

# Serial dependence in visual perception

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Visual input often arrives in a noisy and discontinuous stream, owing to head and eye movements, occlusion, lighting changes, and many other factors. Yet the physical world is generally stable; objects and physical characteristics rarely change spontaneously. How then does the human visual system capitalize on continuity in the physical environment over time?

We found that visual perception in humans is serially dependent, using both prior and present input to inform perception at the present moment. Using an orientation judgment task, we found that, even when visual input changed randomly over time, perceived orientation was strongly and systematically biased toward recently seen stimuli. Furthermore, the strength of this bias was modulated by attention and tuned to the spatial and temporal proximity of successive stimuli. These results reveal a serial dependence in perception characterized by a spatiotemporally tuned, orientation-selective operator—which we call a continuity field—that may promote visual stability over time.

A crucial function of vision is detecting important changes in the environment, and sensory adaptation aids in maximizing sensitivity to change. The visual system adapts to properties such as color, orientation, object and scene properties, and many others<sup>1,2</sup>, thereby optimizing how it responds to changes in these attributes<sup>3–5</sup>. Adaptation is a simple, but powerful, mechanism for leveraging past visual input to maximize change sensitivity, but there is a flip side to the coin: the physical world is largely stable and continuous over time. Objects, scenes and physical properties tend to persist over time, making the recent past a good predictor of the present<sup>6</sup>. The visual system may therefore delicately balance the need to optimize sensitivity to image changes with the desire to capitalize on the temporal continuity of the physical environment. It may often be advantageous to assume that the present visual environment is similar to the one seen moments ago.

One means of combating noise and stabilizing visual estimates would be to introduce serial dependence to visual perception, to systematically bias perception at the present moment toward input from the recent past. The information necessary for such serial dependence to occur may be retained by the visual system—observers can maintain precise information about basic visual features over long delays<sup>7</sup>, sometimes even in the face of intervening stimuli<sup>8</sup>. However, the existence of such a memory trace does not necessarily imply that it alters the perception of future stimuli or that serial dependence occurs in perception. Indeed, maximally independent perception from one moment to the next would carry its own advantages, for example, in reducing systematic biases over time. Furthermore, given the known benefits of adaptation and ubiquitous negative aftereffects<sup>5</sup>, it may be that negative aftereffects dominate over any positive serial dependence in perception. Although serially dependent perception would be a simple means of capitalizing on the continuity of the physical environment, whether such an effect actually arises in perception remains to be tested.

We tested for serial dependence in visual perception using an orientation judgment task. Subjects viewed a series of randomly oriented gratings presented several seconds apart in time and reported the perceived orientation of each grating using an adjustment response. We found that perceived orientation was strongly and systematically attracted toward orientations seen over the last several seconds. This perceptual serial dependence was modulated by attention and was spatially tuned, occurring more strongly for successive stimuli that appeared nearby in space. Several control experiments revealed that the perceptual serial dependence we observed cannot be explained by any known effect of priming, hysteresis, explicit memory or expectation. Our results suggest a systematic influence of recent visual input on orientation perception at any given moment: perceived orientation, even of unambiguous stimuli, is attracted toward visual input from the recent past.

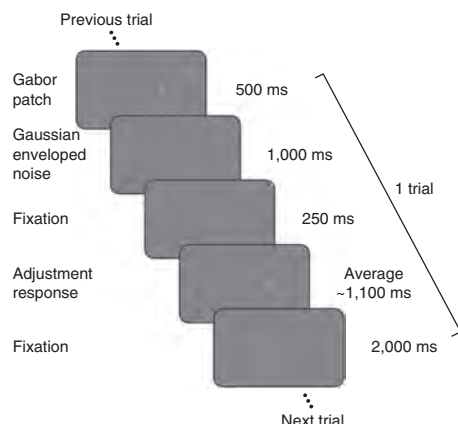
## RESULTS

### Serial dependence in orientation perception

To test for serial dependence in perception, we presented subjects with suprathreshold (25% Michelson contrast) Gabor stimuli and asked them to report the orientation of each Gabor by adjusting a response bar (experiment 1; **Fig. 1**). Stimuli were presented for 500 ms and separated in time by about 5 s (variability in trial duration was introduced by the time it took to make a response). Subjects' error distributions (reported orientation minus correct orientation; **Fig. 2a**) revealed that, although responses were centered on the correct orientations over the course of the entire experiment, on a trial-by-trial basis the reported orientation was systematically (and precisely) biased in the direction of the orientation seen on the previous trial. For example, when the Gabor on the previous trial was oriented more clockwise than the Gabor on the present trial, subjects perceived the present Gabor as being tilted more clockwise than its true

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Received 28 September 2013; accepted 5 March 2014; published online 30 March 2014; doi:10.1038/nn.3689

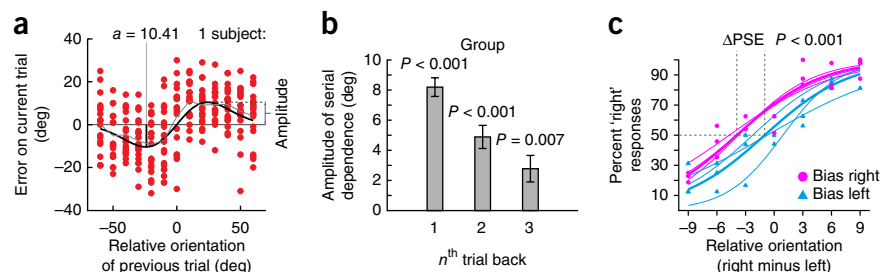


**Figure 1** Experiment 1 event sequence. Participants viewed high-contrast, suprathreshold Gabor patches presented to either the left or right of fixation (on separate, interleaved runs) and reported the perceived orientation of each Gabor by adjusting the orientation of a response bar.

orientation (**Supplementary Fig. 1**). This attraction followed a derivative-of-Gaussian (DoG)-shaped curve (**Fig. 2a**) with an amplitude of  $\pm 8.19^\circ$  in positive and negative directions for the group ( $P = 10^{-6}$ , permutation test, see Online Methods). Each individual subject also showed a significant attraction (all  $P < 0.01$ , permutation tests). On trials in which the Gabor orientation was very similar to the orientation presented on the previous trial, the attraction effect was nearly perfect, revealed by the near unit slope around zero on the abscissa. This means that the reported orientation of a Gabor on the current trial could be completely captured by the previously seen orientation. The effect was tuned to the relative orientations of the present and previous stimuli, peaking in amplitude when the difference in orientation between trials was  $27.78^\circ$  in either the clockwise or counter-clockwise direction. Put in context, two gratings that were separated by more than three times the just-noticeable difference (three JNDs) could look identical depending on what preceded them (**Supplementary Fig. 2**). The amplitude of serial dependence fell off with an increasing number of intervening trials (**Fig. 2b**), but the attraction was still significant for stimuli seen two and three trials (~15 s) back (two-back amplitude of  $\pm 4.89^\circ$ ,  $P = 0.0004$ ; three-back amplitude of  $\pm 2.78^\circ$ ,  $P = 0.007$ ; permutation tests). A control experiment confirmed that serial dependence in perceived orientation arose for both a counter-balanced stimulus sequence (Online Methods) and a fully randomized stimulus sequence (**Supplementary Fig. 3**), both of which were free of correlation between the orientation in a given trial and the relative orientations seen in preceding trials (**Supplementary Fig. 4**).

**Figure 2** Orientation perception is serially dependent. (a) Error plot from experiment 1 for one subject. Positive values on the abscissa indicate that the previous trial was more clockwise than the present trial, and positive errors indicate that the reported orientation was more clockwise than the true stimulus orientation. Gray line is average error; black line shows a DoG curve fit to the data. The peak of the DoG fit gives the amplitude of serial dependence. Each individual subject

showed significant serial dependence in orientation perception (all  $P < 0.01$ ). (b) Serial dependence amplitude computed for stimuli presented one, two and three trials back from the present trial; significant serial dependence was observed in each case. Error bars represent 1 s.d. of the bootstrapped distribution. Data in each bar are based on four subjects and 260 data points per subject. (c) Experiment 3 results. Thin lines are psychometric curve fits to individual subjects' 2AFC data and thick lines are fits to group data. PSE was significantly shifted by the presence of an inducer Gabor at the location of one of the stimuli (mean PSE shift of  $3.44^\circ$ ,  $P = 0.0004$  for the group, all subjects  $P < 0.05$ , based on three subjects, 448 data points each).



### Serial dependence without prior motor responses or recall

It is well established that responses and motor execution can be serially dependent<sup>9,10</sup>. Experiment 1 controlled for any influence of serial dependence in motor execution by randomizing the initial orientation of the response bar on each trial; motor serial dependence (for example, in how long the subject held down the arrow key during the response) would simply add noise that is uncorrelated to the physical or perceived orientation of the stimulus. We further tested whether perceptual serial dependence occurs in the absence of prior motor responses: subjects made no response on 25% of trials (experiment 2); all other aspects of the design were identical to experiment 1. In trials following those in which no response was made (and hence no carryover effect of a motor response was possible), serial dependence was as strong as in trials that followed a response (amplitude of  $\pm 6.76^\circ$ , s.d. =  $\pm 0.91^\circ$ ,  $P = 0.0002$  for trials following a response (104 trials from each of 4 subjects); amplitude of  $\pm 8.75^\circ$ , s.d. =  $\pm 0.93^\circ$ ,  $P = 5 \times 10^{-6}$  for trials in which no response was made on the previous trial (104 trials from each of 4 subjects); difference:  $P = 0.12$ , permutation tests).

Several characteristics of serial dependence distinguish it from the many seemingly similar phenomena previously reported. Unlike prior findings of visual hysteresis using ambiguous<sup>11–14</sup> or rivalrous<sup>15–19</sup> stimuli, serial dependence occurred for suprathreshold, unambiguous stimuli. A follow-up simulation established that the serial dependence that we observed was not a result of trial order effects or statistical artifacts, which can explain some prior reports of autocorrelation in perception<sup>20</sup> (**Supplementary Fig. 5** and **Supplementary Modeling**). We also found that the ability to explicitly recall previous stimuli<sup>21</sup> was not necessary for serial dependence to occur. Two subjects completed a control experiment with stimuli identical to those in experiment 1 except that, in 25% of trials, after reporting the perceived orientation of the stimulus on the current trial, the subjects were asked whether the orientation of the stimulus seen one or two trials ago was oriented clockwise or counter-clockwise of vertical. Participants were at chance in recalling the orientation from two trials back (53% correct,  $P = 0.69$  for a test of above-chance performance, permutation test based on 104 responses), yet we found significant serial dependence in perceived orientation based on stimuli seen two trials back (amplitude of  $\pm 3.12^\circ$ , s.d. =  $\pm 0.90^\circ$ ,  $P = 0.021$ , two subjects, 408 data points each). In fact, on those trials in which subjects misremembered the orientation of a previous Gabor patch, the serial dependence was consistent with the previously presented stimulus, not the falsely recalled one.

