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Serial Dependence in Perception

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Abstract

Much evidence has shown that perception is biased towards previously pre-
sented similar stimuli, an effect recently termed serial dependence. Serial
dependence affects nearly every aspect of perception, often causing gross
perceptual distortions, especially for weak and ambiguous stimuli. Despite
unwanted side-effects, empirical evidence and Bayesian modeling show that
serial dependence acts to improve efficiency and is generally beneficial to
the system. Consistent with models of predictive coding, the Bayesian pri-
ors of serial dependence are generated at high levels of cortical analysis,
incorporating much perceptual experience, but feed back to lower sen-
sory areas. These feedback loops may drive oscillations in the alpha range,
linked strongly with serial dependence. The discovery of top-down predic-
tive perceptual processes is not new, but the new, more quantitative approach
characterizing serial dependence promises to lead to a deeper understanding
of predictive perceptual processes and their underlying neural mechanisms.

Contents

1. INTRODUCTION

Most researchers today agree that perception depends not only on the immediate sensory input but also on contextual information over space and time. **Figure 1*a*** shows a famous demonstration many of us saw as undergraduates: When the image is viewed for the first time, most see only a scrambled set of black and white shapes, with no obvious form. After some time, or with prompting, the clear shape of a dalmatian dog emerges. And once seen, it cannot be unseen! It will emerge instantly every time one views the pattern, even after years. Clearly, perception does not depend only on sensory input, which has not changed from the first viewing. Once the brain has a coherent model of what to see, sensory input can be immediately mapped onto that model. Many regard this as evidence that perception is to some extent generative: The brain forms models of the world and tests these models against sensory input, rather than starting from the input itself.

a   **b**
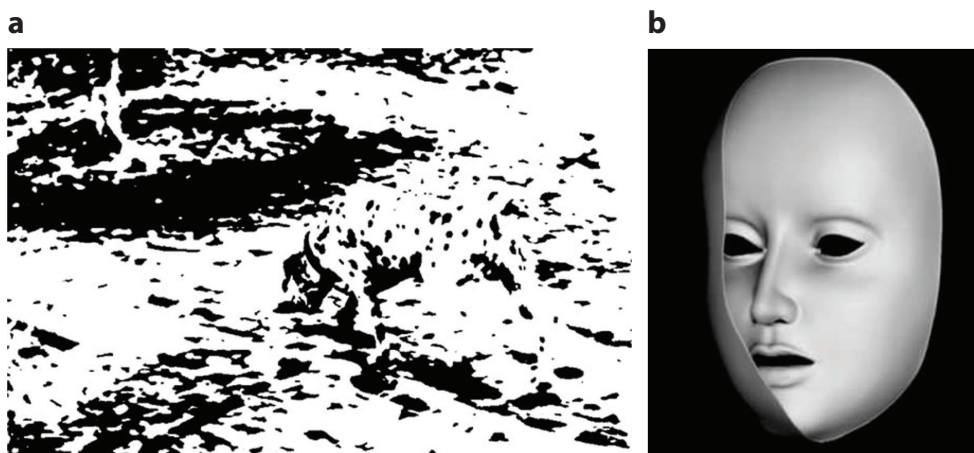
Figure 1

Visual experience shapes perception. (*a*) Classic demonstration of one-shot learning. Initially the picture appears as a bunch of random black and white shapes; but once the dog has been identified, it will pop out immediately on subsequent viewing. (*b*) The hollow mask illusion (Gregory 1970). Although the image is the inside of a mask, it is almost impossible not to see it as a concave face. This demonstrates that the brain learns typical stimulation patterns and formulates decoding strategies to decipher ambiguous sensory information.

The idea that perception may be inferential or generative has been around for a long time, periodically reappearing in the literature. von Helmholtz [1910 (1866)] referred to unconscious inferences to describe the formation of visual impressions that take into consideration converging evidence from the senses and experience. Gregory (1980) famously championed a similar idea, suggesting that perceptual systems construct hypotheses about the world to be verified against sensory data. These ideas are at complete odds with the standard textbook explanation of unidirectional information flow from the retina through the thalamus and the various hierarchically arranged cortical areas; rather, perception should be conceived as a proactive process, where the brain makes best guesses about the world to test against sensory data, updating the guesses as evidence accumulates.

Gregory (1970) drew largely from visual illusions to support his theory, such as the hollow mask illusion illustrated in **Figure 1*b***. Although we are viewing the inside of the mask, we do not see a hollow, concave mask, but a normal convex face (even more persuasive when viewed dynamically).[1] This compelling illusion was taken as evidence that the system makes active hypotheses about the world based on long-term experience: Faces (extremely important for human perception) are all convex, none concave. The sensory data from the concave face differ only in fine detail from a real convex face, so they are interpreted within that framework. Indeed, when watching the hollow mask rotate (see footnote 1), it seems to reverse direction when hollow, as the system attempts to reconcile the local feature movement of a hollow face with the interpretation of a convex face.

Over the past few decades, generative perception has been formulized within two closely related frameworks: Bayesian inference and predictive coding. Within the Bayesian framework, the perceptual hypothesis is termed the prior, which combines optimally with sensory data (the likelihood) to yield the final percept, the posterior (Kersten et al. 2004, Wolpert et al. 1995). Predictive coding is similar, but it further assumes that the actual input is not represented directly in early sensory areas, but only the prediction error needs to be encoded (Rao & Ballard 1999, Srinivasan et al. 1982). The frameworks are somewhat complementary in their focus and implementation but in practice similar in relying heavily on top-down predictions to help disambiguate noisy input and to increase efficiency. All models allow for multistage hierarchies, where feedback loops are stacked so that prediction operates at various levels, dealing with different information content.

