

# Continuity fields enhance visual perception through positive serial dependence

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## Abstract

Positive serial dependencies are phenomena in which actions, perception, decisions, and memory of features or objects are systematically biased towards the recent past. Across several decades, serial dependencies have been variously referred to as priming, sequential dependencies, sequential effects or serial effects. Despite a great deal of research, the functional purpose of positive serial dependencies remains unknown. In this Perspective, we propose that their goal is to promote the stability, accuracy and efficiency of perceptual representations. By continuously inducing serial dependencies, cognition compensates for variability in sensory input and thus stabilizes what would otherwise be a noisy, jittery and discontinuous experience of the world. We theorize that this goal is served by continuity fields: spatiotemporal integration mechanisms that continuously bias perception and cognition towards previously encountered information, thereby smoothing representations to promote the stability, accuracy and efficiency of experience.

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## Introduction

In everyday life, the human visual system is confronted with noisy visual input. Retinal images are often dynamic, and image properties frequently fluctuate from moment to moment as a result of occlusions and lighting changes, as well as internal and external sources of noise. The physical input from the outer world also constantly changes because one's eyes, head and body frequently move, and additional discontinuities are introduced by eye blinks. Still, despite all these factors, people tend to perceive stable object identities within a stable environment and rarely hallucinate or perceive the world as a chaotic environment. One of the fundamental questions in perception science is how this stabilization occurs.

The stability problem is decades, if not centuries, old<sup>1,2</sup>, and has been acknowledged in various guises in many aspects of vision science including eye movements<sup>3</sup>, colour perception<sup>4,5</sup>, change or inattention blindness<sup>6</sup> and adaptation<sup>7,8</sup>. For small fluctuations in visual signals, stability may be achieved passively or because of a lack of sensitivity. For example, changes in stimuli are often below the perceptual threshold<sup>9–11</sup>, suppressed<sup>12</sup>, or outside awareness because of capacity limits in attention or memory<sup>13,14</sup>. Thus, stability in some instances of visual change is achieved 'for free', in that the change is not registered by the perceptual system.

In 2014, it was proposed that perceptual stability is facilitated by an active mechanism, built on positive serial dependence in visual representations<sup>15,16</sup>. Positive serial dependencies are phenomena in which actions, perception, decisions and memory of features or objects are systematically biased towards experiences from the recent past<sup>15,17,18</sup>. Among many labels, positive serial dependencies have been referred to as priming, sequential dependencies, sequential effects or serial effects. This attractive bias contrasts with negative aftereffects<sup>19,20</sup>, a known form of repulsive negative bias.

Positive serial dependencies enhance perceptual stability because the world is autocorrelated: features and objects are relatively unlikely to change location or identity spontaneously over time<sup>21–24</sup>. The visual system could harness this autocorrelation by inducing positive serial dependencies between object representations. For instance, given that objects rarely change colour, size, position or identity over time and space, it is advantageous for their current perception to be influenced by both its current and recent appearance. In this light, the lack of hallucinations is not simply because of insensitivity to changes but an active stabilization process built on serial dependence. In principle, serial dependencies could be introduced at any or every level of analysis, from low-level sensory codes to higher-level cognition, action and memory<sup>25</sup>. Because objects and the environment do not typically change abruptly, neural systems can promote smoother, more stable representations over time by biasing current action, perception, decisions and memory towards the past (at least up to a point).

In this Perspective, we consider evidence for visual positive serial dependencies across a range of sensory and cognitive manifestations. We focus on serial dependence in vision because so much research on this has been published<sup>17</sup>. However, serial dependence effects have been reported in other modalities, including audition<sup>26–29</sup>, timing perception<sup>30</sup>, eye movements<sup>31–34</sup>, pupil modulation<sup>35</sup>, olfaction<sup>36</sup> and multisensory perception<sup>37,38</sup>. Furthermore, serial dependencies can manifest in many realms of psychology, from clinical to social and developmental<sup>39–44</sup>. We will show that serial dependencies occur with a large variety of visual stimuli; they manifest in action, perception, decisions and memory, and are tuned for temporal, spatial and featural properties of the environment, as well as the attentional resources of

the observers. We solidify this converging empirical evidence into a new theoretical account, proposing that serial dependencies underlie integration mechanisms called continuity fields: spatially and temporally tuned operators (analogous to receptive fields<sup>45–47</sup>) that smooth actions, perception, decisions and memory over time. We propose that the computational goal of continuity fields is to improve the efficiency, accuracy and speed of information processing and perception and to facilitate the stability of neural representations over time, without the need to re-analyse the entire visual scene at every moment.

## Positive serial dependencies

Serial dependencies are pervasive and ubiquitous. They alter the representations of almost all kinds of features and objects, occur through many behavioural paradigms, and manifest in different ways.

## Stimuli and behavioural paradigms

Serial dependencies in perception occur with a variety of stimuli<sup>17</sup> (Fig. 1). In the visual modality, serial dependencies occur in basic low-level features, such as luminance<sup>48</sup>, orientation<sup>15,49–56</sup> (Fig. 1a), position<sup>32,33,57,58</sup>, colour<sup>59–63</sup> (Fig. 1b), and shape<sup>64–66</sup> (Fig. 1c).

Beyond these simple features, serial dependencies occur also on more complex properties of the scene. Global object properties, such as numerosity<sup>18,67–69</sup> (Fig. 1d), ensemble orientation and variance<sup>50,70–73</sup> and complex motion patterns<sup>71,74,75</sup> can be extracted and biased towards the past. This kind of serial dependence occurs on global visual input, beyond the local serial dependencies found for single features<sup>70</sup>. In addition, aesthetic ratings of artwork, which could involve low-level and high-level cognitive processes, were found to be biased towards recent visual experience<sup>76,77</sup>.

Serial dependence can also occur on representations of people, including faces. For example, a face seen at one moment appears more similar in identity to similar faces seen in the last several seconds than it actually is<sup>16,78–82</sup> (Fig. 1e). This dependence can even lead to misrecognition of face gender<sup>83</sup>. Face attractiveness is also biased by serial dependence<sup>84–92</sup>. Likewise, perceived facial expression (for instance, degree of happiness) is serially dependent<sup>93–96</sup>, as is the apparent age of faces<sup>97,98</sup>. In addition, past visual experience can bias body size estimations<sup>99</sup> (Fig. 1f), gaze direction<sup>31</sup> and emotional content in natural scenes<sup>100</sup>.

Serial dependencies occur across several behavioural paradigms (Fig. 2), including continuous report in position and orientation<sup>15,50,58,75,101,102</sup> (Fig. 2a), magnitude estimation<sup>38,81,85,87,103</sup> (Fig. 2b), discrimination<sup>15,68,104</sup> (Fig. 2c) and even detection<sup>55</sup> (Fig. 2d). Taken together, serial dependencies affect the representations of virtually all kinds of visual features and objects in a pervasive manner, in a large variety of behavioural paradigms.

## Manifestations

The literature contains reports of positive serial dependencies in vision across four main manifestations: action, perception, decisions and memory (Fig. 3). By manifestation, we refer to the consequence of past visual experience on the present. Manifestations of serial dependence should not be confused with levels of processing, which relate to the underlying mechanism and will be discussed later. For each manifestation, we describe how positive serial dependencies can actively contribute to visual stability.

In action, previous visual experience can influence motor behaviour in response to subsequent visual stimuli. This effect can manifest as a change in response times, a change in error rates, or a motor bias. These findings have been referred to as visuomotor priming<sup>105</sup>, action

priming<sup>106</sup> or response priming<sup>107</sup>. In a typical priming paradigm, motor responses are sped up when current presentations are primed by a previous congruent stimulus compared to an incongruent one<sup>108–111</sup>.