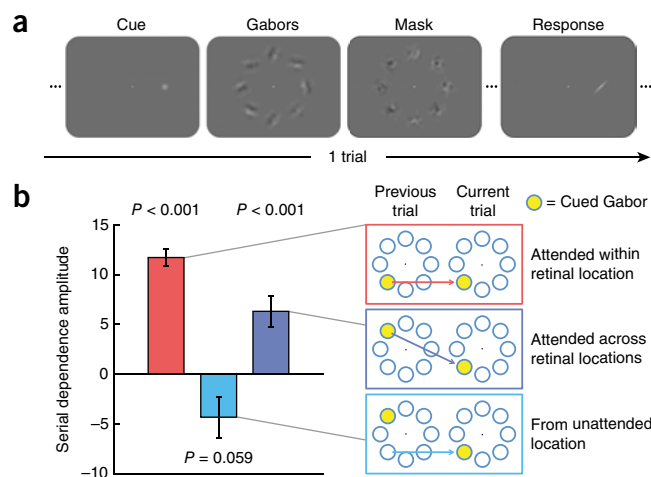
### Serial dependence alters perception

One might still be concerned that the serial effects that we found result not from serial dependence of perception *per se*, but rather

**Figure 3** Attentional modulation of serial dependence. (a) Event sequence for one trial in experiment 4; subjects reported the orientation of the Gabor at the cued location. (b) Serial dependence was strong when the same location was attended on successive trials (red data). There was no serial dependence in a location when the location was unattended on the previous trial (light blue data), but there was significant transfer of serial dependence from one location to another when the two locations were attended on successive trials (dark blue data). Thus, attention is necessary for serial dependence and can carry serial dependence across spatial locations. Error bars represent 1 s.d. of the bootstrapped distribution. Significance testing was conducted with permutation tests based on 104 data points from each of three subjects per test.

from serial dependence in higher level decision processes independent of perception<sup>22</sup>. If serial dependence does indeed alter perception, subjects should experience a visual illusion: the perceived orientation of one stimulus should be altered relative to a comparison stimulus visible at the same time. To test for such an illusion, we had subjects view two Gabors simultaneously on each trial and report which of the two was tilted more clockwise (two alternative forced choice, 2AFC, experiment 3; **Supplementary Fig. 6**). Prior to this 2AFC judgment, subjects saw another pair of Gabors in the same locations and were cued to report the orientation of one; we tested for serial dependence in the 2AFC responses based on the cued (inducer) Gabor (Online Methods). We found that the inducer altered the perceived orientation of the Gabor subsequently presented in the same location (**Fig. 2c**), significantly shifting the point of subjective equality (PSE, offset in orientation required to make the two appear to have identical orientations) for the simultaneously presented Gabors ( $P = 0.0004$  for group PSE shift, all individual subjects  $P < 0.05$ , bootstrap tests). This shift in PSE could not be accounted for by a change in decision criterion or repetition of responses, implying that serial dependence directly alters stimulus appearance.

The results of experiment 3 also demonstrate a key distinction between serially dependent perception and priming<sup>23,24</sup> (and the related notion of object files<sup>25</sup>). Priming yields an improvement in reaction time and/or discriminability of a repeated stimulus. In contrast, our data indicate that serial dependence can effectively reduce the discriminability of simultaneously presented stimuli by altering their appearance. We compared the slope of a psychometric function fit to all of an observer's trials (without regard to the orientation of the inducer, 448 trials per subject) with the slopes of psychometric functions fit separately to trials in which the inducer was expected to bias the subject toward a 'right' response or toward a 'left' response (Online Methods). This comparison tested whether factoring out serial dependence by separating trials according to the expected influence of the inducer yielded an improvement in discrimination over the case of considering all trials together. For the group of three subjects who participated in experiment 3, discrimination slopes were slightly, but significantly, steeper when trials were separated by the expected influence of serial dependence (mean slope of 5.69 for separated trials versus 5.35 for combined trials,  $P = 0.01$ , permutation test comparing the measured slope difference to a permuted null distribution, Online Methods). This result is not surprising given that different inducers had different effects on PSE in the 2AFC judgment; fitting a psychometric curve to the entire data set without taking into account these PSE shifts must yield at least a somewhat shallower slope. Notably, this analysis indicates that the variable influence of serial dependence from different preceding stimuli has the potential to reduce the overall discriminability measured in a 2AFC task.



### Attention gates perceptual serial dependence

We next tested the degree to which endogenous attention influences perceptual serial dependence. Experiment 3 hinted that focused attention may enhance serial dependence, but did not directly measure the influence of attention. In experiment 4, participants viewed eight Gabors organized in a ring around the fixation point and were cued to attend to one of the Gabors before stimulus onset (**Fig. 3a**). The cue indicated with 100% validity which of the Gabors the subject would be required to judge at the end of the trial. Analyzing trials in which the cued location remained constant from the previous to the current trial, we found significant serial dependence, a replication of the effect in experiment 1 ( $P = 10^{-5}$ ; **Fig. 3b**). However, when the cued location changed between trials, perceived orientation was not attracted toward the orientation present at the same retinal location on the previous trial, instead showing a trend toward a negative after-effect ( $P = 0.059$ ). Thus, attention is important for determining the strength of serial dependence. We also found that serial dependence was not strictly tied to retinal position: perceived orientation was attracted toward the previously attended orientation, even when it fell in a different retinal location ( $P = 0.0009$ ). Unlike other aftereffects, notably the tilt aftereffect<sup>26</sup>, serial dependence in perceived orientation is not determined solely by the retinal location of adaptation<sup>27</sup>, and it is more strongly modulated by attention<sup>28</sup>. Attention can carry serial dependence across retinal locations, or, put another way, serial dependence is a property tying together locations that are attended at successive moments.

### The spatial tuning of perceptual serial dependence

Given that serial dependence can occur for stimuli appearing in different retinal locations, we tested its tuning across retinal space. In experiment 5, the location of the Gabor stimulus was changed randomly from trial to trial while subjects maintained fixation at the center of the screen; subjects reported the orientation of the Gabor using an adjustment response as in experiments 1, 2 and 4 (**Fig. 4a**). We computed serial dependence in a rolling window over the distance between successive stimuli (**Fig. 4b**). The amplitude of serial dependence for one-back trials (blue data) was greatest between stimuli that appeared in nearby locations and fell off with increasing distance. A Gaussian curve fit to the data had a s.d. of  $15.2^\circ$ , a broad, but pronounced, spatial tuning. The influence of two-back trials on perceived orientation (**Fig. 4b**) was likewise spatially tuned, with significantly narrower tuning than the one-back case (s.d. of  $8.6^\circ$ ,  $P = 2 \times 10^{-7}$ , bootstrap test for a difference in width between the two curves). We repeated the above binning analysis in two-dimensional space.

**Figure 4** The spatial tuning of serial dependence. (a) Experimental design for experiment 5: stimuli and timing were the same as in experiment 1, but the location of the Gabor was randomized on each trial. (b) Serial dependence computed in a rolling window over the spatial distance between the current and previous trials; one-back data in blue, two-back data in red. The amplitude of serial dependence fell off with increasing spatial separation between successive trials. Shaded regions show  $\pm 1$  s.d. of the bootstrapped amplitude. The width of a Gaussian curve fit to the two-back data was significantly smaller than the width of a Gaussian curve fit to the one-back data ( $P = 2 \times 10^{-7}$ ; bootstrap test based on curves fit to the means in 61 bins in each the one-back and two-back data). (c) Serial dependence computed in a two-dimensional rolling window over the relative positions of the previous and current stimuli, with the current stimulus location plotted at the origin. Color coding shows the amplitude (in degrees) of serial dependence computed at each window location. We found a spatial field in which a prior stimulus attracts the perceived orientation of the present stimulus, which we term a perceptual continuity field.

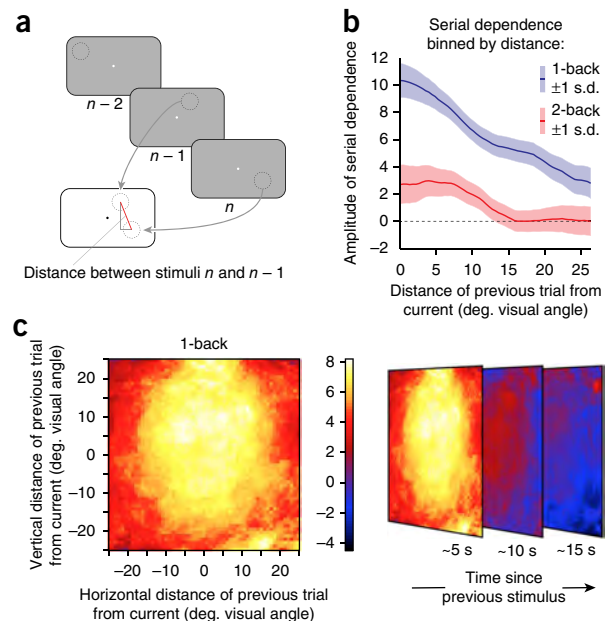
Each pixel in the resulting visualizations (Fig. 4c) is the amplitude of serial dependence for the collection of trials in which the previous stimulus appeared at that location relative to the stimulus location on the present trial. Serial dependence peaked when successive stimuli fell in the same location and dropped off smoothly with increasing distance for both the one-back and two-back cases. In an additional experiment, we found that serial dependence also showed spatial tuning in a spatiotopic (world- or head-centered) coordinate frame (Supplementary Fig. 7).

Using the data from experiment 5, we also tested whether serial dependence occurs for stimuli seen at the fovea. We collected the trials from experiment 5 for which the location of the stimulus on the previous trial was less than or equal to  $3^\circ$  of visual angle away from the location of the stimulus on the current trial (Fig. 4c). In these data, we analyzed trials in which the stimulus was presented at or near the fovea ( $0$ – $2^\circ$  eccentricity). Using the same analysis as in experiment 1 (Supplementary Fig. 1), we found significant serial dependence in orientation perception for these foveally presented stimuli (amplitude of  $\pm 8.46^\circ$ , s.d. =  $\pm 1.55^\circ$ ,  $P = 0.026$ , permutation test based on 268 data points).

## DISCUSSION

We found a previously unknown influence of visual history on perception: orientation perception was systematically biased toward stimuli seen up to ten or more seconds in the past. This serial dependence resulted in a change in appearance, and was not a result of hysteresis in motor responses or decision processes (experiments 2 and 3). Furthermore, the strength of serial dependence was strongly modulated by attention (experiment 4) and was tuned to the spatial and temporal proximity of successive stimuli (experiment 5). Thus, serial dependence operates over nearby, successively attended locations. We use the term continuity field to describe the spatial region, or kernel (Fig. 4c), in which orientation perception is attracted toward previous stimuli, thereby facilitating continuous orientation perception over time.

How is the serial dependence effect that we observed related to negative aftereffects that follow adaptation? Empirically, the two are dissociated in several of our experiments. First, the serial dependence that was observed was not retinally specific, unlike traditional negative tilt aftereffects<sup>29</sup>. Furthermore, serially dependent perception was strongly modulated by attention, did not require long-duration adaptation and had a spatiotopic component. In addition (Supplementary Fig. 8), we found that negative aftereffects could emerge using our stimuli, but only with longer stimulus durations, allowing for adaptation. Finally, experiment 3 pitted negative



aftereffects against serial dependence in the case in which the attended location changed between successive trials. Even though two sequential Gabors were presented in the same retinal location, the perceived orientation of the second one depended more strongly on the orientation of a different (attended) Gabor patch located elsewhere. The prior Gabor at the same retinal location did not produce enough of a negative aftereffect to overcome the serial dependence. Serial dependence may be present (although unnoticed) in many published studies involving brief stimulus exposure, and may actually reduce the measured size of the tilt aftereffect (or other negative aftereffects), at least for briefly presented adapting stimuli.