Demonstrations can be compelling but hard to quantify, and they generally reveal little about the underlying cognitive and neural mechanisms. One of the first quantitative studies of the effect of past perception on current perception was termed priming, the unconscious response facilitation after previous exposure to a relevant stimulus. It was originally introduced by Lashley (1951) and proposed as a mechanism to aid smooth response sequencing. Priming is an important phenomenon for a range of cognitive disciplines, from linguistics to social psychology, and has been studied extensively in perceptual research (Kristjánsson & Ásgeirsson 2019, Maljkovic & Nakayama 1994). Priming typically facilitates perception, measured as increase in accuracy and decrease in reaction times. More recently it has been shown that previous stimuli not only speed up and facilitate current perception but also can bias responses away from veridicality, a phenomenon now termed serial dependence.

2. SERIAL DEPENDENCE

Nearly 10 years ago, Fischer & Whitney (2014) and Cicchini et al. (2014) independently introduced a new technique to study quantitatively the effects of temporal contextual information on perception, termed serial dependence. When judging the orientation or numerosity of sequences

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[1]The rotating mask illusion demo can be found at **https://michaelbach.de/ot/fcs-hollowFace/**.

of stimuli, the judgements were strongly biased toward the orientation (**Figure 2a**) or numerosity (**Figure 2b**) of the previous stimulus. An interesting consequence for numerosity is that the mental number line (the mapping of number to space) is not linear but rather compressed in a logarithmic-like manner, which was previously thought to reflect a native logarithmic representation of numbers (Dehaene 1997). However, the nonlinearity is more parsimoniously explained by the spontaneous bias toward past stimuli that characterizes serial dependence. As shown in more detail in the following section (see **Figure 3b**), the logarithmic-like form of the curve is well predicted from current models of serial dependence.

Shortly after these two reports, Liberman et al. (2014) extended the concept by showing that serial dependence is not limited to basic visual properties such as orientation and numerosity but also applies to more complex stimuli such as face identities, which are also systematically biased toward previously seen face stimuli.

These initial studies had a strong impact on the vision community and kindled a very fruitful line of research using a wide range of stimuli in various modalities. Overall, these studies showed that while serial dependence leads to the misperception of the physical characteristics of stimuli, counterintuitively this misperception is beneficial for perception as a whole, as it increases efficiency and can help to preserve temporal continuity (see Section 3).

Serial dependence affects almost every aspect of perception, including the perception of facial beauty. Taubert et al. (2016b) had participants make binary choices to a series of facial images by swiping right to like a person or left to dislike. Participants were more likely to rate a face as attractive when the preceding face was also attractive (**Figure 2c**), showing that beauty is not absolute but depends on recent experience. Similar results emerged for aesthetic ratings of artwork (Kim et al. 2019): Paintings were rated significantly higher when preceded by an attractive rather than unattractive painting.

Alexi et al. (2018) assessed serial dependence in the perception of body size with a number line–like technique, whereby young women judged the perceived size of a briefly presented body stimulus by positioning a marker along a visual analogue scale. Judgments of body size were biased toward the previously viewed body, so observers perceived bodies as larger than their actual physical size if preceded by a large body, and vice versa. This raises the possibility that distorted body-image perception (which can be linked to eating disorders) could be affected to a certain extent by serial dependence. The fact that these people do not comprehend the extent of their disorder and the large deviation from a healthy weight range could be in part due to their watching themselves continuously in the mirror, blending yesterday's information with the present and not realizing how far the weight loss has built up. This would be consistent with the buildup of serial dependence effects over time (Barbosa & Compte 2020). The timeline of a laboratory experiment is necessarily shorter than that allowing the potential buildup of serial dependence over the course of months or years in real life, so it may well grossly underestimate the effect.

Active blending of past and present information can reduce the salience of gradual temporal changes, giving rise to an interesting illusion (Manassi & Whitney 2022).[2] On viewing a video of a person gradually rejuvenating, the young child shown in the final frame is perceived to be older than the same young child presented in isolation, suggesting that the sequence has been incorporated into the final image and has perceptually aged it. The opposite result was obtained if the runup video was of a gradually ageing person (Manassi & Whitney 2022). This demonstration shows that serial dependence merges and accumulates age information throughout the 30-second