Action priming effects have been documented for many decades<sup>109,112</sup>. However, it is unclear whether these types of priming effect are actually forms of serial dependence. On one hand, they seem to be advantageous effects in line with the continuity fields proposal; in a stable visual environment it is advantageous to increase the speed of one's actions when features and objects are the same (or congruent) over time. On the other hand, there is evidence that priming (changes in reaction time) can be dissociated from serial dependence (biases in reproduction errors; Fig. 2a). For example, repeating stimuli increases priming (reduces reaction time) but does not necessarily change the perceptual biases from serial dependence<sup>113</sup>.

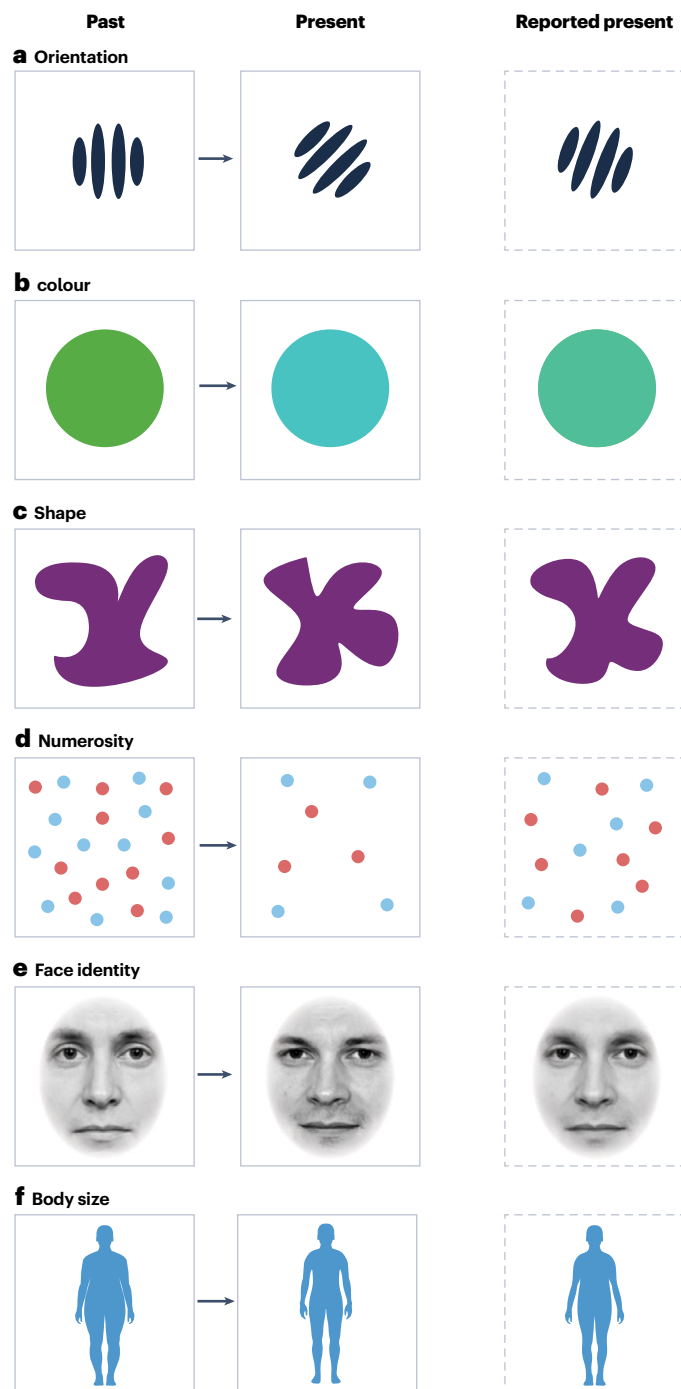
Regardless of whether serial dependence causes changes in reaction time, there are also serial dependencies in actions that do not hinge on priming. For example, one study measured eye movements in response to visual motion cues and found that serial dependence in eye movements is mediated by retinal error signals independently of the spatial context<sup>114</sup>. This pattern indicates a very early, sensory form of serial dependence in eye movements that can therefore facilitate eye movements in an autocorrelated world. This early locus of one instance of serial dependence does not preclude serial dependence in motion perception as well<sup>54,74,75</sup>, but these forms of serial dependence must operate at different stages of processing.

In perception, previous visual experience can change the appearance of subsequent visual objects, leading to a different perceptual experience. Perceptual serial dependencies can induce stability by making different objects look more similar over time<sup>15,98</sup>. This change in appearance, although debated<sup>31</sup>, has been psychophysically demonstrated by dissociating a mere decision-making bias from appearance<sup>15,55,104,115,116</sup>. Furthermore, this manifestation in perception has been exemplified by a specific visual illusion: a continuously seen, physically changing object is misperceived as relatively unchanging because of serial dependence<sup>98</sup> (see a demonstration [online](#)). In a stable visual environment, it is advantageous to continuously recycle previously perceived features and objects, instead of analysing the entire visual scene afresh at every single moment.

In decision-making, previous visual experience can also bias decisions about subsequent visual objects. We defer to previous definitions of 'perceptual choice' as a high-level process that requires interpretation of perceptual experience beyond sensory processing<sup>117</sup> (see discussion of definitions in the section 'Levels of processing'). Depending on the success or failure of past choices, one can implement switch-after-failure or stay-after-success strategies in the present<sup>48,118–122</sup>. In addition, choices<sup>123,124</sup>, expectations<sup>125–127</sup>, confidence<sup>102,128–131</sup> and preference<sup>77</sup> play a crucial role in serial dependence. In a stable environment, it is advantageous to infer regularities in visual input, promoting expectations and preferences with different levels of confidence, and therefore bias decisions accordingly.