At a theoretical level, serial dependence and negative aftereffects following adaptation may reflect different, competing goals of the visual system. If we see something for an extended duration, the visual system adapts because lengthy exposure to such a stimulus indicates something has changed about the world (for example, scene illumination or orientation statistics). Negative aftereffects result from this adaptation<sup>1,5</sup>, which are a byproduct of a recalibration to the (new) world. On the other hand, encountering a brief stimulus that is no longer visible may be more consistent with the interpretation that we, rather than the world, have changed. In this case, adapting (and the consequent negative aftereffects) would not be optimal. Conversely, if the novel aspects of a brief object are attributed to transient events or internal noise (for example, transient occlusions, camouflage, blinks, saccades, etc.), then it may be adaptive to assume that any momentary change in the object attributes at this moment may not be inherent to the object itself. Thus, serial dependence emerges. With sufficient exposure, however, this assumption is overridden and the visual system adapts to the (new) stimulus. Negative aftereffects therefore emerge only with sufficiently long exposure (Supplementary Fig. 8). The mechanisms that mediate adaptation (negative aftereffects) and serial dependence (positive aftereffects) need not be shared, and may operate on different timescales and at different levels in the visual system. The resulting negative and positive aftereffects, however, are simultaneously present under many circumstances, as demonstrated in experiment 3 (Fig. 3b).

Although serially dependent perception is a distinct phenomenon, it could arise from established processes, including neural gain changes or tuning shifts. As a simple confirmation of this, we constructed labeled-line models that compute perceived orientation



by pooling over a population of orientation-tuned channels (**Supplementary Fig. 9** and **Supplementary Modeling**). By incorporating either a gain change at the exposed orientation<sup>30</sup> or a tuning shift away from the exposed orientation<sup>4</sup>, an oriented stimulus in the future will produce a population response that is biased toward the current stimulus. Applying this model to the stimulus sequences presented in experiment 1, we found that the model predictions matched subjects' perceived orientations well (**Supplementary Fig. 9**). Although other similar model frameworks (for example, a Bayesian estimation framework<sup>31</sup>) could be modified to produce serial dependence, this modeling confirms that serial dependence is consistent with known neural mechanisms, even though it is phenomenologically surprising.

A class of findings superficially related to ours comes from studies using multistable and ambiguous stimuli. When there are conflicting potential interpretations of a stimulus, prior visual experience can sway the interpretation in one direction or the other<sup>11–13</sup>. Similarly, in binocular rivalry experiments in which perceptual ambiguity comes from viewing different stimuli in the two eyes, the dominance of one interpretation over another can be modulated by recent visual experience<sup>15–18</sup> or expectation based on prior learning<sup>19</sup>. Unlike these cases, we studied perception of suprathreshold, unambiguous stimuli. In our experiments, even though the visual input from a single trial was sufficient to unambiguously perceive the stimulus, we nonetheless found a robust influence of prior visual input. Furthermore, unlike statistical learning effects, serial dependence in perception does not rely on repeated displays, implicit or explicit learning, or long exposure durations<sup>32,33</sup>. Serial dependence may contribute to the perceptual hysteresis observed with multistable and ambiguous stimuli, but it is a more general mechanism for perceptual stability operating in the absence of conflict.

It was previously reported<sup>34</sup> that, when observers viewed a series of briefly presented gratings over the course of many minutes, orientations seen as many as 2 min before a given trial could influence orientation perception on that trial. On first pass, these results might appear to be related to the serial dependence in orientation perception that we observed. However, the previous study's findings are not related to ours for several reasons. First, the long-term aftereffects that were previously reported may be the result of a statistical artifact. Another study<sup>20</sup> showed that the same pattern of results can arise as a consequence of random fluctuations in the trial sequence coupled with the existence of the well-known negative tilt aftereffect. Our experiments and analysis were designed to avoid such artifacts, and we conducted a simulation (**Supplementary Fig. 5** and **Supplementary Modeling**) to verify that, for the sequences of trials that our subjects saw, it is not possible for a negative aftereffect of any strength or duration to produce our pattern of results. Second, when we specifically looked for a long-term positive aftereffect in our data (as reported previously<sup>34</sup>), it was not present: serial dependence dropped to near zero after the three-back trial, essentially opposite their finding. Finally, the serial dependence we observed is fundamentally different from their proposed effect in other ways, including its spatial tuning, orientation tuning and temporal tuning confined to the past 10–15 s.

Another line of work posited that the brain constructs 'object files'—temporary object representations that tie together an object's features and location—to help us identify a given object as the same object from moment to moment<sup>35,36</sup>. The notion of object files exists as a description of tracking ability rather than a mechanism in itself. There are many possible mechanisms, serial dependence being one, that could underlie the ability to track an object's features in the face of

object translation, eye movements, occlusion and other interference. However, much of the evidence for object files comes from priming studies<sup>25,36,37</sup>, which found that discrimination of an object's features is faster and more accurate when the same object was previewed earlier. Our results differ from these prior findings in that we found that a tracked object looked similar from one moment to the next despite substantial changes in its properties (in this case, orientation); technically, serial dependence causes observers to be less accurate in their perception of instantaneous object properties, but this illusion, similar to countless other illusions such as motion-induced mislocalizations<sup>38</sup>, size illusions<sup>39</sup> and contrast illusions<sup>40</sup>, is adaptive under most circumstances.

In a similar vein to the object file literature, some classes of priming effects have been shown to persist and accumulate over multiple trials. Priming of pop-out<sup>23</sup> is one such example: when viewing pop-out visual search displays (displays in which the target can be rapidly located based on a unique feature), observers are faster to move attention to the target when the pop-out feature of the target is repeated from a previous trial. Similar to our results, this priming effect persists over many trials. Subsequent work has shown similar priming effects, accumulating over trials, for many variants of the search task, including conjunctive visual search<sup>41</sup> (occurring independently for different features<sup>42,43</sup>), as a result of repeated distractors<sup>44</sup>, and as a result of repetition of information at a global versus local scale<sup>45</sup>. These studies point to the existence of a persistent trace of previously seen stimuli that can facilitate detection and discrimination (improving reaction times and accuracy). Notably, our results demonstrate a distinct phenomenon: the contents of perception are systematically biased toward previously seen stimuli in a spatially, temporally and attentionally tuned fashion. As mentioned above, in contrast with priming effects, serial dependence can reduce the discriminability of simultaneously viewed stimuli. Although priming can enhance performance by capitalizing on predictable patterns in visual input, serial dependence stabilizes our perceptual experience by integrating information over time.

The constancy of object properties is the norm in the physical world, but not the rule—object features do sometimes change suddenly and unexpectedly. Does serial dependence work against our ability to detect sudden changes? The results of experiment 1 (**Fig. 2a**) suggest that it does not; we found no serial dependence when the stimulus orientation changed markedly between trials. On the other hand, there is ample evidence that humans are susceptible to change blindness<sup>46–48</sup>: when (unnatural) spontaneous and dramatic changes occur in objects and scenes, they often go unnoticed. Perceptual serial dependence may contribute to change blindness (of orientation information at least) by imposing a stability prior on orientation perception, but, crucially, serial dependence is gated by attention (experiment 4), and is therefore not responsible for failures to detect changes resulting from inattention<sup>49,50</sup>. Under natural conditions, where object properties do not tend to spontaneously change, serial dependence is useful; when unnatural spontaneous changes are introduced, serial dependence may obscure such changes. The characteristics of serial dependence that we observed are therefore well suited to meet the delicate balance between the need for sensitivity to change and the need for sensitivity to physical autocorrelations in the visual environment.

Our results suggest a strong serial dependence in orientation perception, whereby very different stimuli seen in succession can appear to be similar or even identical. This perceptual serial dependence reveals a previously unknown spatially and temporally tuned operator—the continuity field—that could facilitate perceptual continuity of orientation information over time.

## METHODS

Methods and any associated references are available in the [online version of the paper](#).

Note: Any Supplementary Information and Source Data files are available in the [online version of the paper](#).

## ACKNOWLEDGMENTS

We thank J. Shankey for assistance with data collection, and G. Maus, S. Teng and E. Whitney for comments on the manuscript. This work was supported in part by grants from the US National Institutes of Health (EY018216) and the National Science Foundation (1245461) to D.W.

## AUTHOR CONTRIBUTIONS

J.F. and D.W. designed the experiments. J.F. collected the data and carried out the analyses. J.F. and D.W. wrote the manuscript.

## COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

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## ONLINE METHODS

**General methods.** The University of California Berkeley and Massachusetts Institute of Technology Institutional Review boards approved all experimental protocols. A total of 12 subjects participated in the experiments; 6 females and 6 males, ranging in age from 20 to 32 years. We required participants to be adults with normal or corrected-to-normal vision. We obtained written informed consent from all subjects before their participation.

In all experiments, subjects viewed Gabor stimuli from a chin rest positioned 57 cm from a CRT monitor. The Gabors (windowed sine wave gratings) had a peak contrast of 25% Michelson, a spatial frequency of 0.33 cycles per degree, and a 1.5° s.d. Gaussian contrast envelope. Gabors were presented for 500 ms, after which a noise patch was presented for 1 s at the same location. Noise patches were presented to minimize negative aftereffects, and consisted of white noise smoothed with a 0.91° s.d. Gaussian kernel and windowed in a 1.5° s.d. Gaussian contrast envelope. A 0.5° diameter white dot served as a fixation point and subjects were instructed to maintain fixation of the dot for the duration of each experiment while performing the task. In all experiments, with the exception of experiment 3 (see below), on each trial subjects reported the perceived orientation of the Gabor by adjusting the orientation of a response bar (a 0.61° wide white bar windowed in a 1.5° s.d. Gaussian contrast envelope) using the left and right arrow keys. The response bar was initiated in a random orientation on each trial and presented in the same location as the Gabor stimulus.

For the main findings in this study, we report *P* values for individual subjects in addition to reporting group statistics, demonstrating significant within-subject effects. Because the effects are robust even within single subjects, the results do not require large samples, as is established in the psychophysical literature. Statistical tests are two-tailed and Bonferroni-corrected for multiple comparisons.

**Experiment 1. Stimuli and design.** Four subjects participated in experiment 1. Each subject completed ten runs of 104 trials each. **Figure 1** shows the event sequence for one trial in experiment 1: a Gabor stimulus was presented at 6.5° eccentricity (to the left or right of the fixation point in separate, interleaved runs) for 500 ms, followed by a 1-s noise patch. After a 250-ms delay, a response bar appeared at the same location the Gabor was presented in, and subjects adjusted its orientation to match the perceived orientation of the Gabor. After making a response, there was a 2-s delay during which only the fixation point was present before the onset of the next trial.