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[2]The age illusion video can be found at **https://zenodo.org/record/5713857/files/Video%20Material.zip? download=1**.
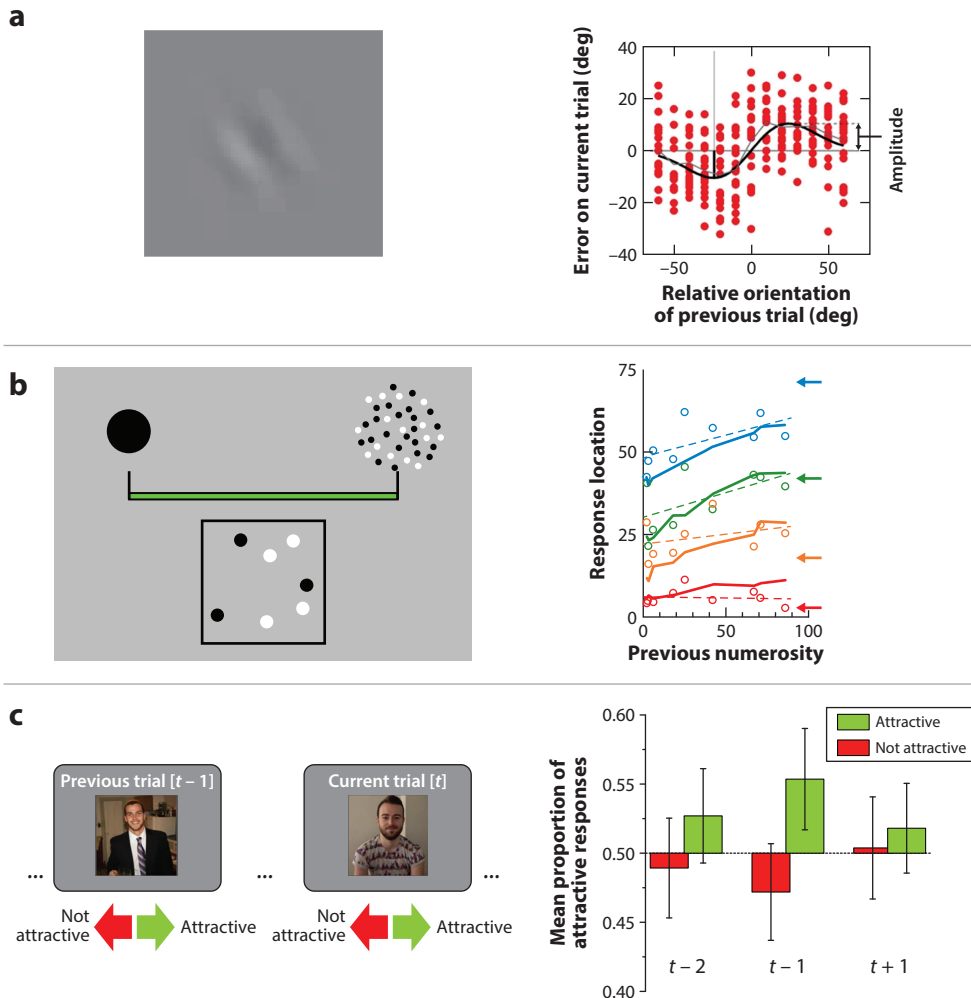
Figure 2

Serial dependence across several visual domains. (*a*) Fischer & Whitney (2014) measured errors in orientation reproduction of a sequence of gratings to demonstrate how the perception of orientation is biased toward the orientation of the previous stimulus. Orientation error is plotted as a function of the difference in orientation between the previous and the current trial. When the previous trial was more clockwise than the current, observers made more clockwise errors, and vice versa. The effect was strongest for smaller orientation differences and waned at higher differences, following a derivative-of-Gaussian pattern. Panel adapted with permission from Fischer & Whiney (2014); copyright 2014 Springer Nature. (*b*) Cicchini et al. (2014) had observers map on a number line the numerosity of a cloud of dots while performing an attention-demanding task. When responses for each current numerosity were analyzed as a function of the previous numerosity, there was a positive linear trend in bias, indicating an assimilative contribution of the previous numerosity. The arrows indicate stimulus numerosity. The effects were particularly strong for higher numerosities, leading to a distortion in the number line (see **Figure 3*b*** and Section 3). Panel adapted from Cicchini et al. (2014). (*c*) Sequential judgments of attractiveness in a Tinder-like paradigm (Taubert et al. 2016b). If the previous trial was an attractive face, the currently judged face was rated as more attractive. The effect extended for stimuli two trials back but not for future trials, ruling out spurious correlations. Panel adapted from Taubert et al. (2016b).
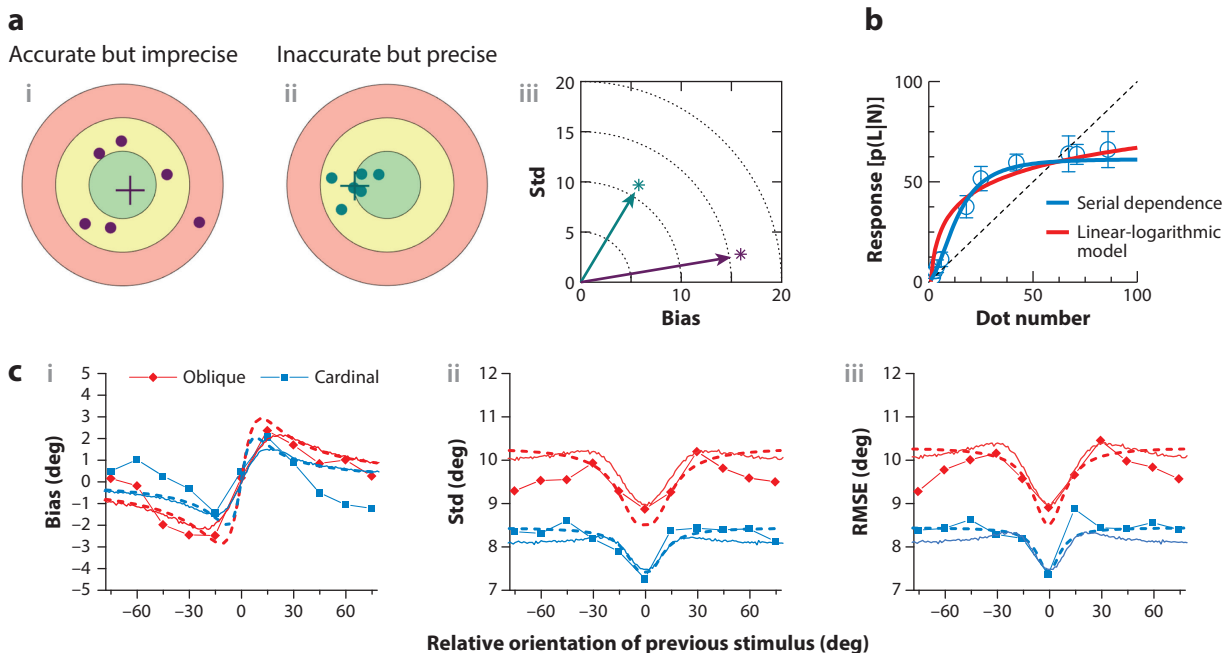
Figure 3