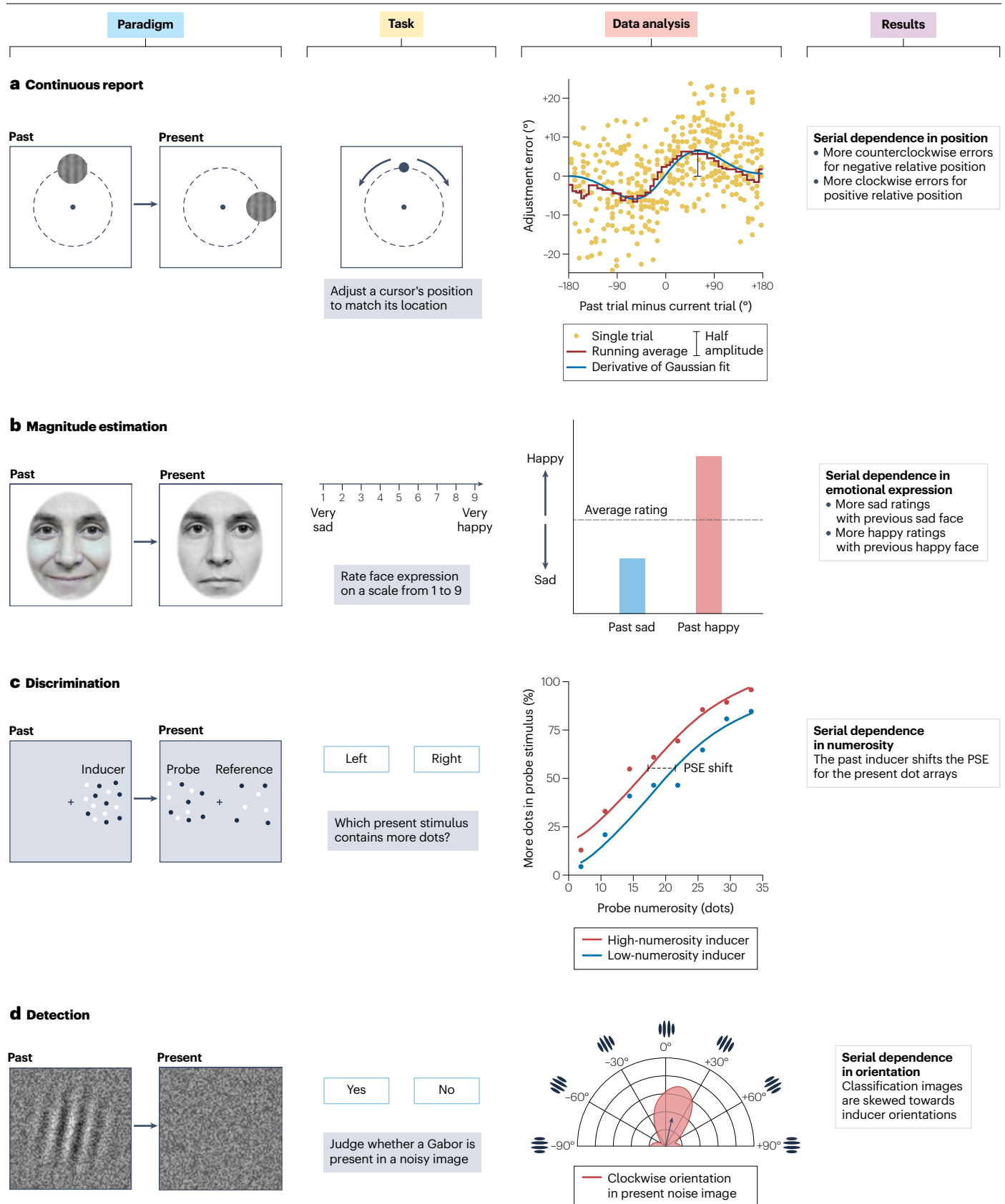
In memory, previous visual experience can also determine the memory of subsequent visual objects<sup>132,133</sup>. For example, visual working memory, here defined as a visual representation of the world that is actively maintained to serve broader cognition<sup>134,135</sup>, can be distorted in its content towards the past. In a stable environment, it has been proposed that the lingering activation of previously relevant stimuli might increase sensitivity for related current information, and thereby increase the cohesion of working memory episodes<sup>25,136</sup>. Conversely, such manifestation in memory could become maladaptive when

previous relevant stimuli are irrelevant to the current situation. This is what happens in proactive interference, when previously memorized visual information detrimentally interferes with the recall of more



**Fig. 1 | Positive serial dependencies across visual stimuli.** In each panel, 'Past' and 'Present' refer to previous and current stimulus and 'Reported present' refers to the reported current stimulus, biased by positive serial dependencies<sup>17</sup>. **a–d**, Orientation<sup>15</sup>, colour<sup>63</sup>, shape<sup>65</sup> and numerosity<sup>68</sup> of objects in a current display are reported as biased towards previous visual stimuli. **e, f**, Face identity<sup>80</sup> and body size<sup>99</sup> are reported as biased towards previously seen individuals.

# Perspective



## Fig. 2 | Behavioural paradigms and data analysis in positive serial dependencies.

**a.** Observers match the location of randomly positioned target grating by adjusting a cursor's position. Adjustment error is plotted as a function of relative difference between previous and current target position. To quantify the magnitude of serial dependence, a derivative of Gaussian (or equivalent) is fitted to the data (blue line) measuring the half-amplitude peak<sup>57,58</sup>. **b.** Observers rate the expression of random faces using a Likert scale. Ratings of current faces are typically biased towards past facial expressions; see similar studies in

refs. <sup>85,87,88</sup>. **c.** Observers are asked which array (probe or reference) contains more dots. Psychometric functions are measured for conditions with and without preceding inducer dots. The point of subjective equality (PSE) is shifted when a previous inducer dot array is presented, in the direction consistent with serial dependence<sup>68</sup>. **d.** Observers detect a Gabor patch embedded in a noisy image. A previously seen Gabor patch biases the detection of orientation information in subsequent noise images, causing classification images to be biased towards previous stimuli<sup>55</sup>.

recent information<sup>132,133,137–141</sup>. In this sense, proactive interference can be considered as a by-product of a type of serial dependence that is generally useful for memory coherence.

It is important to mention that these distinct manifestations of serial dependence (outcomes in action, perception, decision and memory; Fig. 3) do not necessarily imply that serial dependence operates only at those specific levels of processing (their underlying mechanism in perception, decision and memory, from early to late stages). For example, a manifestation of serial dependence in working memory<sup>58,63,137,140,141</sup> is not necessarily evidence of a mechanism of serial dependence taking place solely at the level of memory processing; it can arise and be modulated by other factors at different levels of processing. Likewise, serial dependencies can be strongly tied to basic sensory representations like retinotopy<sup>15,53,142</sup> and can affect visual appearance<sup>15,98,104,116</sup>, but this does not preclude serial dependence occurring at levels of memory and decision<sup>50,141</sup>, or interactions among different levels<sup>58,143</sup>. Thus, although many papers have succumbed to the temptation of arguing for a single level of processing of serial dependence, the most plausible hypothesis is that serial dependence operates at many levels of processing.

Each manifestation of serial dependence continuously interacts through top-down and bottom-up processes. Indeed, serial dependence can be modulated or mediated by higher-level processes, such as attention<sup>15,49,144</sup> confidence<sup>102</sup> and memory<sup>58,74,95,145,146</sup>. Although these influences make it very difficult to pinpoint at which exact processing levels serial dependencies occur, it does suggest that serial dependence is not a monolithic or single modular process. Serial dependencies are a family of phenomena and are not the result of a linear sequential processing pipeline in a single hierarchical order. Instead, each level stems from complex, reciprocal interactions across a large network of areas<sup>147,148</sup>. These phenomena are unified by shared tuning dimensions, as we describe next.

## Tuning properties of serial dependencies

The visual world is autocorrelated over time, meaning that the same features and objects are often presented at the same location, and objects and physical characteristics rarely change spontaneously<sup>21–24</sup>. If serial dependencies promote the stability, accuracy and efficiency of visual representations, we predict that they should be optimized to make use of such properties of the environment, as appropriate for the relevant modality and level of processing. In line with this idea, research has revealed that serial dependencies occur in a selective manner (are 'tuned') for temporal, spatial and featural properties of the environment, as well as the attentional resources of the observer (Fig. 4 and Box 1; see ref. 17 for a meta-analysis).

### Temporal tuning

Serial dependence gradually decays over time or intervening information (Fig. 4a; refs. <sup>15,32,64,71,101</sup>, among others). For example,

orientation perception is systematically attracted by stimuli presented up to 15 seconds in the past<sup>15</sup>. Temporal tuning is typically measured by computing serial dependence strength (Fig. 4a) across the previous trials and was also found to decrease linearly with increasing temporal delay between current and previous trials<sup>58</sup>. The temporal window within which serial dependence occurs is not strictly fixed, but varies depending on the features and objects used, as well as on task and conditions<sup>78,80,149</sup>. For example, prior orientation and faces can influence perception for 15 seconds or more<sup>15,16</sup>, and timing perception seems to hold for at least 8 seconds<sup>150</sup>. In addition, the perceptual states of individual observers can lead to dependencies up to days, weeks and even months in the past<sup>151</sup>.

