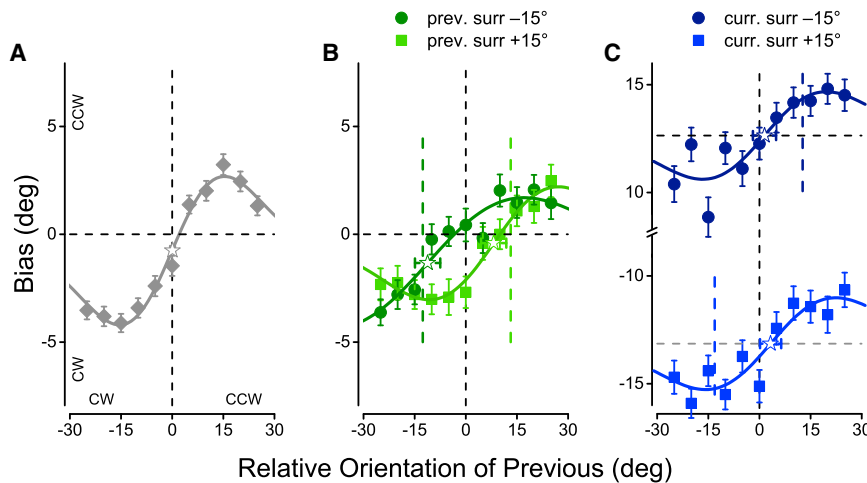


Figure 2. Serial dependence effects for different conditions, for the aggregate observer

(A) Average bias (reproduced minus physical angle) of the current trial for neutral stimuli preceded by neutral stimuli, plotted against the previous minus current physical orientation (by convention, counterclockwise [CCW] is positive). The gray curve is the best fitting δG fit (see STAR Methods), with the star marking its center. Vertical error bars indicate ± 1 SEM of the aggregate observer data (about 250–300 points each) and horizontal error bar ± 1 SEM of the center of curve fit obtained by bootstrapping.

(B) Results for neutral trials preceded by illusory trials, separately for -15° (CW, dark green) and $+15^\circ$ (CCW, light green) flankers (conventions as for A). The color-coded vertical dashed lines show the average bias needed to offset that induced by the flankers for that condition. These

pass within 1 SEM of the centers of the δG fits. Dashed vertical lines indicate point of maximal serial effect if the effect arose after (thick lines) or before (thin line) the illusion had exerted its effect.

(C) Results for illusory trials (navy blue -15° flankers; blue $+15^\circ$) preceded by neutral trials (conventions as for A). Note the difference in the ordinates, reflecting the effect of the flankers on the current trial. Besides this difference, both best-fitting δG curves pass near zero, within 1 SEM. Dashed vertical lines indicate the predicted maximal serial effect, if the priors act after (thick lines) or before (thin line) the illusion had exerted its effect.

DISCUSSION

The analysis of both the aggregate and individual data leads to the same conclusion. The priors that influence future perception incorporate all contextual effects, consistent with their generation at moderately high stages of processing; but they act at a level that does not include the influence of the tilted flanker gratings. As physiological studies suggest that the surround tilt illusion is mediated by specific inhibitory circuitry operating within primary and secondary visual cortex,^{9,18–20} the site of action of the priors must also be relatively early.

Many researchers have suggested that perceptual systems adopt efficient hierarchical generative strategies to boost efficiency of sensory encoding. One clear example is hierarchical predictive coding,^{1,6} where the system predicts the current state of the world from statistical regularities (priors) of the

environment and tests those predictions against current input. The priors, also termed internal templates,²¹ are assumed to be generated by the hierarchical network and fed back to test against input at lower levels.¹ The results of the current study, along with much previous literature,^{10,15,22,23} are consistent with (but do not prove) this idea. Figure 4 schematically illustrates the idea. Prior expectations are constructed from recent perceptual history (which includes the effects of spatial context) and tested against sensory input, leading to a correction signal (ϵ), which is again propagated through the perceptual cascade. That serial dependence curves are centered on the physical rather than the perceived orientation suggests that the expectation error is calculated against a sensory input that does not include the influence of spatial context. The diagram represents this idea conceptually, with the error signal calculated before the site where contextual