Serial dependencies as an optimizing strategy. (*a*) Accuracy and precision. Subpanel *i* shows a hypothetical observer with high average accuracy, subpanel *ii* one with high precision. Subpanel *iii* plots accuracy (bias) against precision (standard deviation) for the two observers; the total root mean square error (RMSE) is given by the length of the vectors. (*b*) Number to space mapping, plotting mapped location against physical numerosity [p(L|N)]. The red curve shows that a linear-logarithmic function fits well the data. The blue curve shows the predictions of a serial dependence model, using Equations 1 and 2. The fit is as good as the logarithmic one, with fewer free parameters. (*c*) Errors in accuracy (*i*), precision (*ii*), and total error (*iii*) in a serial dependence task. The blue points show results for stimuli near the cardinal axes, the red ones show the results for oblique stimuli. The continuous line is the fit of the optimal model using Equations 1 and 2. Although serial dependence leads to biases, the overall effect is a reduction in total error. Figure adapted from Cicchini et al. (2018).

movie, creating the illusion that the age change is perceptually slower. Similar to the distorted body image, this illusion could potentially explain why we can fail to recognize the effect of time passage on our own appearance or that of people with whom we regularly interact, until we see an older photo showing the person at a younger age, where the discrepancies between now and then are much larger.

Serial dependence is not exclusive to the visual system. When asked to reproduce the rate of auditory stimuli in a sequence, the reproduced rate is biased toward the preceding rate (Motala et al. 2020). Serial dependence effects have also been observed in olfaction for intensity and familiarity ratings (Van der Burg et al. 2022).

While serial dependence effects occur in several sensory modalities, current evidence suggests that they may not transfer across sensory modalities. Fornaciai & Park (2019b) had participants judge numerosity, reporting whether a reference or probe stimulus contained more dots. To induce serial dependence, an inducer (either visual or auditory) was presented at the beginning of each trial, prior to the reference and probe stimuli. Visual inducers affected the perceived numerosity of the dot array, but auditory induces did not. This result contrasts with adaptation experiments, which show clear cross-sensory effects of adaptation between visual and auditory stimuli (Arrighi et al. 2014).

3. SERIAL EFFECTS AS AN OPTIMIZING STRATEGY

The most important question to ask about serial dependence is, What is its functional role in perception? Any form of generative perception, including serial dependence, causes current perception to depend to some extent on past perceptual experiences. Is this a bug or a feature? As serial dependence causes a clear bias away from veridicality, its benefits may not be immediately obvious. This section argues, however, that serial dependence will in general be beneficial to the system. The rationale is that as the world tends to remain relatively constant, the system can take advantage of inherent temporal redundancies by incorporating previous signals with current ones, integrating them over time to increase signal-to-noise ratios.

More formally, response error comprises two orthogonal components, average bias (accuracy) and variance (precision), illustrated in **Figure 3a**. As the components are orthogonal, the total root mean square error (RMSE) is given by the Pythagorean sum of the two error types, illustrated as the length of the vectors in **Figure 3a**. RMSE is the term that most ideal-observer models of perceptual efficiency attempt to minimize (Jazayeri & Shadlen 2010, Kersten et al. 2004). Cicchini et al. (2014, 2018) adopted this standard approach to derive an ideal-observer model for optimal perception when the previous stimulus is combined with the current one. They obtain

$$y_{curr} = (1 - w_{prev})x_{curr} + w_{prev}x_{prev}, \qquad\qquad 1.$$

$$w_{prev} = \frac{\sigma_{curr}^2}{\sigma_{prev}^2 + \sigma_{curr}^2 + d^2}, \qquad\qquad 2.$$

where y_{curr} is the response to the current stimulus of magnitude x_{curr}, x_{prev} is the magnitude of the previous stimulus, and w_{prev} is the weight given to the previous stimulus. Put simply, Equation 1 states that the current response should ideally be a weighted average of the current and previous stimuli. The logic is that if the current and previous stimuli are noisy samples of the same object, then an appropriately weighted integration will increase signal-to-noise ratios. Equation 2 defines the ideal weighting of the previous stimulus for maximal efficiency, based on three factors:

■ σ_{curr}^2: the variance (inverse reliability) of the current stimulus. The higher the variance, the more highly the previous stimulus should be weighted.
■ σ_{prev}^2: the variance of the previous presentation. The lower the variance, the more weight it should be given.
■ d^2: the squared difference between the current and previous stimuli. Weighting should be maximal if the two are identical (implying that they are probably both representations of the same object) and steadily decrease as they become less similar.

These three factors make strong predictions that can be and have been tested experimentally. One of the first two demonstrations of serial dependence was designed to determine the cause of the logarithmic-like number line (see Section 1): Mapping numbers to space results in a compressed, logarithmic-like curve, illustrated by the red curve of **Figure 3b**. The blue curve passing through the data is a direct, parameter-free prediction from Equations 1 and 2, based on the measured magnitude of serial dependence and response variance. Intuitively, the shape of the predicted curve is easy to understand. For high numerosities, it is probable that the previous stimulus had a lower numerosity, so serial dependence effects reduce apparent numerosity, while for low numerosities the reverse is true. This on its own should lead to a straight line of lower slope than the identity line. There is another factor, however: Low numbers are reproduced with low variance, while high numbers have proportionally higher errors, approximating Weber's law (Jevons 1871). Therefore, at the lower end of the range, σ_{curr}^2 is low, reducing the distorting effect of serial

dependence compared with the higher end, where it is high. This principle quantitatively predicts the magnitude of the effects, as shown in **Figure 3b**, which has been replicated in other studies (Pomè et al. 2021).

The principle demonstrated for numerosity applies equally well to other features, such as orientation. Grating stimuli around the oblique axis, or of low spatial frequency, are reproduced with more variance (Appelle 1972, Mikellidou et al. 2015) and, as predicted, show stronger serial effects (Cicchini et al. 2018). As before, the results of both the reported bias and response scatter (and consequently total error) are well predicted quantitatively from Equation 2 (**Figure 3c**).