### Spatial tuning

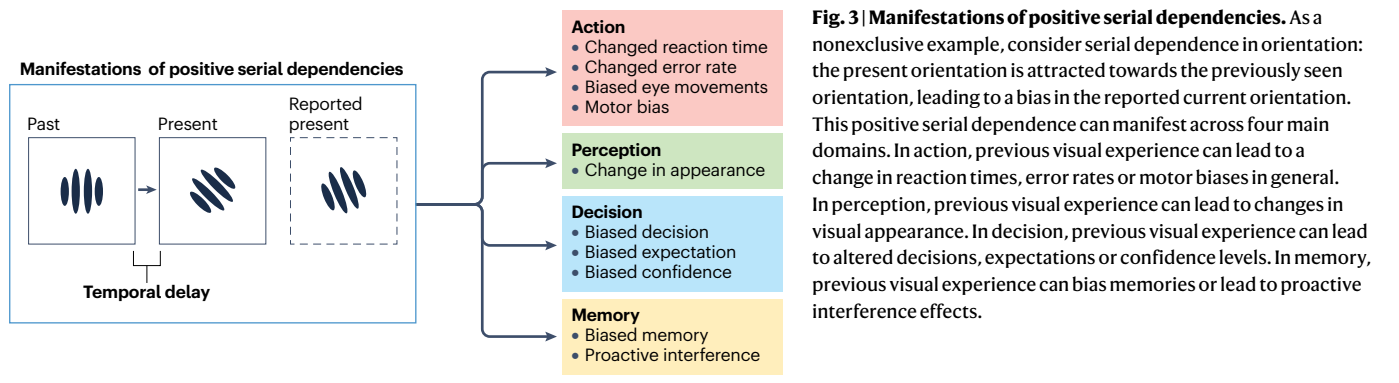
Serial dependence gradually decreases with increasing the relative spatial distance between current and previous objects (Fig. 4b). It is strongest when previous and current objects are presented at the same location, and gradually decreases with increasing the spatial distance between previous and current objects<sup>15,53,57,58,64,68,104,115</sup>. Most research on the spatial tuning of serial dependence has focused on orientation<sup>15,53,104,142</sup>, but spatially selective serial dependence was also found for faces<sup>66</sup>, position<sup>57</sup> (see tuning in Fig. 2a)<sup>58</sup>, numerosity<sup>67</sup> and shape<sup>64,65</sup>. The coordinate frame(s) of the spatial tuning are substantially retinotopic, at least for orientation<sup>15,53,104,142</sup>, but it has also been reported in allocentric<sup>152</sup> and cartesian coordinates<sup>153</sup>. It is conceivable that the spatial tuning of serial dependence operates in more than one coordinate frame<sup>15</sup> or it may depend on the level of processing and particular stimuli involved. For example, retinal motion generates serial dependence<sup>114</sup>, and so does perceived motion or relative motion<sup>54,75</sup>, but the coordinate frames of these effects are dissociable.

### Feature tuning

Serial dependence occurs for more similar sequential objects, but not for dissimilar ones (Fig. 4c). This kind of tuning was found with low-level basic features such as orientation<sup>15,50,51</sup>, position<sup>32,33,57,58</sup>, colour<sup>59–63</sup> and shape<sup>64,65</sup>. Serial dependence is also tuned to similarity in higher-level object representations, like faces<sup>16,80,94</sup>. For instance, serial dependence was found to occur across different face viewpoints<sup>16,80</sup> but not for rotations around the roll axis or for invariances that disrupt face recognition<sup>80,89</sup>. In addition, within the same object, positive serial dependencies occur at the level of features and at the level of integrated representations<sup>66</sup>. Negative aftereffects can occur at the same time in other stimulus dimensions, such as expression and orientation<sup>54,83</sup> (Box 2). These findings point to multifaceted feature-tuning interactions for complex stimuli.

Not all studies that have reported serial dependence have found strong feature tuning; for instance, it was not found for motion variance estimates<sup>71</sup>, face attractiveness<sup>85</sup>, or aesthetic judgements of artwork<sup>76</sup>. However, the null result in these studies should not be taken as strong





**Fig. 3 | Manifestations of positive serial dependencies.** As a nonexclusive example, consider serial dependence in orientation: the present orientation is attracted towards the previously seen orientation, leading to a bias in the reported current orientation. This positive serial dependence can manifest across four main domains. In action, previous visual experience can lead to a change in reaction times, error rates or motor biases in general. In perception, previous visual experience can lead to changes in visual appearance. In decision, previous visual experience can lead to altered decisions, expectations or confidence levels. In memory, previous visual experience can bias memories or lead to proactive interference effects.

evidence against feature tuning, even in those domains. What counts as similar in complex features and objects can be difficult to define or manipulate, so the tuning might still be present but not adequately captured by the stimulus range or data analysis in a given study (Box 1). In particular, two common limitations occur in the work that reports an absence of feature tuning. First, the stimulus range might be small compared to sensitivity (that is, ratio of the stimulus range to a just-noticeable difference). Second, the tested stimulus dimensions are often prothetic or linear, in contrast to metathetic or circular dimensions (such as orientation). These two factors are often intertwined, so it is important to be cautious about concluding that tuning is absent when the real culprit might be discriminability, range and/or a more general lack of statistical power.

## Attentional tuning

Serial dependence is, in at least some forms, gated by attention (Fig. 4d). Spatial attention toward previous objects is required for serial dependence to occur on the current object<sup>15,52,68,154,155</sup>. Consistent with this pattern, serial dependence only occurs for stimuli that are within the focus of attention and awareness, and does not occur when features are suppressed by binocular rivalry<sup>144</sup>. In addition, feature-based attention has an important modulatory role: attending to a specific feature in a complex object leads to higher serial dependence in that dimension compared to when a different dimension is attended to<sup>49</sup>. For instance, serial dependence in orientation increases when the previous orientation is attended to compared to the previous size. Along the same lines, it was found that serial dependence increases when objects share the same context features (colour, serial position or spatial position) across trials, therefore showing that attentional selection to multiple features and objects plays a role<sup>75</sup>.

Taken together, serial dependencies do not indiscriminately and automatically occur in all situations, but rather are tuned to specific properties (see ref. 17 for meta-analyses of the four tunings). Serial dependencies induce perceptual stability between sequentially viewed objects for a limited period of time, at a similar location, when the objects are relatively similar, and if the features and objects are attended. These tunings need not be hardwired and can continuously interact with each other; for example, attention can modulate the decay of serial dependence in time, as well as in space and feature similarity.

## Continuity fields

We propose that positive serial dependencies are a manifestation of a broader psychophysically defined theoretical construct called

continuity fields<sup>15,16</sup> (Fig. 5). Continuity fields are spatiotemporal regions within which the visual system treats visual features and objects as being more similar than they actually are. Within these spatial, temporal and featural windows (Fig. 4), actions, perception, decisions and memory of features or objects are systematically biased towards experiences from the recent past (Fig. 5).

Continuity fields are operationally defined by their tuning properties (Fig. 4): the specific conditions in which serial dependence occurs. Continuity fields are analogous to but different from receptive fields. The concept of receptive fields, originally defined behaviourally as regions of the body that drive reflexes<sup>45</sup>, was extended to refer to specific regions of sensory space in which an appropriate stimulus elicits a neuronal response<sup>156</sup>. Like receptive fields, continuity fields are mechanisms, but their function is distinct. By biasing action, perception, decisions and memory towards the past (through serial dependence), continuity fields promote stability<sup>15,70,98,157</sup>, accuracy and efficiency<sup>111,158</sup>. Thus, continuity fields as a mechanism reflect the computational goal of serial dependencies: to enhance perception of an otherwise jittered and noisy visual input. We next outline the implications of continuity fields, and review their possible levels of processing, neural correlates and models.