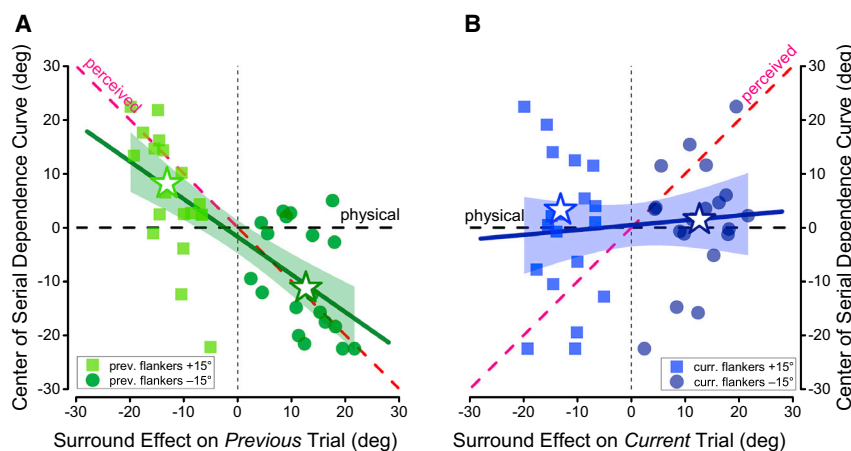


Figure 3. Dependence of the shift of serial dependence on the magnitude of the surround illusion

(A) Neutral trials preceded by illusory trials. For each participant ($N = 19$), we plot the center of the curve describing serial effects (the locus of maximal effect) as function of the average illusory bias for that participant. Star symbols show results of the aggregate observer. Light green symbols show results when the previous flanker orientation was $+15^\circ$ (CCW), dark green -15° (CW). The thick green line shows the best linear regression along with confidence bands. Black and pink dashed lines represent the predictions if the serial dependence were based on physical or perceived orientation, respectively.

(B) Same as in (A) but for conditions where an illusory trial succeeds a neutral trial. Blue and navy-blue symbols refer to previous flanker orientations of $+15^\circ$ or -15° , respectively. The thick blue line shows the best linear regression.

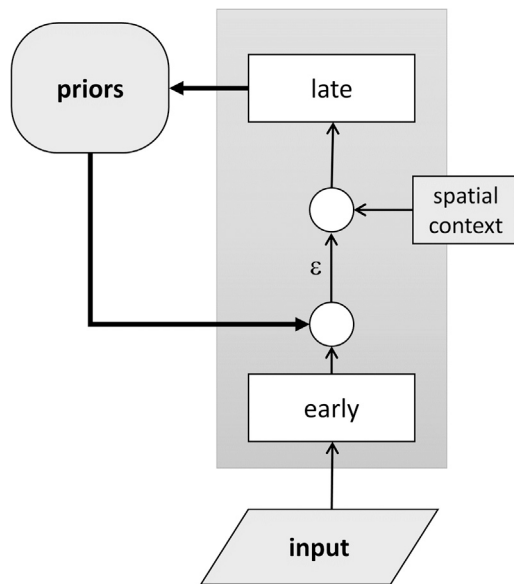


Figure 4. Serial dependence in a predictive coding framework

Predictive coding assumes that perception arises from the interaction of prior expectations with bottom-up signals carrying new information. Perceptual expectations, generated at higher levels, are fed back to earlier brain sites (thick arrow loop) so that only unexpected information (prediction error [ϵ]) is carried over. Our results suggest priors are compared to sensory information that does not include spatial context of the current trial. Spatial context, however, contributes to the formation of the priors that affect subsequent presentations.

effects of tilted surrounds influence perception. In practice, the two processes could be performed independently in parallel, leading to a similar result. However, the error could not be calculated at a later decisional stage¹⁶ that includes the spatial context effects, as that would lead to a horizontal shift of the serial dependence curves in the illusory trials, which was not observed.