The scaling of the effects with stimulus reliability could explain several other nonobvious facts of serial dependence. For example, it has been reported that serial effects are stronger if the previous stimulus was perceived with high confidence (Samaha et al. 2019, Suárez-Pinilla et al. 2018). The strength of the neural representation of the stimulus may fluctuate from one trial to another, so some stimuli will be more reliable and seen with more confidence, and they will generate more serial dependence. Similarly, serial effects are stronger if responses are delayed (Bliss et al. 2017, Fritsche et al. 2017). Although this has been attributed to the delay allowing more time for working memory to activate (as discussed in the next section), it is also possible that delayed responses are more variable, predicting stronger serial dependence. Given the relevance of stimulus reliability to the predicted and measured magnitude of serial dependence, it is important to take this possibility into account when drawing conclusions about the effects of manipulations such as response delay.

A fundamental term in the denominator of Equation 2 is d^2, the squared difference of magnitude between the current and previous stimulus dimension. This term predicts that the strongest effects will occur when the two stimuli are most similar and will fall off as they become more dissimilar. The obvious intuitive advantage of this strategy is that only stimuli that are similar enough to be both noisy samples of the same object will be combined. This means that perception will gain from integration with the similar past stimulus, increasing signal-to-noise ratios, but will not integrate inappropriately when there has been a change in the object being viewed (Burr & Cicchini 2014).

We have already seen a clear example of this behavior in orientation judgments: Serial dependence does not increase monotonically with the difference in orientation of previous and current stimuli, but it initially increases and then decreases (**Figure 2a**). This signature behavior, first observed by Fischer & Whitney (2014), is well fit by a derivative-of-Gaussian function (the product of a linear and a Gaussian function); but it is also fit well by Equation 2, as the d^2 term brings the weight back to near zero for large angular differences. Again, this is a general property, observed not only for orientation but also for numerosity (Cicchini et al. 2014), attractiveness of art (Kim et al. 2019), perceived body size (Alexi et al. 2018), and even odor perception (Van der Burg et al. 2022).

A complementary and fascinating discussion of how serial dependence can adaptively enhance perception and decision making for incoming stimuli is presented by Kiyonaga et al. (2017), who compare serial dependence with working memory. Serial dependence is generally adaptive, leading to stability, but can on occasion become maladaptive when it sustains representations that are irrelevant to the current situation, akin to the phenomenon of proactive interference in working memory.

4. AT WHAT LEVEL DO SERIAL DEPENDENCIES OPERATE?

Serial effects were reported in the literature long before the term serial dependence was coined, but they tended to be considered a nuisance rather than an efficient perceptual strategy (Busse et al. 2011, Fründ et al. 2014). Are they simply a response bias, or do they act on perceptual

and sensory processes? That they lead to increased efficiency, as shown in the previous section, argues against artifacts such as response biases, and this is supported by much other evidence. In one of Fischer & Whitney's (2014) initial experiments, observers withheld their response on a quarter of the trials: Serial dependence was equally strong after the no-response trials, showing that response was not driving the effects. Along similar lines, Cicchini et al. (2017) had observers respond with a vertically flipped mirror response on every second trial. Serial dependence followed the pattern of the actual physical stimuli, not the mirror response, clearly implicating perceptual processes. Further evidence against simple response biases is that serial effects are selective for spatial position (Fischer & Whitney 2014), and this is inconsistent with their being generated by the response, which is independent of stimulus position.

Having excluded trivial response biases, we can ask at what level of perceptual processing they do operate. This question is often posed in terms of whether serial dependencies act on early sensory coding mechanisms or on later perceptual decision-making mechanisms. Early in the debate, Fritsche et al. (2017) claimed that serial dependence acts on perceptual decision mechanisms. They showed that when more time was allowed for response, serial effects increased, suggesting that the longer the current stimulus lingers in working memory, the more it is exposed to the effects of serial dependence. This has been replicated several times, with various paradigms (Bliss et al. 2017, Manassi et al. 2018). However, as argued in the previous section, while this result is consistent with stronger memory encoding for longer pauses, there are other plausible explanations for the increase in serial dependence, such as the lower reliability of the stimulus after a long delay. Additionally, for low-contrast stimuli, the positive attraction occurs even for rapid presentations (Manassi et al. 2018), providing a further possible explanation for the role of delay: Adaptation to high-contrast stimuli with short delays (see Section 6) may counteract the positive attraction of serial dependence (Manassi et al. 2018).

A second line of evidence comes from experiments using a clever technique in which no perceptual decisions about stimulus magnitude are required, but only a judgement of whether two stimuli appear to be identical or not. This results in a Gaussian distribution for perceived equality, whose peak gives the best estimate of the point of perceived equality: Any bias introduced by serial dependence should shift the peak. Fritsche et al. (2017) claimed that previous stimuli caused no such shift, suggesting that serial dependence requires perceptual decisions and therefore does not act on early encoding stages.

This claim catalyzed much research, leading to interesting conclusions. Cicchini et al. (2017) replicated Fritsche et al.'s (2017) study but showed that under more appropriate conditions, with successive stimuli more similar in orientation, serial dependence was as strong with their technique as it was when decisions of orientation magnitude were required. As mentioned previously, serial dependence operates over a limited range, clearly evident in **Figure 2a**. The inducing stimuli in Fritsche et al.'s (2017) study differed by 20° from the test stimuli, and they were therefore too different to expect strong attractive effects. Cicchini et al. (2017) used smaller differences in orientation to reveal strong serial effects, questioning the conclusion that serial dependence acts only on perceptual decisions.