## Implications

Continuity fields, with their serial dependence effects, can be beneficial for visual stability, accuracy and efficiency. By continuously recycling previous visual information, continuity fields can promote visual stability (see a demo [online](#) of visual stability induced by serial dependence)<sup>98</sup>. In the autocorrelated visual world, it is advantageous for the visual system to continuously bias representations towards the past for the sake of interacting in a stable environment<sup>15,18,70</sup>. Similarly, when watching a film, the human visual system tricks the viewer into perceiving a stunt double as the principal actor for the sake of continuously perceiving the same person in action<sup>16</sup>. Importantly, continuity fields also lead to more accurate and faster responses when previous and current visual stimuli are similar than when they are dissimilar. They can therefore improve sensitivity and confidence in an autocorrelated environment in which previous and current visual stimuli are routinely similar<sup>18,111,131,158,159</sup>. On a neural level, continuity fields also reduce the number of potential neural computations across time for each perceived object. In this sense, biased perception of features and objects can be an efficient strategy because the visual system exploits natural temporal redundancies to its advantage<sup>104,111,158</sup>.

However, trading some accuracy in favour of stability by biasing representations towards the past can have detrimental consequences

when dealing with non-auto-correlated sequences of images. For example, perceptual decisions biased toward the past might have life-changing consequences for clinicians performing medical image perception tasks (such as cancer screening) and officers conducting airport security screenings. In fact, it was found that classification errors of simulated tumours are 7% more often biased towards the previous image content than towards other tumour categories<sup>64,65,160,161</sup>. In addition, previously memorized visual content can interfere with the retrieval and acquisition of present information, thereby leading to proactive interference<sup>137–140</sup>. In another real-life context with non-auto-correlated sequences of images, when looking at random face images in dating apps, observers are more likely to rate a face as attractive when the previous face was attractive than when it was unattractive<sup>85,87,88,90,162</sup>.

At a more general level, the existence of continuity fields would have methodological implications for behavioural research studies<sup>48</sup>. Although there has been a great deal of work on response perseveration and other order effects in responses<sup>118,119,163</sup>, visual judgements about trials presented in a sequence are usually assumed to be independent of previous trial content<sup>48</sup>. This assumption is important for most common psychological and psychophysical approaches, including putatively bias-free constant stimuli and adaptive procedures. However, serial dependence can manifest as a temporally varying criterion<sup>164,165</sup>, or horizontally shifting psychometric functions<sup>166,167</sup>. In fact, by removing history biases such as negative and positive serial dependence, discrimination thresholds were found to be lower and more reliable<sup>48</sup>.

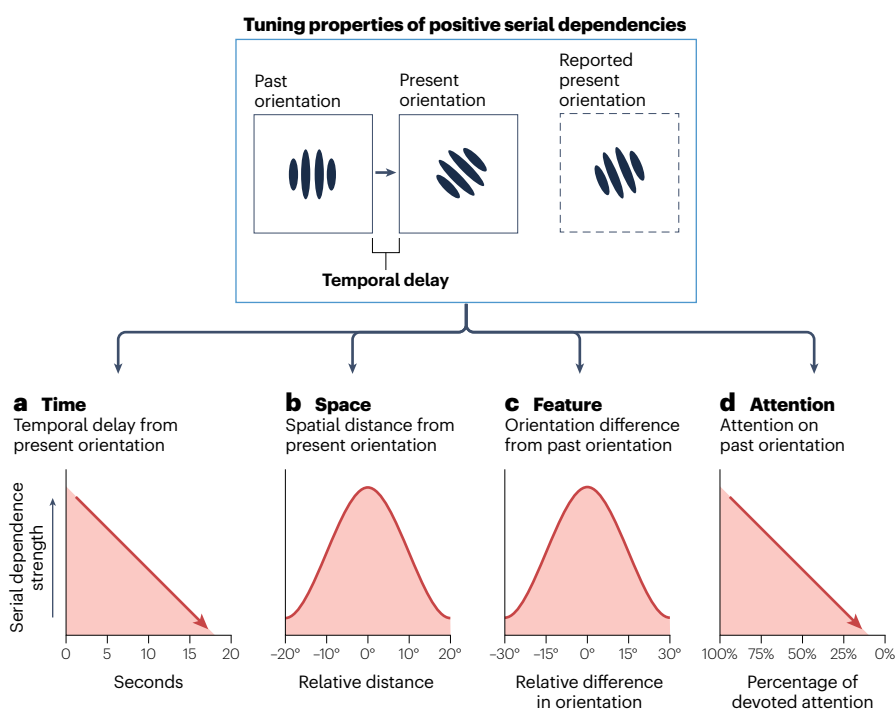
We have so far operationally defined continuity fields by their psychophysically measured tuning properties (Fig. 4). Although the computational goal of continuity fields (and the resulting positive serial dependencies) has been characterized in the literature, their neural loci and implementation are still under investigation. To effectively

isolate, identify and visualize continuity fields (similar to what is shown in Fig. 5), it is crucial to uncover the neural mechanisms responsible for serial dependence. In the following sections, we examine the levels of processing, neural loci and algorithms that have been proposed for generating serial dependence, therefore serving as an indicator of the presence of the continuity field operator.

## Levels of processing

Serial dependencies have been proposed to occur on the level of perception<sup>15,57,68,98,104,114,116</sup>, decision<sup>50,51,122,143,168,169</sup>, and memory<sup>32,63,74,136,141</sup> and debate continues about their locus or loci. It is important to mention that, when referring to levels of processing, there is no consensus on the operational definitions of these concepts; there is an unavoidable fuzziness in what counts as ‘perception’, ‘decision’ and ‘memory’ processes. We bear this in mind and offer only pragmatic placeholders for these indistinct and overlapping categories. The links to actual processing levels – and corresponding brain mechanisms – should not be taken for granted.

Serial dependencies cannot be considered purely low-level or high-level phenomena. There is a substantial literature on top-down modulation of serial dependence from attention<sup>15,49</sup>, awareness<sup>115,144</sup>, memory<sup>51,58,95,146</sup>, task<sup>75,87,170</sup>, context<sup>75</sup> and confidence<sup>102,168</sup>, among other factors<sup>127</sup>. At the same time, serial dependencies cannot be considered as a purely high-level process because they are strongly tied to the visual properties of visual stimuli, can occur independently of explicit decision<sup>68,69,94,98,104,114,171</sup>, can be response- and task-independent<sup>55,98,104,114,171</sup>, and can manifest in perception<sup>98,104,116</sup>. For particular feature dimensions such as orientation<sup>15</sup>, the truth might lie somewhere in the middle: serial dependence might be the result of top-down mechanisms that propagate down to early levels of visual processing<sup>55,172</sup> which might act in the form of perceptual templates<sup>55</sup> after contextual effects are incorporated<sup>172</sup>. Serial dependence might also



**Fig. 4 | Tuning properties of positive serial dependencies.** When an oblique grating (for example, at  $-25^\circ$  orientation) is preceded by a vertical one ( $0^\circ$ ), the oblique orientation is perceived as biased towards the past ( $-25^\circ + 5^\circ = -20^\circ$ ). **a**, Serial dependence decreases as the temporal delay between past and current orientation is increased. **b**, Serial dependence occurs only within a limited spatial window; it is strongest when previous and current orientations are presented at the same location ( $0^\circ$  degrees of visual angle), and it gradually decays as the relative distance increases. **c**, Serial dependence occurs only between similar features and not between dissimilar ones. **d**, Serial dependence is tuned for attentive resources devoted to the past orientation.