The overall weighting given to perceptual history varies predictably with many factors, such as the noisiness of the current and previous stimuli.^{7,8} Crucially, it also depends on the difference between the current and previous stimulus attribute (orientation in this case): if the orientations are similar (leading to relatively small error signals), both past and current signals were probably generated by the same stimulus, so it is efficient to integrate them; but if they differ greatly, it is more probable that there has been a discontinuity, and integration would be disadvantageous. It is this property that distinguishes the intelligent “Kalman filter-like” operation of serial dependence from simple low-pass smoothing;²⁴ and this causes the data to follow the characteristic signature δG pattern, with effects falling off with orientation difference to tail off around 30°. An important unsolved problem is how the system determines whether the previous stimulus was similar to the present. The current results suggest that, for simple tasks, such as orientation judgments, the integration weight is determined at relatively low levels of sensory analysis, before the illusory inducers act. Under the predictive coding model, integration weight could depend on the size of the error signal, attenuating with error following a Gaussian function.

An alternative, somewhat speculative (but testable) mechanism for the selective effects of serial dependence is that orientation priors feed back to primary visual cortex to sensitize neurons tuned to that orientation, perhaps by increasing their gain. Subsequent stimulation of that orientation would evoke a stronger response, which would bias the population response (and perception) toward that orientation. This bias would be limited to the extent of the tuning width of orientated detectors: unless the current stimulus falls within the tuning spectrum of the sensitized orientation-selective neurons, it will not stimulate them, and its response will not be boosted. This idea is highly speculative but is broadly consistent with the orientation tuning bandwidth of cells in primary visual cortex, in the order of $\pm 15^\circ$,²⁵ comparable to the selectivity of serial dependence. It is also consistent with the phenomenon of “repetition priming,” the improvement in accuracy and response times for repeated stimuli,^{26–28} as well as with fMRI studies decoding the presence of priors in primary visual cortex.²² Future studies could test the notion directly, examining whether repetitive priming is affected by the tilt surround illusion.

Although the mechanisms mediating serial dependence remain far from clear, our findings with orientation judgments point to a relatively early site of action of the priors, a site encoding raw orientation signals unaffected by spatial context. Obviously, this does not exclude the role of other factors, like attention^{10,29} and confidence,^{30–32} or processes such as short-term memory.^{16,33–36} How these interact with the early mechanisms revealed in this study remains open, subject to further research.

It is interesting that different forms of contextual effects can operate together, superimposing their effects. The tilt surround illusion is an antagonistic, negative effect induced by simultaneous presentation of slanted flanker gratings (akin to negative after effects over time), well modeled by assuming gain control operations operate over extended regions.⁹ Serial dependence operates over time, rather than space, and results in a positive biasing of orientation (again, possibly via gain control mechanisms, as mentioned above). The two effects coexist in the current experiment and, within our simplistic design, seem to sum linearly. However, in real-world situations, where both objects of interest and non-attended objects providing context may all undergo history effects, the interactions could be considerably more complex. This remains an interesting problem, requiring further investigation with more complex experimental designs.

It has been known for decades that perception depends strongly on contextual effects.³⁷ The present results show how one form of contextual influence, perceptual expectations or priors, are high-level constructs incorporating contextual information and that these priors can act on lower level incoming signals. This underlines the fact that serial effects operate through a network rather than at a single, local level, a feedback network similar to that assumed by predictive coding models of vision.¹

STAR★METHODS

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AUTHOR CONTRIBUTIONS

A.B. conceived the original idea. All authors contributed to the experimental design, and A.B. and G.M.C. collected and analyzed the data. All authors contributed to the interpretation of the results and to writing the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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REFERENCES