We used two approaches for generating trial sequences in experiment 1: a fully random sequence of orientations (**Supplementary Fig. 3**) and a counterbalanced trial sequence. For counterbalanced runs (**Fig. 2a,b**), in the beginning of a run, two baseline orientations were chosen at random from the range of 0–180 degrees. The trial sequence for a run contained trial pairs, where the baseline orientation was presented in the second trial of the pair and an orientation in the range of –60 to 60° (in increments of 10°) relative to the baseline orientation was presented in the first trial of the pair. All possible pairings of the baseline orientations with orientations in the range of –60 to 60 degrees relative to the baseline orientations were presented within a run. For example, in a run with a baseline orientation of 100°, a 100° oriented Gabor was presented in a trial following a 40° Gabor, in a trial following a 50° Gabor, in a trial following a 60° Gabor, and so on. This counterbalancing was conducted for 1-, 2- and 3-back trial pairings. We measured serial dependence for the baseline trials only. This approach provided a stringent means of measuring serial dependence because it required that a given orientation could be pulled in both the clockwise and counter-clockwise directions, depending on the preceding stimulus. Thus, although this counterbalancing approach reduced the number of usable trials, it had the advantage of requiring serial dependence to occur within a given orientation. A comparison of serial dependence measured in the counterbalanced design versus a randomized design (experiments 3–5) in the same subjects revealed no difference in the amplitude of serial dependence.

**Analysis.** The general approach to measuring perceptual serial dependence is outlined in **Supplementary Figure 1**. Within a subject, we first plotted the error on each trial (reported orientation minus presented orientation; positive values indicated errors in the clockwise direction) as a function of the difference in orientation between the Gabor presented on the current and previous trials (previous orientation minus current orientation; positive values indicate that the stimulus on the previous trial was more clockwise than the stimulus on the present trial). Thus, for points where the *x* and *y* values had the same sign, the

subject's error on that trial fell in the direction of the orientation on the previous trial. To measure the amplitude of serial dependence, or the degree to which subjects' errors were pulled toward the orientation of the previous stimulus, we fit the error plot with a first derivative of a Gaussian curve (DoG), given by  $y = xawce^{-(wx)^2}$  where *x* is the relative orientation of the previous trial, *a* is the amplitude of the curve peaks, *w* scales the curve width, and *c* is the constant  $\sqrt{2}/e^{-0.5}$ . The constant *c* rescales the curve so that the *a* parameter numerically matches the height of the positive peak of the curve for ease of interpretation: the amplitude of serial dependence (*a*) is the number of degrees that perceived orientation was pulled in the direction of the previous stimulus for the maximally effective difference in orientation between trials. Error bars were computed by bootstrapping the DoG curve fit 5,000 times, sampling from the data with replacement on each iteration, and taking the s.d. of the *a* parameters from the resulting bootstrapped distribution. Significance testing was conducted with a permutation test that similarly refit a DoG curve 100,000 times, shuffling the data labels (relative orientation of the previous trial) on each iteration. This permutation procedure generated a null distribution against which the measured amplitude of serial dependence was compared to obtain a *P* value. *P* values were taken as the proportion of amplitude estimates in the bootstrapped null distribution that were equal to or larger in absolute value than the subject's measured amplitude of serial dependence. In the analysis of experiment 1 and in subsequent analyses where a permutation test was used to assess significance, the exchangeability requirement for a permutation test is met because under the null hypothesis (here, no systematic relationship between orientation judgment errors and relative previous orientation; a flat line), error distributions would not be expected to differ at different locations along the abscissa, and are hence exchangeable.

**Experiment 2. Stimuli and design.** Four subjects participated in experiment 2. Each subject completed two runs of 208 trials each. The experiment was identical to experiment 1, except that in 25% of trials (randomly selected, but constrained to maintain stimulus sequence counterbalancing as described for experiment 1), the response bar did not appear and the subject made no response. In these trials, in lieu of the response bar, subjects saw the fixation point alone for a period of time determined by the running average of the response period duration for previous trials within the same run. This procedure ensured that trials in which the subject did not make a response had the same average duration as the trials in which the subject made a response.

**Analysis.** Trials in which the subject made no response were discarded. The remaining trials were separated into two groups: those in which a response was made on the previous trial (response trials) and those in which no response was made on the previous trial (no-response trials). We separately analyzed the two groups of trials using the same curve fitting method as in experiment 1 to determine whether the execution of a response on the previous trial influenced the strength of serial dependence.

**Experiment 3. Stimuli and design.** Three subjects participated in experiment 3. Each subject completed four runs of 112 trials each. The event sequence for one trial in experiment 3 is shown in **Supplementary Figure 6**. Subjects performed two tasks on each trial; a cue reminded subjects of which task to perform for the upcoming stimuli. At the onset of a trial a cue (a white dot windowed in a 0.7° s.d. Gaussian contrast envelope) appeared at 6.5° eccentricity to the left or right of the fixation point. This cue instructed the subject to judge the orientation of the Gabor that subsequently appeared at the cued location. Following the 350-ms cue and a 350-ms delay period, two Gabors were presented simultaneously to the left and right of fixation at 6.5° eccentricity. The Gabors were presented for 500 ms, followed by the presentation of noise patches for 1 s. The subject then adjusted a response bar, presented at the location of the cued Gabor, to report its orientation. Following the subject's response there was a 1.5-s delay period (fixation only), followed by a central cue: the fixation point dimmed for 350 ms. This cue instructed the subject to compare the orientations of the subsequent Gabors, judging which was oriented more clockwise (on separate, randomly interleaved runs, subjects judged which Gabor was more counter-clockwise). Following the 350-ms central cue and a 350-ms delay period, two Gabors were presented simultaneously to the left and right of fixation at 6.5° eccentricity. The Gabors were present for 500 ms, followed by the presentation of noise patches for 1 s. Subjects then reported which Gabor was oriented more clockwise (or counter-clockwise) with a button press



(2AFC). Following the subject's response, there was a 1.5-s delay period (fixation only) before the onset of the next trial.

For the second set of Gabors presented in a trial (2AFC judgment), the difference in orientations between the two Gabors varied from  $-9^\circ$  to  $9^\circ$  in increments of  $3^\circ$ ; the orientations were constrained to the range of  $\pm 14.5^\circ$  around vertical. For the first set of Gabors presented in a trial (adjustment response), the orientation presented at the cued location was either  $20^\circ$  clockwise or  $20^\circ$  counterclockwise relative to the Gabor that would appear at the same location later in the trial. The Gabor at the uncued location had a random orientation, constrained to the range of  $-34.5$  to  $34.5$  degrees, the same range that all Gabors in the experiment fell in.

**Analysis.** We term the cued Gabor in the first set of Gabors that appeared in a trial the 'inducer', as the goal of experiment 3 was to test whether the orientation of this cued Gabor induced a change in the perceived orientation of the Gabor subsequently presented in the same location in the same trial. We binned trials by the influence that we predicted the inducer would have on the subject's 2AFC response. Say that on a given trial a  $20^\circ$  oriented inducer was presented in the right visual field, followed by  $6^\circ$  and  $0^\circ$  oriented Gabors in the left and right visual fields, respectively. Because the inducer was oriented more clockwise than the subsequent Gabor that appeared in the same location (the right visual field), we predicted that the inducer would bias the subject to perceive the Gabor in the right visual field as oriented more clockwise than its true orientation. This effect of the inducer would make the subject more likely to report that the Gabor in the right visual field was oriented more clockwise than the Gabor in the left visual field in his/her 2AFC response. Similarly, if an inducer appearing in the left visual field was oriented more counter-clockwise than the subsequent Gabor appearing in the left visual field, it would bias the subject to perceive the Gabor in the left visual field as more counter-clockwise than its true orientation. As in the first example, this effect of the inducer would make the subject more likely to report that the Gabor in the right visual field was oriented more clockwise than the Gabor in the left visual field in his/her 2AFC response. Both of these example trials would be collected together into one bin because the inducer had the same predicted influence on the subject's 2AFC response. In a second bin, we collected the trials in which we predicted the inducer would make the subject more likely to report that the Gabor in the left visual field was oriented more clockwise than the Gabor in the right visual field in his/her 2AFC response. We then fit psychometric functions to the data in each bin separately (Fig. 2c) using logistic regression of the form  $y = 1/(1 + e^{-a(x-b)})$  where  $y$  is the proportion of 'right' responses,  $x$  is the relative orientation of the left and right Gabors, and  $a$  and  $b$  scale the slope and intercept of the curve fit, respectively. The PSE for each curve fit was taken as the  $x$  value at which  $y = 0.5$  (subjects were equally likely to respond 'left' or 'right' in the 2AFC judgment). We tested for a significant difference in the PSE for the data in the two bins using a bootstrapping approach, resampling the data in each bin with replacement 5,000 times, recomputing the PSE estimates on each iteration, and recording the difference in PSE estimates for the data in the two bins ( $\Delta$ PSE). The bootstrapped distribution of  $\Delta$ PSE estimates was tested against a null hypothesis of no difference in PSE for the data in the two bins. Note that this approach provided a conservative estimate of the true PSE shift that can be induced by perceptual serial dependence. While the analysis assumed that in the 2AFC judgment only the Gabor at the same location as the inducer Gabor was influenced by it, the results of experiment 5 show that the influence of serial dependence spreads over a broad region of space (Fig. 4). Thus, in the 2AFC judgment, both Gabors were influenced by the inducer, but the Gabor in the same location as the inducer was influenced more, resulting in the significant PSE shifts that we found. We also verified that the response on the first (adjustment) judgment was not correlated with the response on the second (2AFC) judgment, or with whether the subsequently appearing Gabor would be clockwise or counter-clockwise from the inducer.

To test for a difference in the discrimination slopes found when all trials were analyzed together versus when trials were separated by the expected influence of the inducer, we averaged the slopes of psychometric functions fit separately to trials in which the inducer was expected to bias the subject toward a 'left' response and trials in which the inducer was expected to bias the subject toward a 'right' response. We subtracted from this average the slope of a psychometric function fit to all trials. We compared the group average of this difference score to a group null distribution, generated by repeating the above procedure 5,000 times and permuting the trial labels on each iteration.

**Experiment 4. Stimuli and design.** Three subjects participated in experiment 4. Each subject completed four runs of 78 trials each. The event sequence for a trial in experiment 4 is shown in Figure 3a. At the onset of a trial subjects saw a cue (a white dot windowed in a  $0.7^\circ$  s.d. Gaussian contrast envelope) in one of eight possible locations along a  $9.0^\circ$  ring around the fixation point. The cue instructed subjects to attend to the orientation of the Gabor that subsequently appeared at the cued location; all other Gabors were task-irrelevant. The cue was present for 350 ms, followed by a 350-ms delay period (fixation point presented alone). Following the cue and delay period, eight Gabors were presented simultaneously in a  $9.0^\circ$  isoeccentric ring around the fixation point. The Gabors were present for 500 ms, followed by 1-s noise patches presented in the same eight locations. Following a 250-ms delay, a response bar appeared at the cued location and subjects adjusted the bar to report the perceived orientation of the Gabor at that location. There was a 2-s delay period (fixation only) following a subject's response before the onset of the next trial. Given that experiments 1 and 2 established that serial dependence occurs within a given orientation using a counterbalanced stimulus sequence, in experiment 4 the orientations of the Gabors presented on each trial were randomly drawn from the range of  $0$ – $180$  degrees to increase the number of usable trials.