## Box 1

### Measuring serial dependence

Continuity fields reflect an underlying serial dependence in how the brain processes information. Measuring serial dependencies, however, is not trivial; they are easily confused with other effects that can masquerade as sequential biases. In fact, many psychophysical findings can look like serial dependence but in reality represent something different. The following is an incomplete list of artefacts that can imitate serial dependence but that are not, and therefore none of these can be considered to be the core mechanism of continuity fields.

#### Stimulus artefacts

When investigating serial dependence in a sequence of trials, it is important to consider and control the stimulus distribution. Most studies use stimuli drawn from a metathetic (circular, like orientation) or prothetic (linear, like size or gender) stimulus distribution. With prothetic stimulus spaces (for example, ranging from happy to sad), edge intensities in the stimulus can become perceptual anchors<sup>221</sup> or predictive (an extremely happy face is likely to be followed by something less happy). These kinds of edge effects can lead to biased responses that masquerade as a serial dependence effects but are not. They are, in fact, an artefact arising from a linear stimulus space. This problem also applies if the stimulus space is circular but the dimensions of the presented stimuli are restricted to an effectively prothetic portion of the stimulus distribution. These kinds of artefact can be controlled in several ways in experiment design and analysis, as described below.

#### Response artefacts

Central tendency<sup>222</sup> effects can lead to something that appears similar to serial dependence. For example, judgements constantly biased towards the mean value of a stimulus scale would lead to a seeming serial dependence. Serial dependence consists of a dynamic prior on a trial-by-trial basis, whereas central tendency is a static one (mean of the stimulus set<sup>223</sup>). Hence, central tendency is not serial dependence and can be dissociated from it<sup>30</sup>, controlled<sup>16</sup>, or taken into account in a model<sup>85</sup>. Along the same lines, response hysteresis (responding the same way on successive trials)<sup>166,224</sup> can be confused with serial dependencies<sup>225</sup>, but response hysteresis is independent of the visual stimulus, is not tuned in the same ways (Fig. 4) and has been dissociated from serial dependence in many papers<sup>15,70,104</sup>.

#### Observer-specific biases

Observers have idiosyncratic biases in many perceptual and cognitive functions<sup>151,226–229</sup> that could masquerade as serial dependence. Unique observer-specific biases in perceptual localization or pattern, object and face recognition could, for example, cause observers to over-report some stimuli and under-report others<sup>32,50,58,102,230</sup>. This reporting can happen even in a circular stimulus space<sup>227</sup> and would appear to indicate a serial dependence effect, even when none is present. This pattern also highlights how artefacts can interact with each other, introducing unforeseen biases. For example, it has been shown that there are individual differences in perceived position, size and motion direction<sup>151,226,227</sup>. These biases are related to individual observers but are not generated through serial dependence nor do they serve as a clear mechanism of perceptual stabilization.

#### Cognitive biases

Observers might rely on past information to make subsequent judgements independently of the visual stimulus<sup>231–233</sup>. Anchoring effects like this can look like serial dependence at first, but anchoring does not conform to the operational definition of serial dependence because it is not tuned to the same dimensions. For example, anchoring is not spatially or retinotopically tuned<sup>15,53,104</sup>. Anchoring is also not known to display the other tuning properties of serial dependence<sup>234</sup> (Fig. 4). That said, some reports of anchoring might be forms of high-level serial dependence. The possible links between serial dependence and anchoring remain an interesting and open area of investigation.

This list of potential pitfalls and artefacts is, of course, incomplete, but it highlights the importance of considering in all experiments how artefacts might introduce spurious sequential effects or imitate serial dependence. These artefacts can be controlled through stimulus design, experiment design, analysis controls, appropriate null distributions and statistical tests, ideal observer modelling, or a combination of these approaches. It is also worth noting that all of these concerns hold not just for psychophysical experiments but for all experiments that use behavioural and/or physiological methods. More importantly, these pitfalls and artefacts do not have any beneficial implication for stability, accuracy, or efficiency in the processing of the visual environment, and thus cannot be considered as the basis of the continuity fields.

encompass multiple stages, as in the motion domain: retinal motion can generate serial dependencies<sup>114</sup>, and so can perceived motion<sup>54</sup>, indicating that serial dependencies are introduced redundantly.

Importantly, serial dependence at any level of visual processing is consistent with the proposal of continuity fields as stabilization mechanisms. Even if continuity fields took place at a specific level of processing, their manifestations would still serve the purpose of stabilizing actions, percepts, decisions or memories in the noisy environment. Crucially, there is broad evidence for the manifestation of serial dependencies in perception<sup>15,55,98,104,114,116,173</sup>, independently of the level of processing. Thus, any underlying mechanism of serial dependence

needs to take into account these perceptual manifestations. Finally, evidence for the role of top-down factors such as attention<sup>15,49,144</sup> confidence<sup>102</sup> and memory<sup>58,74,95,145</sup> does not go against the proposal of serial dependence as a stabilization mechanism: visual mechanisms do not act in isolation, but they have a role within complex systems whose reciprocal interactions operate across large networks of areas and at multiple levels of visual processing<sup>147,148</sup>.

#### Neural correlates

Research on the neural correlates of continuity fields is still preliminary<sup>174</sup> but has pointed to several potential loci, ranging from early



visual cortex to frontal cortex. Some kind of serial dependence might arise in the initial feed-forward processing of information, very early after stimulus onset and maintained for a relatively long retention period<sup>175</sup>. Potentially consistent with this, orientation signals in early visual cortex were found to be biased toward previously presented orientations<sup>176</sup>, but see ref. 177, implying that serial dependence might act at very early stages of visual processing. However, identifying a neural correlate does not necessarily localize the source of the effect or the cortical networks that support it.

Several studies have proposed that serial dependence involves higher-level cortical regions, which might involve feedback to earlier levels of processing (see also Box 3). For example, transcranial magnetic stimulation of dorsal premotor cortex<sup>178</sup> and lateral frontal cortex<sup>179</sup> leads to reduced serial dependence, therefore showing that these areas have a role in storing previous trial history. Based on single-cell recording data in rats, posterior parietal cortex carries a substantial amount of information about sensory-stimulus history<sup>180</sup>; see also ref. 181. Similarly, ventrolateral prefrontal cortex in primates also encodes prior stimuli and decisions<sup>182</sup>. Human intracranial recordings reveal that

medial prefrontal cortex activity correlates with perceptual memory of previous trials<sup>183</sup>. Previous stimulus information is also decodable from single-unit spiking activity in the frontal eye field<sup>33,184</sup>; it was found that the firing patterns of neurons in this area (and their resulting eye movements) are a weighted combination of prior and current sensory visual information<sup>184,185</sup>. Past visual information is also stored in a more global manner, as reflected by large-scale activity patterns in human EEG<sup>186–189</sup> (but see ref. 190) and alpha oscillations<sup>27</sup>. Finally, activity-silent traces inferred from spiking synchrony in the prefrontal cortex were found to modulate serial dependence; from this data it was proposed that serial dependence in the working memory arises from a combination of sustained firing and synaptic augmentation<sup>136,191</sup>.