1. Rao, R.P., and Ballard, D.H. (1999). Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nat. Neurosci.* *2*, 79–87.
2. Mamassian, P., Landy, M., and Maloney, L.T. (2002). Bayesian modelling of visual perception. In *Probabilistic Models of the Brain: Perception and Neural Function*, R.P.N. Rao, B.A. Olshausen, and M.S. Lewicki, eds. (MIT), pp. 13–36.
3. Kersten, D., and Yuille, A. (2003). Bayesian models of object perception. *Curr. Opin. Neurobiol.* *13*, 150–158.
4. Kersten, D., Mamassian, P., and Yuille, A. (2004). Object perception as Bayesian inference. *Annu. Rev. Psychol.* *55*, 271–304.
5. Knill, D.C., and Pouget, A. (2004). The Bayesian brain: the role of uncertainty in neural coding and computation. *Trends Neurosci.* *27*, 712–719.
6. Friston, K. (2009). The free-energy principle: a rough guide to the brain? *Trends Cogn. Sci.* *13*, 293–301.
7. Cicchini, G.M., Mikellidou, K., and Burr, D.C. (2018). The functional role of serial dependence. *Proc. Biol. Sci.* *285*, 20181722.
8. Cicchini, G.M., Anobile, G., and Burr, D.C. (2014). Compressive mapping of number to space reflects dynamic encoding mechanisms, not static logarithmic transform. *Proc. Natl. Acad. Sci. USA* *111*, 7867–7872.
9. Clifford, C.W.G. (2014). The tilt illusion: phenomenology and functional implications. *Vision Res.* *104*, 3–11.
10. Fischer, J., and Whitney, D. (2014). Serial dependence in visual perception. *Nat. Neurosci.* *17*, 738–743.
11. Liberman, A., Fischer, J., and Whitney, D. (2014). Serial dependence in the perception of faces. *Curr. Biol.* *24*, 2569–2574.
12. Cicchini, G.M., and Kristjánsson, Á. (2015). Guest editorial: on the possibility of a unifying framework for serial dependencies. *i-Perception* *6*, 2041669515614148.
13. Taubert, J., Van der Burg, E., and Alais, D. (2016). Love at second sight: sequential dependence of facial attractiveness in an on-line dating paradigm. *Sci. Rep.* *6*, 22740.
14. Kiyonaga, A., Scimeca, J.M., Bliss, D.P., and Whitney, D. (2017). Serial dependence across perception, attention, and memory. *Trends Cogn. Sci.* *21*, 493–497.
15. Cicchini, G.M., Mikellidou, K., and Burr, D. (2017). Serial dependencies act directly on perception. *J. Vis.* *17*, 6.
16. Fritsche, M., Mostert, P., and de Lange, F.P. (2017). Opposite effects of recent history on perception and decision. *Curr. Biol.* *27*, 590–595.
17. Gibson, J.J. (1937). Adaptation, after-effect, and contrast in the perception of tilted lines. II. Simultaneous contrast and the areal restriction of the after-effect. *J. Exp. Psychol.* *20*, 553–569.
18. Gilbert, C.D., and Wiesel, T.N. (1990). The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat. *Vision Res.* *30*, 1689–1701.
19. Sengpiel, F., Sen, A., and Blakemore, C. (1997). Characteristics of surround inhibition in cat area 17. *Exp. Brain Res.* *116*, 216–228.
20. Cavanaugh, J.R., Bair, W., and Movshon, J.A. (2002). Selectivity and spatial distribution of signals from the receptive field surround in macaque V1 neurons. *J. Neurophysiol.* *88*, 2547–2556.
21. Pascucci, D., Mancuso, G., Santandrea, E., Della Libera, C., Plomp, G., and Chelazzi, L. (2019). Laws of concatenated perception: Vision goes for novelty, decisions for perseverance. *PLoS Biol.* *17*, e3000144.
22. St John-Saaltink, E., Kok, P., Lau, H.C., and de Lange, F.P. (2016). Serial dependence in perceptual decisions is reflected in activity patterns in primary visual cortex. *J. Neurosci.* *36*, 6186–6192.
23. Collins, T. (2019). The perceptual continuity field is retinotopic. *Sci. Rep.* *9*, 18841.
24. Burr, D., and Cicchini, G.M. (2014). Vision: efficient adaptive coding. *Curr. Biol.* *24*, R1096–R1098.
25. Blakemore, C., and Campbell, F.W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *J. Physiol.* *203*, 237–260.
26. Tulving, E., and Schacter, D.L. (1990). Priming and human memory systems. *Science* *247*, 301–306.
27. Wiggs, C.L., and Martin, A. (1998). Properties and mechanisms of perceptual priming. *Curr. Opin. Neurobiol.* *8*, 227–233.
28. Kristjánsson, A., and Campana, G. (2010). Where perception meets memory: a review of repetition priming in visual search tasks. *Atten. Percept. Psychophys.* *72*, 5–18.
29. Fritsche, M., and de Lange, F.P. (2019). The role of feature-based attention in visual serial dependence. *J. Vis.* *19*, 21.
30. Braun, A., Urai, A.E., and Donner, T.H. (2018). Adaptive history biases result from confidence-weighted accumulation of past choices. *J. Neurosci.* *38*, 2418–2429.
31. Suárez-Pinilla, M., Seth, A.K., and Roseboom, W. (2018). Serial dependence in the perception of visual variance. *J. Vis.* *18*, 4.
32. Bosch, E., Fritsche, M., Ehinger, B.V., and de Lange, F.P. (2020). Opposite effects of choice history and evidence history resolve a paradox of sequential choice bias. *J. Vis.* *20*, 9.
33. Papadimitriou, C., Ferdoash, A., and Snyder, L.H. (2015). Ghosts in the machine: memory interference from the previous trial. *J. Neurophysiol.* *113*, 567–577.
34. Bliss, D.P., Sun, J.J., and D’Esposito, M. (2017). Serial dependence is absent at the time of perception but increases in visual working memory. *Sci. Rep.* *7*, 14739.