**Analysis.** Trials were divided into those in which the cued location was the same as in the previous trial and those in which the cued location differed from the previous trial. We then measured the amplitude of serial dependence as in experiments 1 and 2 in three separate analyses: i) when the cued location was the same as in the previous trial, we used the orientations of the cued Gabors on the current and previous trials to compute serial dependence; ii) when the cued location differed between successive trials, in one analysis we used the orientations of the cued Gabors on the current and previous trials to compute serial dependence; and iii) when the cued location differed between successive trials, in a second analysis we used the orientation of the cued Gabor on the current trial and the orientation of the (uncued) Gabor presented in the same location on the previous trial (Fig. 3b). This analysis generated three separate estimates of the amplitude of serial dependence, measuring serial dependence within an attended location, across two different attended locations, and within a location that was not previously attended.

**Experiment 5. Stimuli and design.** Three subjects participated in experiment 5. Each subject completed ten runs of 100 trials each. The event timing within a trial was identical to that in experiment 1 (see Fig. 1), but the Gabor stimuli appeared at random locations within  $\pm 12.5^\circ$  from fixation in the  $x$  and  $y$  directions (Fig. 4a). In each trial, the response bar appeared in the same location as the Gabor stimulus. The orientation of the Gabor presented on each trial was chosen randomly from the range of  $(0, 180]$  degrees.

**Analysis.** To measure the spatial tuning of serial dependence in experiment 5, we binned trials according to the spatial separation between the current and previous stimulus locations. We first binned trials according to the distance between the current and previous stimulus locations (distance between successive stimulus locations was computed as  $\sqrt{(x_{\text{current}} - x_{\text{previous}})^2 + (y_{\text{current}} - y_{\text{previous}})^2}$ ) within a  $3^\circ$  rolling window. For the data within a given window, we computed serial dependence amplitude as in experiment 1. This analysis yielded a plot depicting the drop-off in the amplitude of serial dependence with increasing distance between the stimuli presented in successive trials (Fig. 4b). We fit Gaussian curves separately to the one-back and two-back data and tested for a significant difference in the width (s.d.) of these curves using a bootstrapping approach as in experiment 3. We resampled the data from each curve with replacement 100,000 times, recomputing the s.d. estimates on each iteration and recording the difference in s.d. estimates for the two curves. The bootstrapped distribution of difference scores was tested against a null hypothesis of no difference in the s.d. of the two curves. We repeated the analysis using the two-dimensional spatial separation between successive trials (that is, considering  $x$  distance and  $y$  distance separately). In this case, the rolling window was a circle with a radius of  $3^\circ$ . This analysis yielded a two-dimensional visualization of the drop-off in amplitude of serial dependence with increasing spatial separation between the stimulus positions on successive trials (Fig. 4c). In Figure 4c, the location of the stimulus on the present trial is represented at the origin, and the position of the stimulus on the previous trial relative to the current trial is represented along the  $x$  and  $y$  axes.



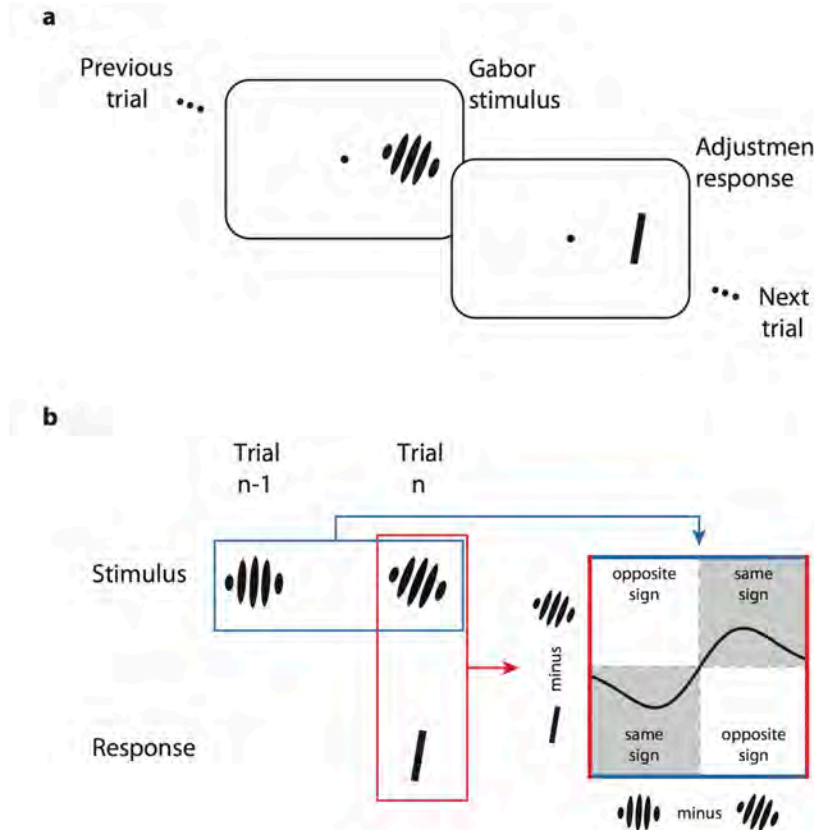
Given that the stimuli were positioned randomly on each trial, the number of trials could vary across bins in the above analyses. For the statistical analysis of the data shown in **Figure 4b**, we used a subsampling approach to equate the effective number of trials across bins. Within each bin, we sampled 200 trials from the total set within the bin and computed serial dependence based on those 200 trials. We repeated this subsampling 5,000 times and used the mean serial dependence amplitude across iterations as the measure of serial dependence within the bin. This approach equated the statistical power across bins.

**Negative aftereffect and labeled-line models.** The procedures for constructing and testing the negative aftereffect and labeled-line models are described in the

**Supplementary Modeling.** For the negative aftereffect model (**Supplementary Modeling**), we based the parameters of the negative aftereffect on data from ref. 51. For the labeled-line models (**Supplementary Modeling**), we based the tuning of orientation-selective channels on data from ref. 52.

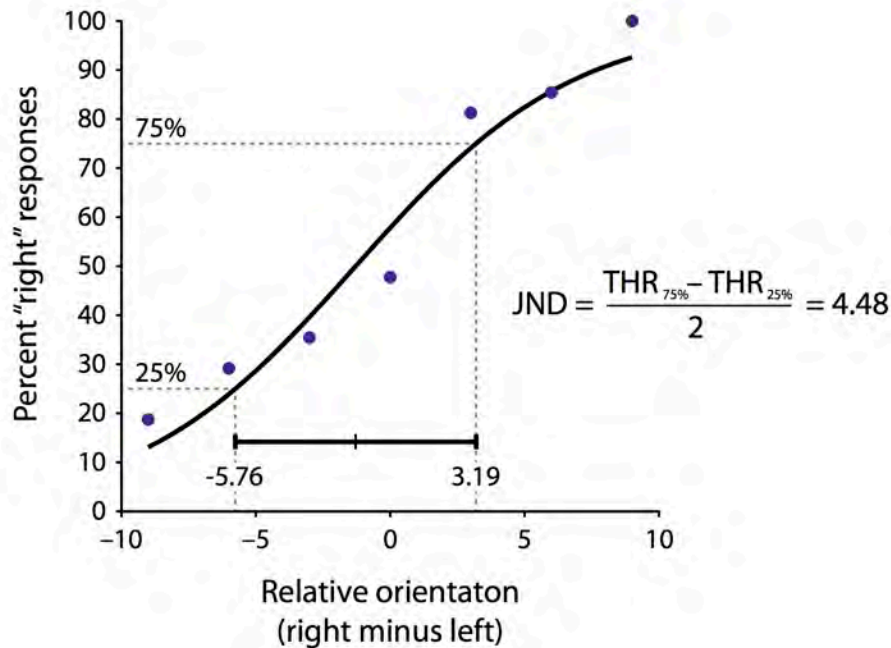
- 51. Mitchell, D.E. & Muir, D.W. Does the tilt after-effect occur in the oblique meridian? *Vision Res.* **16**, 609–613 (1976).
- 52. Ringach, D.L., Shapley, R.M. & Hawken, M.J. Orientation selectivity in macaque V1: diversity and laminar dependence. *J. Neurosci.* **22**, 5639–5651 (2002).

### Supplementary Figure 1



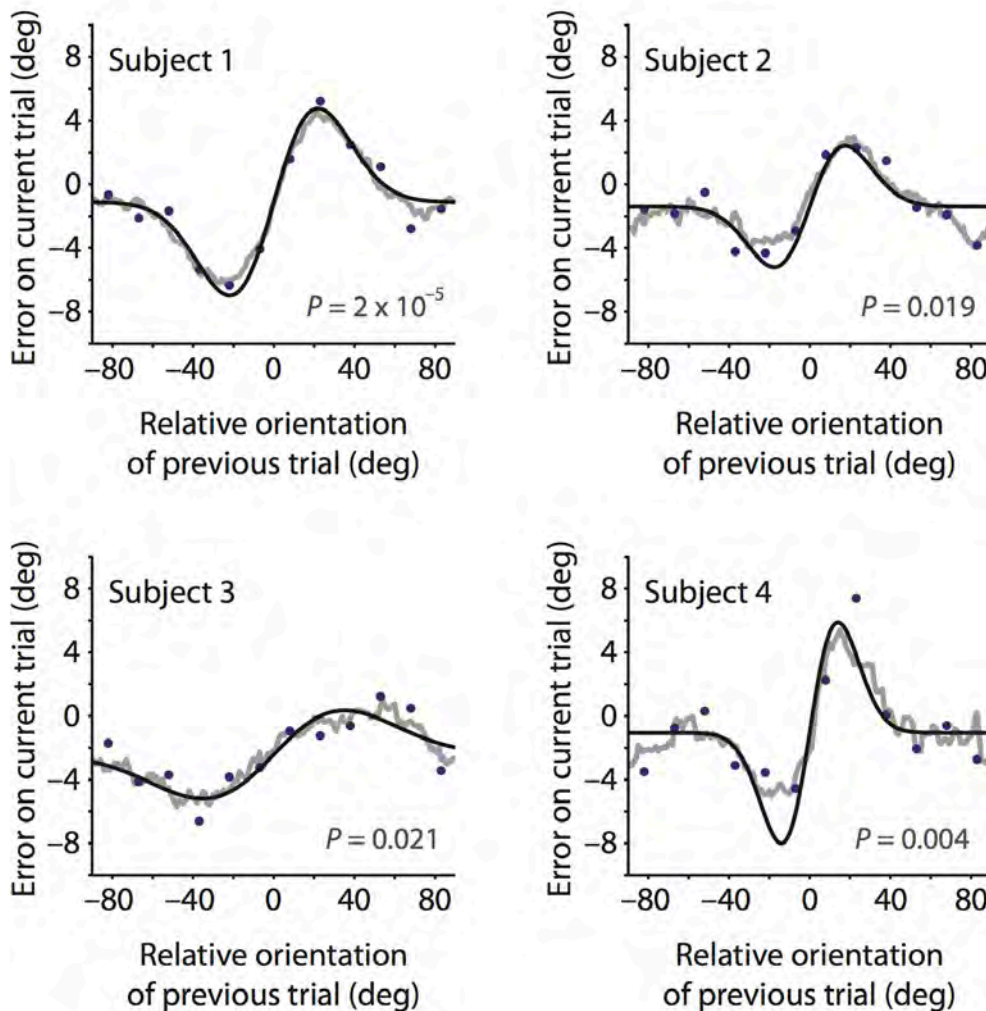
**Supplementary Figure 1:** Measuring perceptual serial dependence. To measure serial dependence in orientation perception, we presented subjects with an oriented grating (Gabor) on each trial and asked subjects to report the orientation of the grating by adjusting a bar using the arrow keys (panel **a**). Of interest was whether the reported orientations were systematically dependent on the stimulus orientations seen in previous trials. We constructed a plot capturing the relationship between the perceptual error on each trial and the orientation presented on the previous trial (panel **b**). For each trial we computed the relative orientation of the previous stimulus to the present one (e.g., by how much was the previously seen orientation clockwise or counter-clockwise of the present orientation; indicated by the blue box) with positive values indicating that the orientation seen on the previous trial was clockwise of the orientation seen on the present trial. We also computed the error on the present trial with positive values indicating perceptual errors in the clockwise direction (indicated by the red box). Plotting error as a function of the relative orientation of the previous trial allowed us to examine whether subjects' errors were drawn in the direction of the previous stimulus (shaded region on the plot), or repelled away from the orientation of the previous stimulus as would be found for traditional negative aftereffects at short inter-stimulus intervals (unshaded region on the plot). A preponderance of points within the shaded region of the plot, as was the case in the actual data (see **Fig. 2a**), indicates that perceived orientation was attracted toward the orientation seen on the previous trial.