Collins (2020) has shown that even tasks not requiring explicit representation of orientation, such as visual search for the odd-oriented bar (**Figure 4a**), can result in local serial effects that distort the bar's apparent orientation to impact on search performance. When the previous target was orientated away from current distractors, performance in the current trial improved, and vice versa (see **Figure 4a**).

Murai & Whitney (2021) adapted the elegant noise image classification technique to measure the perceptual templates during the presentation of a sequence of stimuli (**Figure 4b**). These templates are thought to reflect the perceptive field of the mechanisms responsible for the task
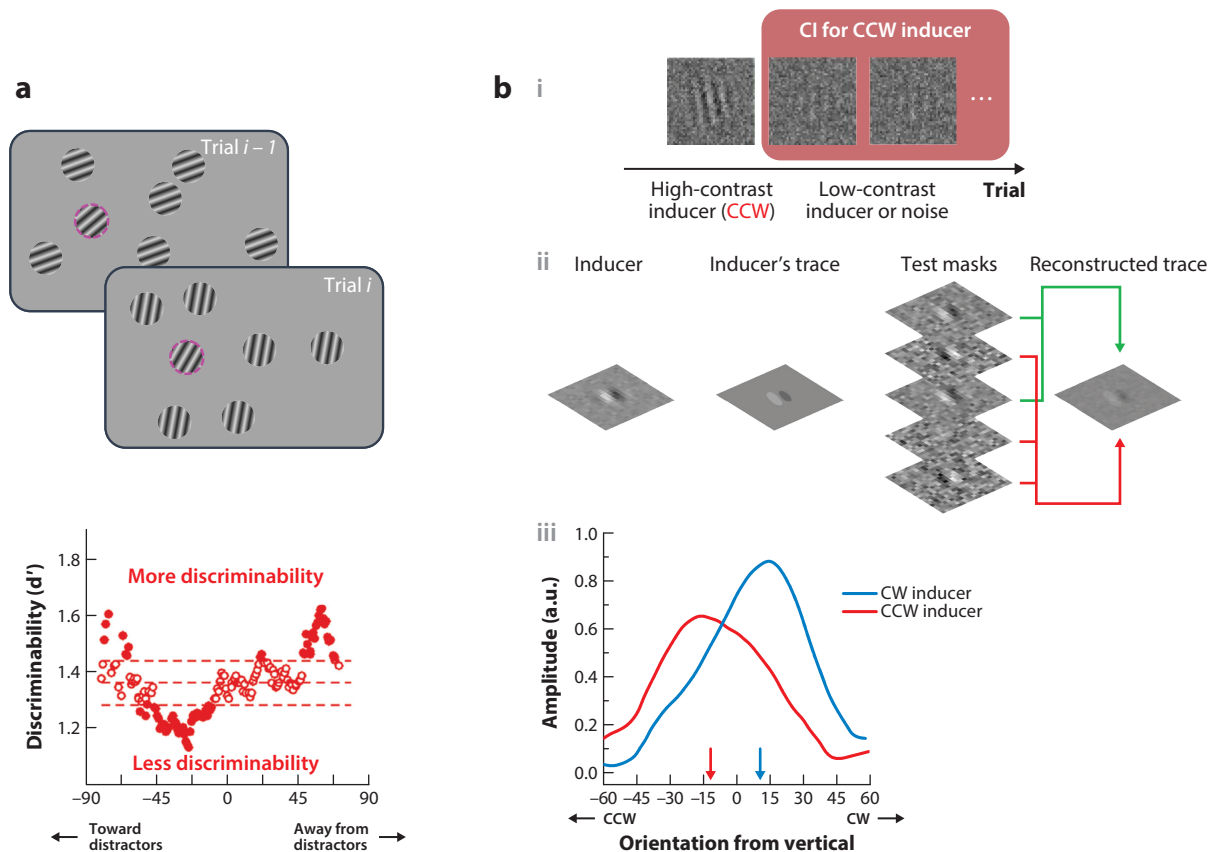
a

Trial *i − 1*

Trial *i*

Discriminability (d′)

More discriminability

Less discriminability

Toward distractors

Away from distractors

b i

CI for CCW inducer

High-contrast inducer (CCW)

Low-contrast inducer or noise

Trial

ii Inducer   Inducer's trace   Test masks   Reconstructed trace

iii

Amplitude (a.u.)

CW inducer
CCW inducer

CCW

CW

Orientation from vertical

Serial dependence of orientation without explicit orientation encoding. (*a*) Collins (2020) tested serial effects in a search paradigm in which all but one array of grating-patch stimuli had the same orientation. The target whose orientation had to be identified was oriented ±5° from the distractors. Discriminability (d′) was affected by the orientation of the previous stimulus, improving when oriented away from current distractors (illustrated here) and becoming worse when oriented toward it, as shown by the lower graph. (*b*) Noise image classification paradigm by Murai & Whitney (2021). (*i*) After presentation of a high-contrast Gabor (inducer), observers were shown a low-contrast Gabor embedded in noise (classification image, CI) and reported whether they saw it or not. (*ii*) Noise image classification aims to recover latent information in the visual system. If the inducer leaves a trace in sensory regions, on the following trial some noisy patterns will interact constructively with the trace and assist detection (as for the first and the third trace), while others add destructively to make detection harder (as for the second and the fifth trace). Subtracting trials where the target was not seen (*red*) from when it was (*green*) leads to a reconstruction of the hypothetical trace present in the brain at the time of presentation. (*iii*) Orientation of the biasing traces after an inducer 15° clockwise (CW) (*blue*) or 15° counterclockwise (CCW) (*red*) from vertical. Average orientation of the trace is indicated by arrows.