Despite the accumulating evidence, the neurophysiological mechanisms of serial dependencies are still inconclusive; several brain areas are believed to be involved in serial dependence, without any unanimous consensus on their involvement and/or interactions. Perceptual history is stored in many brain regions and in many forms, and any or all of these could be involved in functionally biasing present action, perception, decisions and memory. This diverse body of findings on serial

## Box 2

### Serial dependence and adaptation

Adaptation produces negative aftereffects, whereas positive serial dependence is a kind of positive aftereffect. The two can occur at the same time<sup>15,51,52,54,71,83,101,115,204,212,235–237</sup>, but they are empirically distinguishable. First, they have different tuning properties, in the time, space and feature domains<sup>17</sup> (Fig. 4). Negative aftereffects are often retinotopically specific<sup>238,239</sup>, do not spread far in space and do not require attention<sup>19,20,49,240–243</sup>. Serial dependence, on the other hand, is very broadly tuned in space, more broadly tuned to feature dimensions, and it is gated by attention (Fig. 4). Although adaptation (and consequent negative aftereffects) and serial dependence can be dissociated, we theorize that adaptation and serial dependence are two sides of the same coin.

There are overlapping computational goals of adaptation and serial dependence: to achieve constancy and stability in perceptual interpretations, respectively. Stability refers to features or objects being represented as having the same identity over time. Constancy is the recovery or perceptual inference of the true object properties (such as colour, size, shape, lightness or identity) despite varying input. Constancy can be achieved by adapting (and discounting) prevailing conditions<sup>719,244,245</sup>. Adaptation, in turn, results in negative aftereffects (like the motion aftereffect and the tilt aftereffect) in controlled conditions. Often the two goals of constancy and stability are very similar, but they are not always the same. For example, one can fail to achieve constancy (such as misperceiving the colour or size of an object) and yet still have stability (that is, a persistent misperception of the wrong colour or size of an object). Most of the time, however, these two goals are aligned: when an observer has accurate constancy calculations, they have achieved a kind of stability. Complementarily, when an observer has stability via serial dependence, they can forgo the calculations required for constancy by recycling previous representations.

The role of attention in adaptation and serial dependence might be different. It is often suggested that adaptation operates

predominantly passively on bottom-up information, with relatively little modulation by attention or awareness<sup>49,246–248</sup>. Conversely, a growing body of evidence suggests that visual serial dependence involves top-down guidance<sup>249</sup>: serial dependence requires attention<sup>15</sup> (see section 'Attentional tuning') and awareness of an object identity<sup>115,144</sup>, and is modulated by top-down factors like feature attention<sup>49</sup>, confidence<sup>71,168,169</sup> and memory<sup>32,51,58,75,191</sup>. That top-down attention might be necessary for (at least some forms) of serial dependence does not mean that serial dependence arises in a single module or that a single source explains it. On the contrary, attention and feedback can operate separately at many levels of the visual hierarchy<sup>250–252</sup>. Moreover, the putative dissociation in the spatial, temporal and feature tuning of serial dependence in different domains is less consistent with a single source or module.

The fact that serial dependence and adaptation generate opposing perceptual outcomes does not mean that their goals conflict. Indeed, the goals of adaptation and serial dependence could be largely overlapping and complementary: to achieve constancy and stability, respectively. The fact that the two phenomena are opposed could help to produce a sort of equilibrium in which neither effect dominates. Domination of one over the other might otherwise occur if adaptation were left unchecked, resulting in excessive sensitivity to changes, or the 'coding catastrophe'<sup>22,253,254</sup>, in which downstream neural populations mistakenly attribute changes in activity due to adaptation as changes in the stimulus itself<sup>7</sup>. In either of these cases, adaptation for the sake of constancy could, in principle, result in rampant negative aftereffects in which object identities constantly seem to fluctuate<sup>255,256</sup>. Serial dependence is a possible antidote. It promotes a stable representation of previously encountered objects and features and thus counteracts over-zealous negative aftereffects that could otherwise arise. Continuity fields, in this view, are the cure for the coding catastrophe.

dependence suggests that continuity fields might be implemented at different levels of visual processing and reflect canonical operations that are ubiquitous in neural processing.

Strikingly, although continuity fields are relatively easy to measure behaviourally and must be a product of neural processing, there has not yet been a clear visualization of continuity fields in neurophysiological data. It might be that the neural signals that carry information related to continuity fields are too subtle, are silent or are multiplexed with other stronger signals. Perhaps continuity fields manifest in second-order effects. There are a number of other possibilities. An intriguing idea arises from the observation that positive serial dependencies can manifest in virtually all kinds of stimuli, modalities and tasks. Rather than residing in a single dedicated module, continuity fields might occur at many stages of processing<sup>192</sup>. All (or many of) the proposed levels of processing and neural correlates might lead to serial dependencies depending on the stimuli, task, manifestations, processing level and so on. Accordingly, the existence of continuity fields at one level would not invalidate continuity fields at other levels (in contrast to ref. 143).

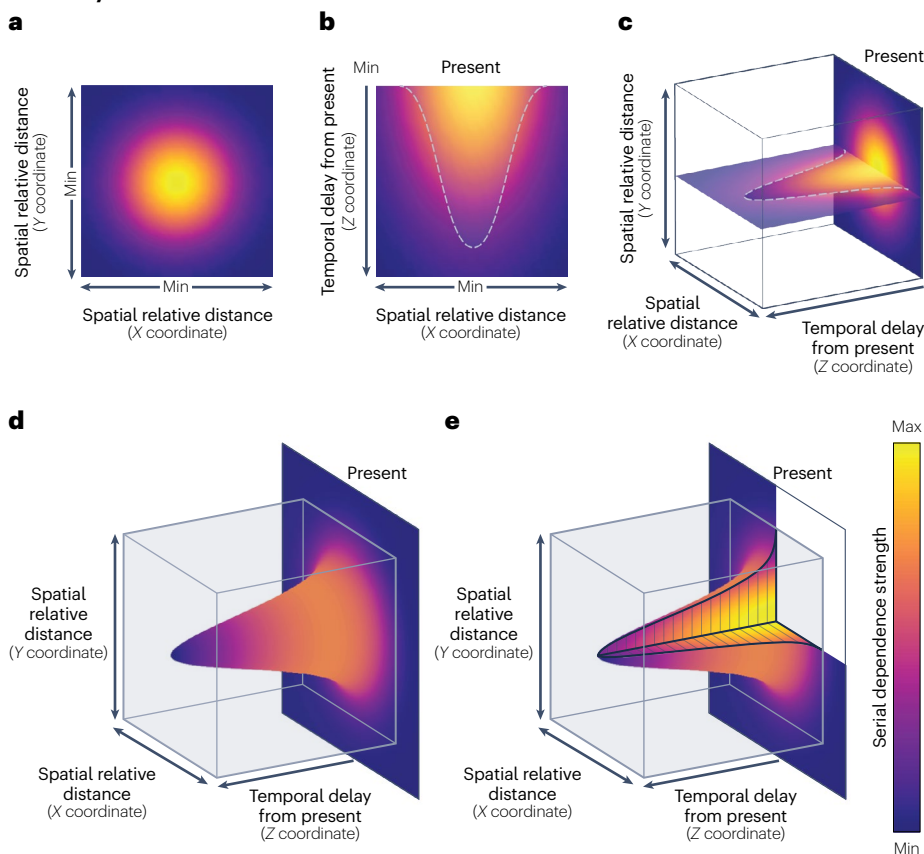
## Models

There is no shortage of modelling work on serial dependence and therefore on the underlying algorithm of continuity fields<sup>193,194</sup>. Almost every paper on the topic has tried to quantify and predict the strength of serial dependence with some sort of algorithm. Serial dependence is often modelled with Kalman filters, a standard approach in signal processing, which incorporate information from the past<sup>18,76,83,99</sup>. Along the same