## Supplementary Figure 2



**Supplementary Figure 2:** Computing the just noticeable difference (JND) from two alternative forced choice data. To compute the just noticeable difference (minimum orientation difference that can be reliably discriminated) for the Gabors presented in our experiments, we used the 2AFC discrimination data from Experiment 3, this time using only the information from the 2AFC judgments. For each individual subject, we plotted the percent of the time that the subject responded "right" as a function of the relative orientations of the Gabors presented in the left and right visual fields (positive values on the abscissa indicate that the right-hand Gabor was more clockwise). Data shown here are from one example subject. We fit a logistic function to the resulting plot as in the analysis of Experiment 3, and found the x values for which the logistic curve had a y value of 25% and 75%. One half of the difference between these two x values was taken as the JND. The mean JND for the three subjects who participated in Experiment 3 was 5.39. The same three subjects participated in Experiment 1; the mean amplitude of serial dependence for these subjects was 8.21; that is, two orientations that differed by 16.42° could appear identical based on the stimulus that preceded them, an effect that is 3.05 times the JND as measured here in the same subjects.

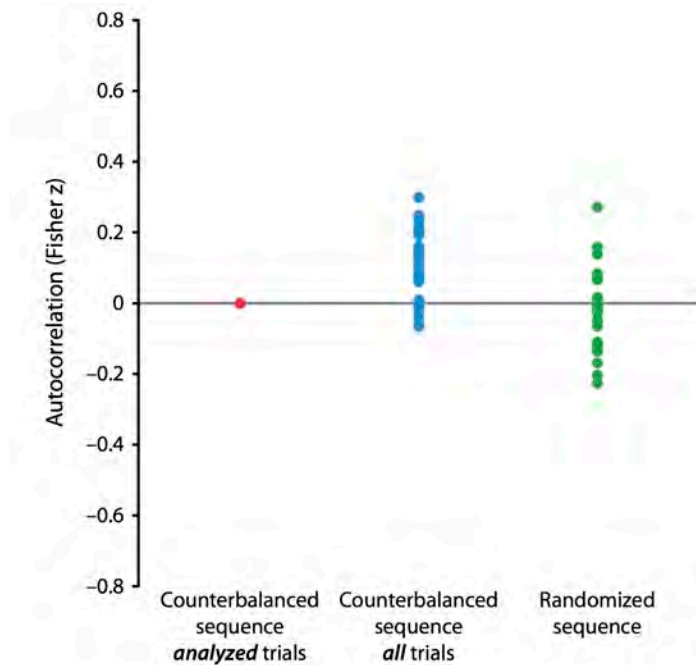
### Supplementary Figure 3



**Supplementary Figure 3:** Serial dependence measured using randomized trial sequences. We repeated Experiment 1, this time presenting a random sequence of orientations on each run. All aspects of the experimental design were identical to the counterbalanced version of Experiment 1 except that a random orientation was presented on each trial, and we analyzed all trials in the sequence. Four participants each completed eight 104-trial runs. The gray line in each plot shows a running average of the subject's orientation judgment errors, and data points show mean error within 20 deg. bins along the abscissa. Black lines show derivative of Gaussian (DoG) fits to subjects' error distributions (the DoG model included a constant term to account for overall bias). Each subject individually showed significant serial dependence in orientation judgments (permutation tests; 824 data points per subject). The amplitude of serial dependence found with this randomized design did not differ from the amplitude measured with the counterbalanced design (group mean amplitudes were  $\pm 8.19^\circ$  for the counterbalanced design (4 subjects, 260 data points per subject) and  $\pm 4.85^\circ$  for the randomized design (4 subjects, 824 data points per subject); permutation test comparing amplitudes from the randomized and counterbalanced versions;  $P = 0.15$ ).

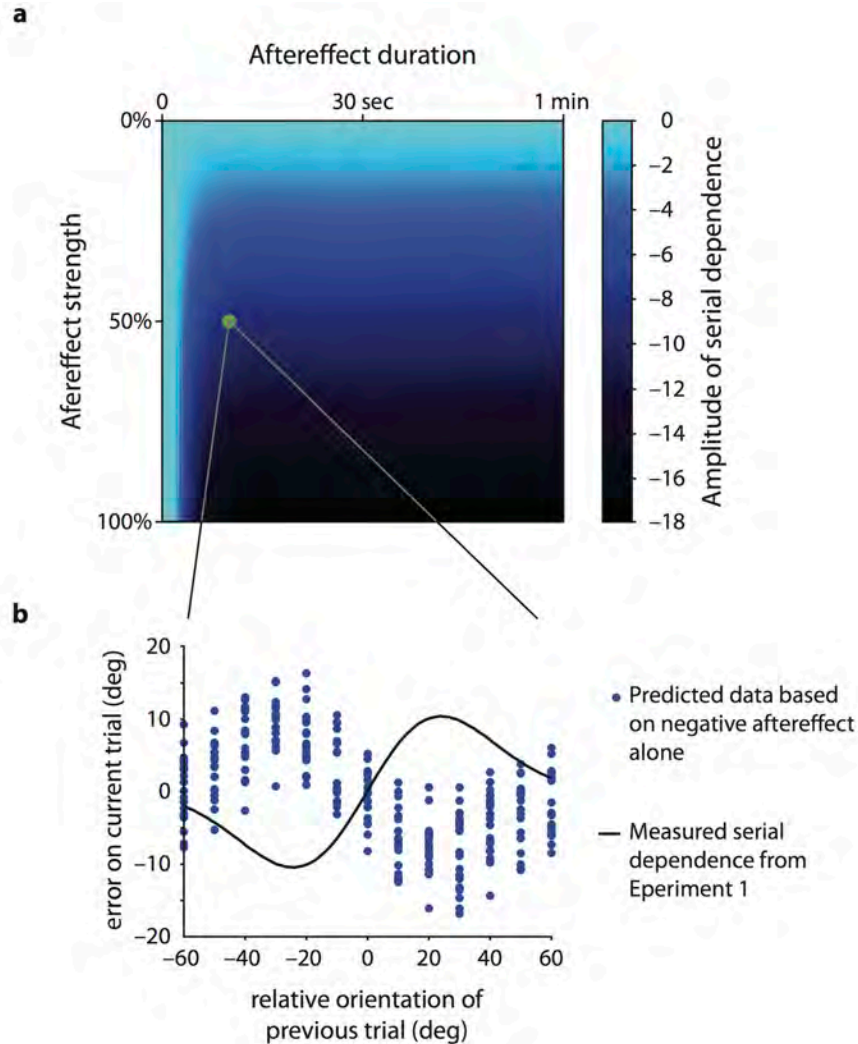


### Supplementary Figure 4



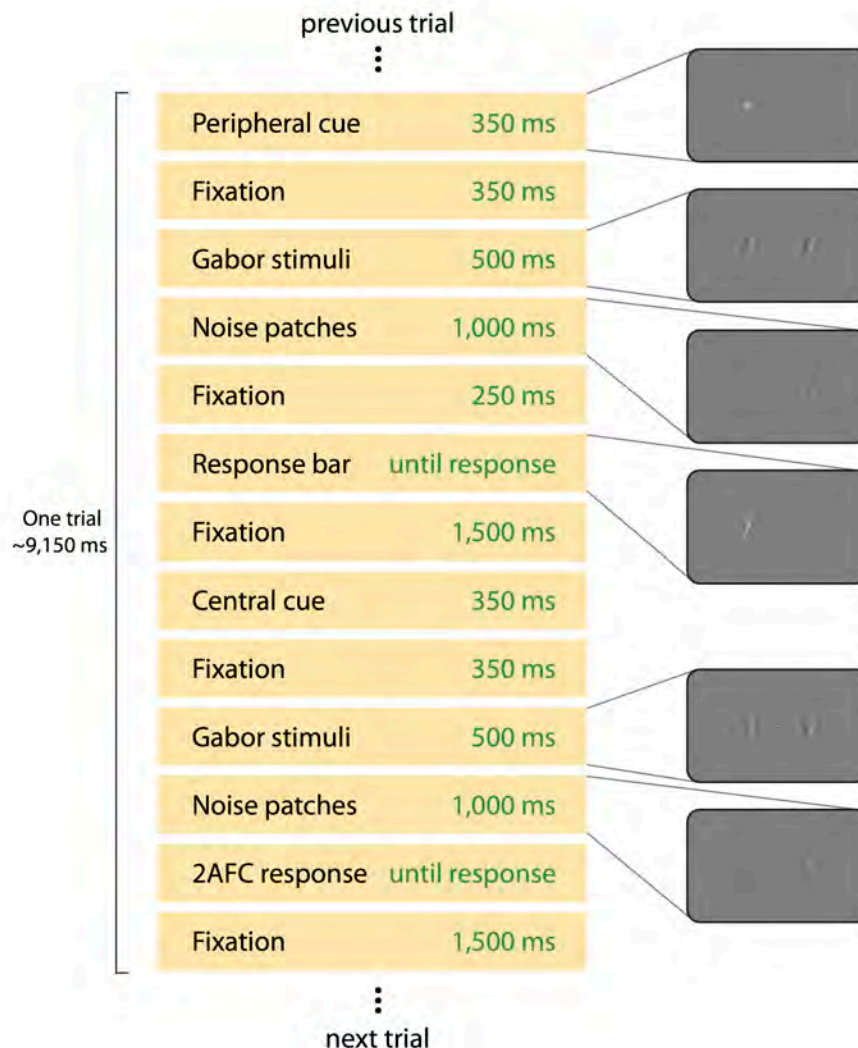
**Supplementary Figure 4:** Statistics of Experiment 1 trial sequences. Experiment 1 used two approaches for generating trial sequences: a fully random sequence of orientations and a counterbalanced sequence designed to ensure that every orientation used in the analysis was preceded equally often by all orientations in the range of -60 to 60 degrees relative to it (see Methods). Data points here show the autocorrelation (correlation between the orientation presented on a given trial and the relative orientation of the previous trial) for each run that subjects completed in Experiment 1; one point represents one run. Within the counterbalanced design, the autocorrelation was exactly zero for all runs when considering the trials used in the analysis (“baseline” trials; red data). Considering all trials within the counterbalanced runs including those not intended for analysis and discarded prior to computing the strength of serial dependence, the correlation tended to be positive (blue data) and the mean was significantly greater than zero (mean correlation of  $z = 0.11$  across 40 runs;  $P = 1 \times 10^{-5}$ , evaluated by a permutation test in which we shuffled the trial ordering within runs and recomputed the mean correlation 100,000 times to generate a null distribution). However, there was no significant difference in the amplitude of serial dependence measured within only baseline trials vs. all trials in the counterbalanced sequences (group mean amplitudes were  $\pm 5.51^\circ$  for all trials (1030 trials per subject) and  $\pm 8.19^\circ$  for baseline trials (260 trials per subject);  $P = 0.10$ ; permutation test). Within the randomized stimulus sequences, the autocorrelation was never exactly zero (which is why we also employed a counterbalanced design), but across all runs the autocorrelation centered on zero and did not significantly differ from zero (green data; mean correlation of  $z = -0.025$  across 32 runs;  $P = .15$  evaluated with a permutation test as above). Within both the counterbalanced and randomized paradigms, we found significant serial dependence in orientation perception for all subjects. These results, together with the negative aftereffect modeling (**Supplementary Fig. 5**), confirm that perceptual serial dependence is not the result of statistical dependencies in the presented trial sequences.