(Ahumada 1996, Neri et al. 1999). After a high-contrast inducer, the observer had to detect a low-contrast stimulus embedded in noise. Using the standard technique of subtracting misses and correct rejections from hits and false alarms, they constructed the perceptual template for the task. Importantly, the template revealed not only the current stimulus but also a latent trace of the previous stimulus. As the perceptive field for a simple detection task is thought to represent the action of early visual mechanisms, notably the primary visual cortex (V1), this experiment provides very strong evidence for the action of serial dependence at a sensory encoding site. As the task was simply to detect the stimulus rather than report its orientation, the results point to
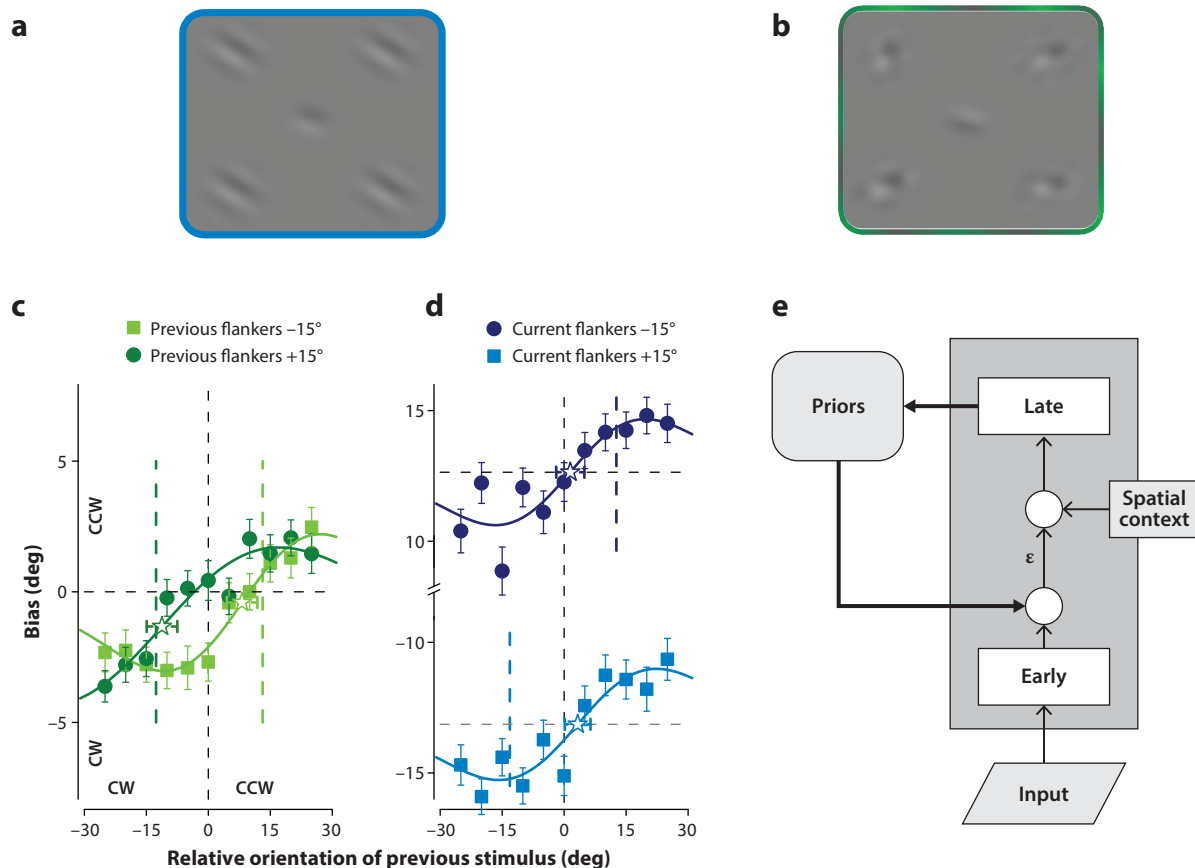
Figure 5

Site of generation and action of serial effects. (*a*) Example of the tilt-surround illusion used by Cicchini et al. (2021). The test stimulus is surrounded by Gabor stimuli tilted ±15° away from the test, inducing an illusory opposing tilt in the target. (*b*) Example of a neutral stimulus, where the surrounding Gabor stimuli are oriented randomly. (*c*) Reproduced orientation of neutral test stimuli preceded by illusory stimuli oriented either +15° (*dark green*) or −15° (*light green*) from the target. The pattern of responses is clearly affected by the illusion, as the center of the derivative of the Gaussian function is shifted toward the apparent orientation of the inducer. This shows that the priors driving the serial dependence incorporate the effects of the tilt illusion, probably generated at a high level. (*d*) Reproduced orientation of illusory test stimuli preceded by neutral stimuli oriented either +15° (*light blue*) or −15° (*dark blue*) from the target. The illusion shifts the pattern of responses vertically, but they remain horizontally aligned at 0, indicating that the trace of previous presentations acts early, before the illusion caused by the surround has taken place. (*e*) The findings are consistent with a network explanation of serial effects acting within a predictive coding network that compares current inputs to prior expectations and carries forward only the error (ε), with priors derived from recent sensory history incorporating all possible information, including spatial context; however, this information feeds back to earlier levels of visual analysis, before the site of action of spatial context.

the automatic emergence of a sensory memory of the previous stimulus, even in the absence of a specific orientation-related task.

Taking a completely different approach, Cicchini et al. (2021) asked two complementary questions: At what level are the serial dependence priors generated? And at what level do they act? Note that these two questions are not necessarily the same, even though they are often confused. The experimental technique exploited another strong contextual visual illusion, the tilt surround illusion (**Figure 5a**), which is thought to occur at early stages of visual processing (Cavanaugh et al. 2002, Clifford 2014, Gilbert & Wiesel 1990), together with the fact that serial dependence

for orientation follows the characteristic tuning curve shown in **Figure 2a**. By randomly intermingling illusory trials where the target was biased by the tilt illusion (**Figure 5a**) with neutral trials where the target was surrounded by non-oriented inducers (**Figure 5b**), they measured whether the signature tuning curve followed the physical or the perceived orientation of the current and previous stimuli.