lines, Bayesian models<sup>195</sup> were shown to be very powerful in predicting serial dependence when considering past stimuli as priors for perception in the present<sup>101,158,177,196–199</sup>. This latter class of model fits well with previous findings that serial dependence is modulated by noise: weaker sensory stimuli in the present moment display stronger serial dependence<sup>48,50,57,98,111,196,200–202</sup>. Other models were developed specifically to deal with delay-dependent serial dependence effects<sup>203</sup> or were based on neurophysiological correlates<sup>204</sup>, theorizing that serial dependence arises because of memory traces from prior stimuli<sup>136,191,205,206</sup>, or that it originates from lingering perceptual decision templates at a ‘read-out’ level<sup>50,143</sup> (but see refs. 55,94,98). Serial dependencies could also arise from heuristic-like processing<sup>207–209</sup>. Finally, several models have tried to predict the interplay between positive serial dependence and negative aftereffects<sup>50,101,210–214</sup>.

Computational models are an invaluable tool with which to quantify and predict serial dependence formally under different conditions. However, the behavioural and neurophysiological evidence on the topic is still too scattered to develop sufficiently precise tests of competing models. More importantly, all kinds of proposed models agree in principle with the continuity field proposal. Models focus on the algorithmic level of explanation, whereas we propose that continuity fields reflect the unique computational goals of each stage of neural processing. Regardless of the algorithms used at the stage or stages of visual processing (low, mid and/or high-level) and of whether the associated neural mechanisms are common or distinct, continuity fields are a key functional mechanism that acts through serial dependence

## Continuity field



**Fig. 5 | Continuity field operators.** **a**, Positive serial dependencies occur in a limited relative distance: they are strongest when current and previous stimulus are presented at the same location (min), and gradually decrease with increasing the spatial relative distance ( $X$ – $Y$  coordinates). **b**, Serial dependencies decay over time. They decrease with increasing the temporal delay from the present ( $Z$  coordinate). An attractor field can be extrapolated from this pattern (dashed line). **c**, Temporal and spatial tuning of serial dependencies can be combined into a 3D representation that covers their spatial and temporal characteristics. **d**, Serial dependencies decrease with increasing temporal delay from the present. The grey cube indicates the continuity field when serial dependence biases actions, perception, decision and memory towards the past. The degree of tuning might depend on several factors, including the relevant level of analysis, task or the brain’s attempt to match the autocorrelations of the particular representation (of whatever feature, object, person or scene is attended or coded) with the autocorrelation of the corresponding thing in the world. **e**, Within the continuity field, serial dependencies are highest when spatial relative distance and temporal delay from the present are zero (carved-out section).

## Box 3

### Continuity fields and predictive coding

On the one hand, the idea of serial dependencies as stabilization mechanisms can be interpreted with respect to the predictive coding theoretical framework<sup>257,258</sup>. According to predictive coding, the brain generates predictions about incoming sensory stimuli and compares these predictions with the actual sensory input, with the goal of minimizing the prediction error. Perception reflects these mismatches between predictions and sensory signals<sup>259</sup>. The predictions — priors — can be generated at high levels of visual processing and then back-propagated by feedback<sup>257</sup>. Because the visual world is autocorrelated, the visual system can use past experiences of visual information as a prior to make predictions about the future<sup>158</sup>. Therefore, serial dependencies might be consistent with predictive coding.

On the other hand, serial dependence reduces the apparent difference between sequential stimuli: it makes similar stimuli appear even more similar than they actually are. This outcome seems to contradict the function of prediction errors and might even seem antithetical to the goals of predictive coding. Predictive coding provides a way to efficiently process information by prioritizing the processing of unexpected or novel stimuli, but serial dependence diminishes these differences by making sequential stimuli seem more similar than they are. However, when a stimulus changes and generates a prediction error, it is not necessarily important to notice this change. Prediction errors are useful only if they do not generate too many false alarms. Physically identical sequential objects could nevertheless generate prediction errors simply

because of internal or external noise or other sources of uncertainty, but these are not prediction errors the perceptual system should be sensitive to.

Too much predictive coding is too much of a good thing. It could make the system constantly hypersensitive to tiny deviations in visual input over time by generating prediction errors that are uninformative, irrelevant, or too specific for the purpose of interacting in a stable environment. Runaway prediction errors could pervasively distort perception, decisions and actions. Continuity fields (and the serial dependence they generate) could serve as the counter-balance for predictive coding, dampening the effect of noise-generated prediction errors. The tuning properties of serial dependence seem well suited to this role: serial dependencies only occur for a limited time, at similar locations, with similar objects, and if the objects are attended to. For autocorrelated visual input, serial dependence improves efficiency and accuracy, speeds up processing, facilitates stable interpretations, and dampens errant prediction errors that would arise from noise. Viewed in this light, serial dependence is neither a necessary consequence of nor contradictory to predictive coding. Serial dependence complements and is compatible with predictive coding.

Continuity fields and the serial dependence generated by them might serve a critical check to maintain an equilibrium between the need for sensitivity to novelty and the desire to represent the world as stable. Future theoretical and empirical research should directly explore how continuity fields dovetail with the computational goals of predictive coding.

to enhance the perceptual stability, accuracy and efficiency of visual representations.

### Conclusions

Positive serial dependencies are ubiquitous and essential in human visual experience; they continuously shape actions, perceptions, decisions and memories. Despite decades of research, their functional purpose has remained unknown. In this Perspective, we propose that these serial dependencies are expression of a purposeful stabilization mechanism, continuity fields: spatially and temporally tuned mechanisms that bias and therefore smooth perception, decision, action, and memory over time (Fig. 5). By exploiting the regularities of the visual environment, continuity fields enhance perceptual stability, accuracy and efficiency in everyday visual experience (Fig. 4).

Future research will reveal the underlying mechanisms and neural correlates of serial dependencies and thereby provide a deeper understanding of the functioning of continuity fields. There might be good reasons that a clear picture has not emerged thus far. For example, continuity fields might occur at multiple stages of visual processing and each stage might have peculiar properties and mechanisms, therefore making difficult to pinpoint the exact source and mechanism. In addition, continuity fields might vary depending on the kind of manifestation. Thus, there might not be a single continuity field, but many, at different levels, each with its own unique functioning. Continuity

fields might also underlie several types of visual illusions reported in the literature<sup>215–220</sup>.

Beyond research on serial dependencies per se, future research will test the link between serial dependence manifestations and their functional goal of enhancing perception. For example, an interesting prediction of continuity fields as a stabilization mechanism is that serial dependence in a particular feature or object should mimic autocorrelations in the feature statistics in the external world. If this is true, the temporal tuning of serial dependence in orientation should correlate with temporal fluctuations in visual information about orientation statistics in natural scenes<sup>196</sup>. Initial research on autocorrelations in emotion perception seems to be in agreement with this idea<sup>100</sup>. A direct link between serial dependencies and perception enhancement could be considered foundational evidence for our continuity fields proposal.

Intriguingly, continuity fields might exist and act even beyond the visual modality, enhancing the stability of other senses such as audition and olfaction. In this sense, the human brain might generally adopt this efficient strategy to bias the senses towards the past to minimize a noisy input. Continuity fields might even act across senses and domains of cognition to serve the same purpose of promoting the stability, accuracy and efficiency of our experience.

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