## Supplementary Figure 5



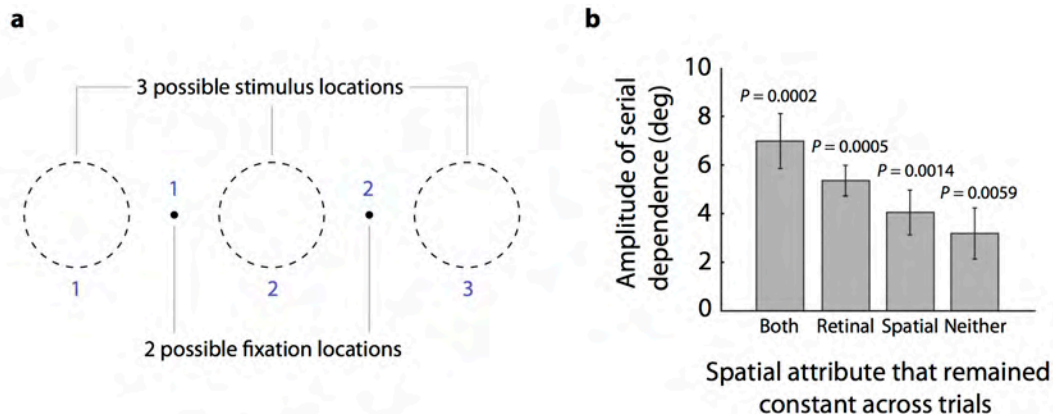
**Supplementary Figure 5:** Serial dependence does not arise from negative aftereffects alone. We conducted a simulation to test whether apparent serial dependence in perceived orientation could arise from negative aftereffects alone, for example due to an interaction between negative aftereffects and random fluctuations in the stimulus sequence. Using the same trial sequences presented to subjects in Experiment 1, we simulated subjects' responses based on negative aftereffects of varying strength and persistence over time. We found that regardless of the aftereffect strength or duration, negative aftereffects alone predict a negative amplitude in the measured serial dependence (repulsion rather than attraction; panel **a** shows the simulation results for the stimulus sequence presented to one subject; all subjects showed comparable results), contrary to what we observed in subjects' responses. Panel **b** shows a sample position discrimination plot from the simulation. Predicted responses based solely on negative aftereffects are qualitatively dissimilar to the pattern of responses that subjects made in Experiments 1-6. This simulation shows that it is not possible for negative aftereffects alone to produce an apparent attraction of perceived orientation toward previously seen orientations within our experimental design and analysis.

## Supplementary Figure 6



**Supplementary Figure 6:** Event sequence for one trial in Experiment 3. Subjects made two judgments per trial; a cue reminded subjects which judgment to perform on the upcoming stimuli. At the outset of a trial, a cue (white dot) appeared to the left or right of fixation. This cue instructed the subject to judge the orientation of the Gabor that appeared at that location; the Gabor in the opposite visual field was task-irrelevant. After a delay, two Gabors appeared simultaneously to the left and right of fixation for 500 ms, followed by noise patches presented for 1 s. The subject then adjusted a response bar to match the perceived orientation of the Gabor at the cued location. After the subject's response, there was a delay period of 1.5 s during which only the fixation point was present. Following the delay period, the fixation point dimmed slightly for 350 ms to indicate that the subject was to judge the relative orientations of both upcoming Gabors, deciding which was oriented more clockwise (or, on separate runs, which was more counter-clockwise). Two Gabors then appeared to the left and right of fixation for 500 ms, followed by noise patches presented for 1 s. The subject then indicated which of the Gabors was oriented more clockwise (or counter-clockwise) in a two alternative forced choice (2AFC) response. Following the subject's response there was a delay period of 1.5 s prior to the onset of the next trial.

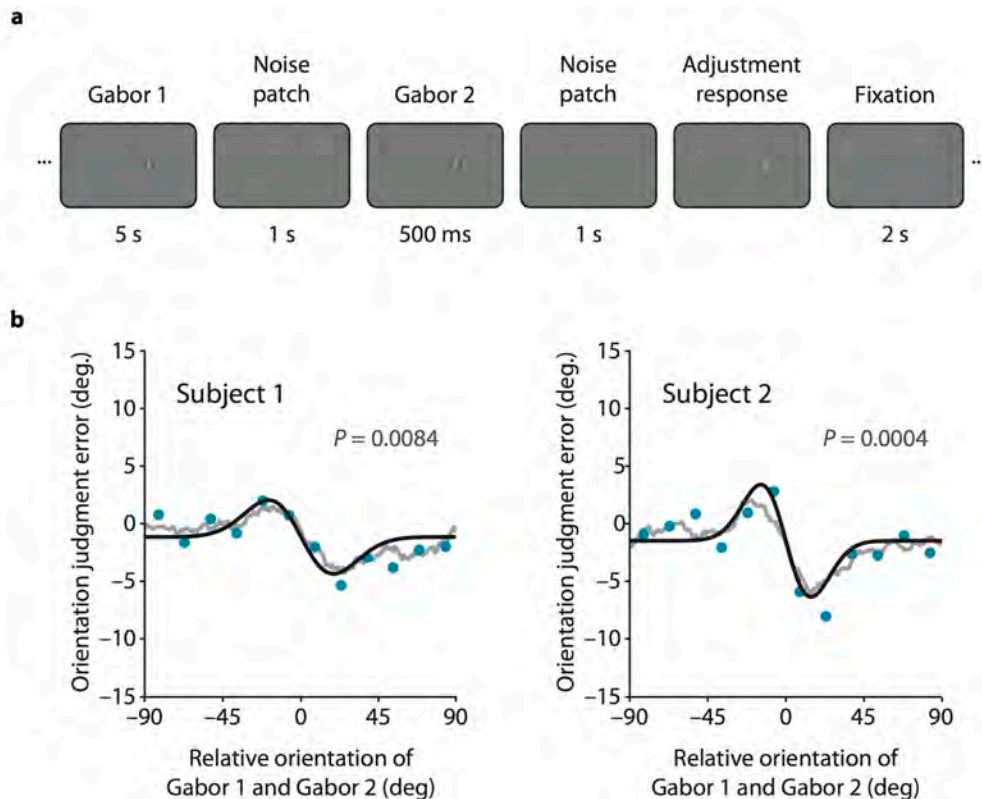
## Supplementary Figure 7



**Supplementary Figure 7:** Experiment 6: The coordinate frame of serial dependence. We compared the strength of serial dependence in perceived orientation in retinotopic vs. spatiotopic (head-centered) coordinates by varying the stimulus and fixation locations across trials (panel **a**). On each trial the fixation point appeared in one of two locations, at  $6.5^\circ$  to the left or right of the center of the screen, and the Gabor patch appeared in one of three locations, at  $6.5^\circ$  or  $19.4^\circ$  to the left or right of fixation depending on the location of the fixation point. Trials were paired, and every second (baseline) trial was analyzed. We manipulated the change in fixation-Gabor positioning between the trials in each pair: on  $\frac{1}{4}$  of trial pairs both the spatial and retinal positions stayed the same (“*both*” trials), on  $\frac{1}{4}$  of trial pairs the spatial position of the Gabor changed while its retinal position remained the same (“*retinal*” trials), on  $\frac{1}{4}$  of trial pairs the retinal position of the Gabor changed while its spatial position remained the same (“*spatial*” trials), and on the final  $\frac{1}{4}$  of trial pairs both the retinal and spatial position of the Gabor changed (“*neither*” trials; hence the trials are named for the aspect of the stimulus position that remained constant between the two successive trials in a pair). We counterbalanced the orientations presented so that subjects saw exactly the same set of orientations on all four of the spatial conditions – the only thing that differed among the spatial conditions was the change in the relative positioning of the fixation point and Gabor between trial pairs. We found significant serial dependence within each of the four conditions (panel **b**; permutation tests based on 180 trials from each of four subjects in each condition; error bars are  $\pm 1$  s.d. of the bootstrapped group mean). Serial dependence was significantly stronger in those trials in which the retinal stimulus position was the same as in the previous trial (retinal & both trials) than in trials when the retinal position changed (spatial & neither trials), replicating the tuning of serial dependence to retinal position found in Experiments 4 and 5 ( $P = 0.019$ ; permutation test based on 360 trials per condition from each of four subjects). At the same time, serial dependence was also stronger when the spatiotopic stimulus position stayed constant between trials (spatial & both trials) than when it changed (retinal & neither trials;  $P = 0.037$ ; permutation test based on 360 trials per condition from each of four subjects), indicating that serial dependence is tuned to an object’s spatiotopic position as well. This tuning to both spatiotopic and retinotopic stimulus position suggests that serial dependence likely operates at multiple levels in the visual processing hierarchy.