35. Fischer, C., Czoschke, S., Peters, B., Rahm, B., Kaiser, J., and Bledowski, C. (2020). Context information supports serial dependence of multiple visual objects across memory episodes. *Nat. Commun.* *11*, 1932.
36. Stein, H., Barbosa, J., Rosa-Justicia, M., Prades, L., Morató, A., Galan-Gadea, A., Ariño, H., Martínez-Hernández, E., Castro-Fornieles, J., Dalmau, J., and Compte, A. (2020). Reduced serial dependence suggests deficits in synaptic potentiation in anti-NMDAR encephalitis and schizophrenia. *Nat. Commun.* *11*, 4250.
37. Gregory, R.L. (1980). Perceptions as hypotheses. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* *290*, 181–197.
38. Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., and Broussard, C. (2007). What's new in psychtoolbox-3? *Perception* *36*, 1–16.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
MATLAB r2016b	The MathWorks	SCR_001622
Psychophysics Toolbox 3	http://psychtoolbox.org/	SCR_002881
JASP 0.9.2	https://jasp-stats.org	SCR_015823

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to the Lead Contact, David Burr (dave@in.cnr.it).

Materials availability

There is no restriction for distribution of materials.

Data and code availability

For data analysis, we used off-the-shelf routines available in MATLAB (version R2016b) in combination with the JASP (version 0.9.2). Experimental data are downloadable at Zenodo repository: <https://zenodo.org/record/4362291#.X94jCthKhPY>.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

19 healthy human participants with normal or corrected-to-normal were recruited for the experiment (18–55 years-old, mean age = 32, 11 females). Experimental procedures are in line with the declaration of Helsinki and were approved by the regional ethics committee (*Comitato Etico Pediatrico Regionale – Azienda Ospedaliero-Universitaria Meyer – Firenze, FI*). Written informed consent was obtained from each participant, which included consent to process and preserve the data and publish them in anonymous form.

METHOD DETAILS

Measurements were made in a quiet room in dim lighting conditions. The stimuli were generated in MATLAB (r2016b; MathWorks) with Psychtoolbox,³⁸ and displayed on a linearized LCD monitor (refresh rate of 60 Hz) positioned 57 cm from the observer.