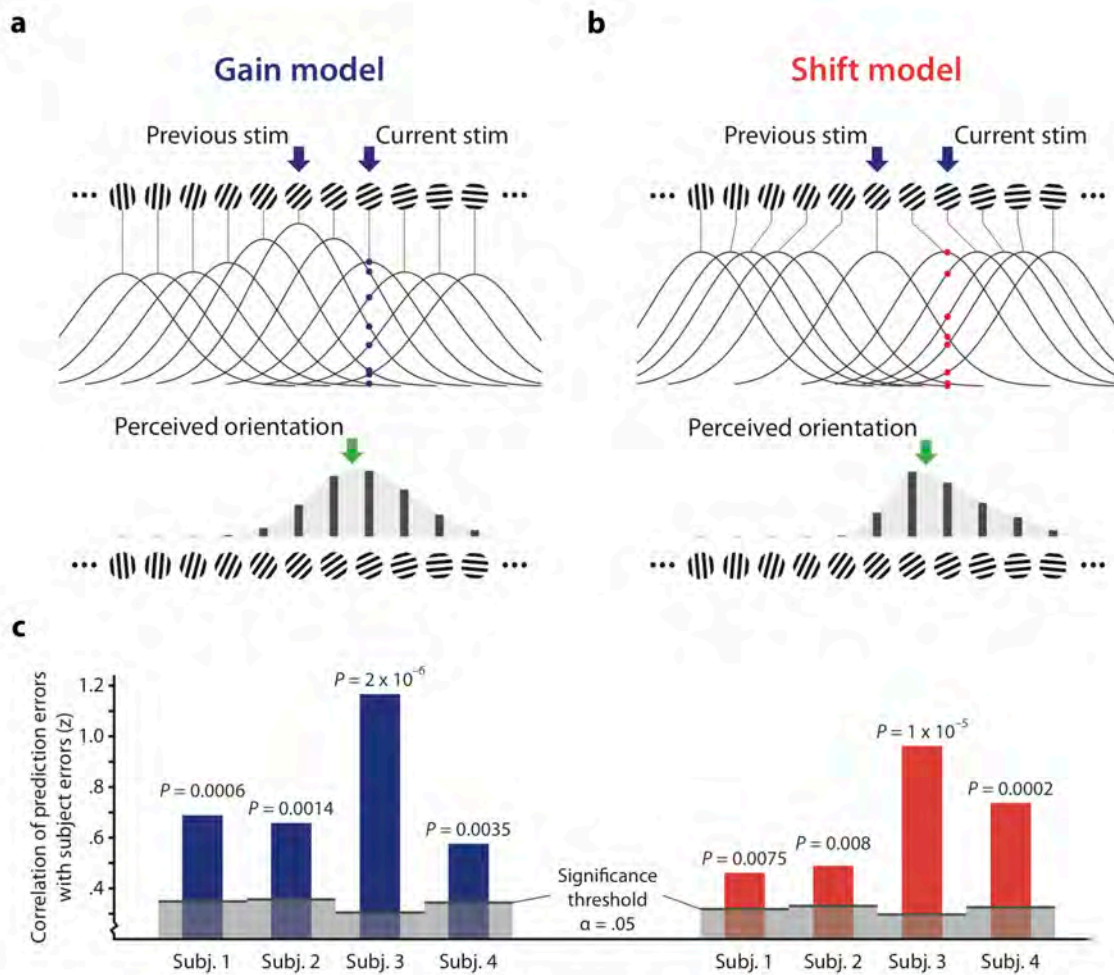


## Supplementary Figure 8



**Supplementary Figure 8:** Experiment 7: Negative aftereffects in orientation judgments. We tested whether negative aftereffects would arise in a similar experimental paradigm to the one used in Experiments 1 and 2 if the stimulus presentation was longer, allowing for orientation adaptation. **a**) In each trial, subjects saw two Gabors: a long duration Gabor (5 s) and a short duration Gabor (500 ms). Each Gabor was followed by a 1 s noise patch, and subjects were instructed to report the orientation of the second (short duration) Gabor using an adjustment response. This design was intended to be as similar as possible to the one used in Experiments 1 and 2 while allowing for orientation adaptation to occur and minimizing the time between the adapting (long duration) and test (short duration) stimuli. The absence of a response between the first and second Gabors is akin to Experiment 2, where we found serial dependence in orientation judgments even in the absence of a response on the previous trial. Both Gabor orientations were randomized on each trial. Two participants each completed six 104-trial runs. **b**) We analyzed the data as in Experiment 1 (see **Supplementary Fig. 1**) by plotting orientation judgment errors as a function of the difference in orientation between the first and second Gabors (Gabor 1 minus Gabor 2). Gray lines show a running average of subjects' errors, and data points show mean error within 20 deg. bins along the abscissa. Black lines show derivative of Gaussian (DoG) fits to subjects' error distributions. Crucially, the sign of the curve fit for each subject was flipped as compared with the data from Experiment 1 (see **Fig. 2a** and **Supplementary Fig. 3**) – both subjects showed significant negative orientation aftereffects (permutation tests; 618 data points per subject). These data show that both negative and positive aftereffects (serial dependence) can arise within the same paradigm depending on stimulus duration and the time between successive stimuli.

## Supplementary Figure 9



**Supplementary Figure 9:** Labeled-line models of how serial dependence may arise from changes in single-unit orientation tuning. **a)** Gain model: channels tuned to recently-seen stimuli temporarily become more responsive. This increased sensitivity shifts the population response to a current stimulus toward the orientations of previous stimuli. **b)** Shift model: single-unit orientation tuning is temporarily shifted away from the orientations of recently-seen stimuli. Shifts in orientation tuning skew the population response to a current stimulus toward the orientations of previous stimuli. **c)** We fit the models to subjects' responses from the fully randomized version of Experiment 1 using one half of the data (odd numbered runs; 412 trials per subject) and tested model performance on the remaining (independent) half of the data (even numbered runs; 412 trials per subject). Both the gain model (blue data) and shift model (red data) performed significantly above chance in predicting subjects' errors on the left-out data (permutation tests; shaded region shows the permuted chance distribution). While the gain model produced somewhat better fits in three of four subjects, both models provide plausible accounts of how serial dependence in orientation perception might arise from simple changes in single-unit tuning.

## Supplementary Modeling for *Serial dependence in visual perception* by J. Fischer and D. Whitney

### *Negative aftereffect model*

To evaluate whether the serial dependence we report could arise simply as a result of classic negative aftereffects, we ran a simulation that estimated the strength of serial dependence we would expect to find in the presence of negative aftereffects alone. Using the counterbalanced trial sequences presented to subjects in Experiment 1, we estimated the perceived orientation on each trial based on the presented orientation and negative aftereffects from the orientations seen on previous trials. The modeled negative aftereffects peaked in strength for previous orientations that were 10 rotational degrees away from the present stimulus and fell off in strength for smaller or larger separations<sup>51</sup>. We allowed the overall strength of the aftereffects to vary as a free parameter in the simulation, ranging from zero (no aftereffect) to 100%, meaning that a previous stimulus rotated 10° from the present stimulus could repel the perceived orientation of the present stimulus by 10° (100% of the orientation difference). The falloff of the influence of negative aftereffects over time was a second free parameter in the model: aftereffects fell off in a Gaussian fashion with the standard deviation of the Gaussian ranging from zero (instantaneous falloff, hence no negative aftereffects) to one minute (trials seen several minutes ago still had some influence on the perception of the present trial). For a given pair of aftereffect strength and temporal falloff parameters, we computed the perception of the present stimulus as the orientation of the present stimulus (correct response) plus the Gaussian-weighted sum of negative aftereffects from all previous trials. After estimating the perceived orientation for each trial, we constructed a serial dependence plot (see **Supplementary Fig. 1**) and fit a DoG (first derivative of a Gaussian) curve to the data to measure the strength of serial dependence. We recorded the predicted serial dependence at each point in the parameter space to determine whether any combination of parameters could lead to results that resemble the serial dependence we found in subjects' responses. The results are shown in **Supplementary Figure 5**, and demonstrate that serial dependence does not emerge as a product of a negative aftereffect of any strength or duration.

### *Labeled-line models*

How might serial dependence in orientation perception arise? We considered two possibilities: cells tuned to the orientations of recently-viewed stimuli might have increased sensitivity for a period of time following the stimulus presentation (a possible result of lingering feature-selective attention), or orientation tuning of single units might shift away from previously viewed stimuli. For each case we constructed a labeled-line model to examine whether such a

phenomenon would result in serial dependence in the decoded orientation from a population of modeled cells. Each model consisted of 180 orientation-tuned Gaussian channels with a standard deviation of 28.2 degrees<sup>52</sup>, tiled over orientation space in increments of one degree. Each channel always signaled the orientation for which it was optimally tuned prior to any stimulus presentation (hence a “labeled line” model). That is, in the “shift” model, the range of orientations to which a channel was responsive could shift, but the orientation signaled by a response from that channel remained constant. Perceived orientation was computed as the centroid of the population response: a Gaussian curve was fit to the responses of all channels (allowing for a skewed distribution by estimating sigma for the rightward and leftward tails separately), and the centroid of the distribution was computed as  $-\sqrt{\frac{2}{\pi}}(\sigma_1 - \sigma_2)$ .

In the “gain” model (**Supplementary Fig. 9a**), channels tuned to the orientation of a recently seen stimulus became more sensitive, i.e. they responded more strongly to subsequent stimuli that fell within their tuning range. The amount of gain applied across channels was governed by a Gaussian distribution centered on the orientation of the most recent stimulus, and the amplitude and standard deviation of the Gaussian distribution were free parameters in the model. A third free parameter was a relaxation parameter, which determined how quickly the gain in channels relaxed back to zero after stimulation.

In the “shift” model (**Supplementary Fig. 9b**), the orientation tuning of the channels was shifted away from a recently seen orientation. The distribution of shifts over channels was determined by the first derivative of a Gaussian (DoG) centered at the stimulated location, such that the shift at the stimulated location was zero and neighboring channels were repelled away with an amplitude that peaked at the maxima of the DoG function and fell to zero beyond that. The width and amplitude of the DoG function were free parameters in the model; subjects were allowed to have different maximal shifts at different distances from the stimulated orientation. As in the “gain” model, a third relaxation parameter determined how quickly the shifted channel tuning relaxed back to its default state after stimulation.

Predicted responses for a given set of parameters were generated by using the trial sequences presented to subjects in the fully randomized version of Experiment 1. For each trial, the model generated a prediction for the perceived orientation of the stimulus based on the present and prior stimuli in the trial sequence. We split the data from the randomized version of Experiment 1 into two halves for each subject and conducted model fitting on the first half of the data and model testing on the second half. Model fitting was conducted with least-squares fitting, finding the parameters that minimized the summed squared difference between the model’s predicted responses and subjects’ actual responses. Within the second half of the data, model performance was evaluated based on the correlation between the model’s errors and subjects’ errors. Testing performance based on errors rather than raw responses required the model to



make the same pattern of errors that subjects made (rather than simply reporting the true stimulus orientations) in order to perform above chance.

**Supplementary Figure 9c** shows model performance for the gain model (blue data) and the shift model (red data). Chance performance was determined by permuting the trial correspondence between model errors and subjects' errors 5,000 times and recording the correlation on each iteration; p values were taken as the proportion of the permuted null distribution that was larger than the true correlation between model errors and subjects' errors. While the gain model tended to perform somewhat better than the shift model, both models performed significantly above chance for all subjects. Both models also have a plausible basis in known neural phenomena. If feature-selective attention remains tuned to the channels that responded to recent stimuli<sup>30</sup>, it could increase sensitivity within those channels as posited in the gain model. There is also evidence that orientation tuning of single cells can shift in the manner specified in the shift model<sup>4</sup>, although such shifts resulted from longer adapting stimuli and may or may not arise for the short stimulus presentation in our paradigm. Further tests will be needed to distinguish among these and other models (e.g., a Bayesian estimation framework<sup>31</sup>) that could accommodate our findings, but our labeled-line models demonstrate that serial dependence in orientation perception can arise from simple tweaks to neural tuning based on recent visual input.