Orientation reproduction

The stimulus comprised a visual target surrounded by four visual flankers, presented against a uniform gray background. The target was a grating (15% contrast; 0.56 cycles-per-degree) vignetted within a Gaussian window (FWHM = 1.04°), and presented in the right upper quadrant (centered at +10°, +6°). The four flankers were either grating patches (15% contrast, 0.8 cpd, FWHM = 1.56°) tilted ± 15° away from the target orientation, or band-limited noise patches created by summing five gratings of frequency 0.56 ± 0.1 cpd with pseudo-random orientations and phases. The random patches were windowed by a Gaussian function (FWHM = 1.56°), then normalized to have a peak contrast of 15%.

Experimental sessions were a sequence of quadruplets of trials, each comprising two initial *neutral* trials with flanking noise patches, one *illusory* trial with tilted flankers, then a further neutral trial (Figure 1B). Each quadruplet started with a new orientation extracted at random to ensure that all possible orientations were presented, with several large inter-trial changes of orientation. The other trials in the quadruplet increased or decreased in orientation by 0–30°. A typical session included 15 quadruplets (60 trials).

Participants maintained fixation on a small red dot (0.25°) at the center of the display. After a random delay the stimulus appeared on the screen for 250 ms, to be replaced by a rotatable bar controlled by mouse, presented below the fixation point. Participants reproduced the orientation of the grating and initiated the next trial by pressing a button on the keyboard.

Trials with a reproduction error greater than 35° were discarded and excluded from further analysis (2.9% of trials). All participants responded to between 975 and 3516 trials.

2AFC Orientation judgment

The tilt surround illusion was also measured with a 2AFC procedure where participants were presented with two stimuli (one to the left one to the right) and chose which was more clockwise. The stimulus on the right was the same as that of the illusory trials of the main experiment, thus surrounded by four gratings all oriented 15 clockwise or counter-clockwise from the target orientation. The stimulus

on the left was presented in isolation at the same horizontal and vertical eccentricity, and had a variable orientation respect to the target (ranging between $\pm 30^\circ$). For each participant, responses were separated according to the relative surround orientation, binned according to orientation difference between probe and target, and fitted with a cumulative Gaussian curve, whose median estimates the point of subjective equality between the probe and the target. 10 participants from the main experiment took part in these measurements, each contributing with minimum 60 trials per curve.

QUANTIFICATION AND STATISTICAL ANALYSIS

Trials were divided into three types: 1) neutral trials preceded by neutral trials; 2) illusory trials preceded by a neutral trial; 3) neutral trials preceded by illusory trials. Illusory trials were separated into positive and negative flankers. For each trial type we plot the bias in the current response (the difference between the reproduced and physical angle) as function of the orientation difference between the previous and the current stimulus (see Figure 2), where by convention positive is Counter-Clockwise (CCW) and negative Clockwise (CW). For each condition we fit the data with a first derivative of Gaussian function (∂G), approximated by a point by point multiplication of a linear and a Gaussian tuning function.

$$y = A x e^{-\frac{(x-\mu)^2}{\sigma^2}} + B \quad (\text{Equation 1})$$

Where μ indicates the center of the Gaussian tuning (the orientation difference leading to maximal effect), σ the width of the Gaussian (the range of the effect), A the maximal amplitude of the effect and B a constant response bias (independent of the previous trial).

For the aggregate participant fits (like those displayed in Figure 2) we allowed all parameters to vary freely. For individual data we first fitted the serial dependence occurring in trials with no bias, to determine all parameters, then fixed σ for subsequent fits for that participant (three free parameters).

For data analysis, we used off-the-shelf routines available in MATLAB (version R2016b) in combination with the JASP (version 0.9.2). Bayes Factors were calculated using JASP 0.9.2 (<https://jasp-stats.org>). When comparing two linear regressions we calculated the two BFs of the best fitting line either against a flat line (null hypothesis, serial dependence independent of the orientation illusion) or against the identity line (serial dependence incorporating the illusion). The ratio between these two values yields the Bayes factor of the “incorporating the illusion” model against the null.