The answer was clear: When the illusory stimulus preceded a neutral stimulus, the serial dependence tuning curves for the neutral stimuli shifted leftward or rightward to align with the perceived orientation of the inducing stimulus (**Figure 5c**). This shows that the priors of serial dependence include the effect of the surround tilt, so they must be generated at a higher level than the site of action of the illusory surround. On the other hand, when the current stimulus was itself illusory and was preceded by a neutral stimulus, the curves shifted vertically (reflecting the direct effect of the tilted surrounds) but remained horizontally aligned with the physical orientation of the stimulus (**Figure 5d**). This shows that the site of action of the priors comes before the site of action of serial dependence. Thus, while priors are generated at a high stage—incorporating all contextual information—they act at a low stage before the contextual tilt aftereffects. This is expected from a typical feedback loop (such as **Figure 5e**), where the prior represents the current hypothesis about the stimulus, incorporating all available contextual information, which then feeds back to interact with early levels of sensory analysis.

It is important to differentiate between the site of generation of serial dependence priors and their site of action. For example, Ceylan et al. (2021) showed that serial effects generalize across stimuli with completely different low-level features, by intermingling trials of oriented Gabor patches with dot stimuli symmetric with respect to an oriented axis. Serial dependence was equally strong between the two different type of stimuli as within each class, which was taken as evidence that serial dependence acts at high levels of perceptual analysis, on the concept of orientation rather than its low-level representation. However, this is perfectly compatible with **Figure 5e**, where the prior itself is generated at a later stage (from either Gabor or random-dot patterns), but may act at an early stage of analysis, separately for the two types of stimuli. Similarly, Turbett et al. (2021) showed that serial dependence for faces persisted across changes in viewpoint, arguing against an entirely low-level locus for the bias. However, the distinction between the site of generation and the site of action of the priors must again be considered. In addition, most models of predictive coding (Rao & Ballard 1999) involve a hierarchy of predictions and error-checking loops. Serial dependence for faces could well occur at a higher level than for, say, orientation, but the principle that they operate at the level of perceptual rather than decisional mechanisms remains the same.

Further evidence for whether serial effects occur early or late in the visual system comes from studying their reference frames. Serial dependence is spatially specific—it is strongest when the past and present stimuli overlap in space—so we can ask whether this spatial selectivity is retinotopic (solid with the retina) or spatiotopic (solid with external space). Early stages of visual processing are typically retinotopic, with receptive fields linked directly to the retinal location of the stimulus, while both physiological and behavioral evidence suggests that later visual processes work in craniotopic or spatiotopic coordinate systems (i.e., anchored to the head or to external space, respectively; see Melcher & Colby 2008). Therefore, whether the serial effects are retinotopic or spatiotopic may provide evidence of where they are generated and where they act.

Interestingly, the evidence is somewhat mixed. Fischer & Whitney (2014) initially reported a spatial tuning of about 20° for serial effects, with evidence for both retinotopic and spatiotopic selectivity. Collins (2019) followed up with a paradigm involving large saccades every second trial, with sequences of stimuli corresponding in either retinal or spatial coordinates. She found stronger positive serial effects when stimuli matched retinotopically. Mikellidou et al. (2021) used a different

approach to dissociate retinal from spatial coincidence, requiring participants to tilt their heads leftward or rightward between trials, changing the orientation of the stimuli on their retinae but not on the screen. At odds with Collins, they found the strongest serial effects when the stimuli were similar in external coordinates, not on the retina.

Why is the evidence for retinal or spatial selectivity so ambiguous, varying with the experimental paradigm? Perhaps this is to be expected if serial dependence involves multiple sites, with priors generated at high levels but acting at low levels. This may activate both spatiotopic (high-level) and retinotopic (low-level) mechanisms, as Fischer & Whitney (2014) reported. In Mikellidou et al's. (2021) study, the effective orientation of the prior was in world rather than retinal coordinates, consistent with the idea that priors should provide useful information about the state of the physical world and not change each time we tilt our heads. This does not imply, however, that they do not act at early, retinotopic levels, as Collins's (2019) study suggests.

5. ARE ATTENTION AND AWARENESS NECESSARY FOR SERIAL DEPENDENCE?

Having established that serial dependencies act at low levels of processing, but are probably generated at high levels, incorporating other contextual information, it is interesting to ask about the role of attention and awareness. In their initial work, Fischer & Whitney (2014) included a condition in which eight stimuli were presented simultaneously and the observer cued which to report: Only cued (and presumably attended) stimuli elicited positive serial effects on the subsequent trial. However, in the same year, Cicchini et al. (2014) reported seemingly contrary results. They showed that serial dependence for numerosity was strongest in dual-task conditions, where little attention is available for the numerosity task. They attributed the increase of serial effects not directly to attention but to increased stimulus uncertainty in the dual task (see Section 3), but the results nevertheless show that serial dependence can occur without full attention.

More recently, Fritsche & de Lange (2019) manipulated feature-based attention by intermingling pairs of trials that both required an orientation judgment with pairs where the first trial required a size judgment and the second was an orientation trial, thereby cuing attention either toward the same or toward a different feature. The strongest serial effects occurred for successive orientation judgements (**Figure 6a**). However, it is worth noting that significant serial effects were also found in the cross-feature condition, when attention was directed to size, showing that while serial effects can be strengthened by attention, they can also occur without it. Fischer et al. (2020) showed that serial dependence is strongest when the previous stimulus was task relevant; but again, serial dependence also occurred for nonrelevant stimuli if matched for position and, under some circumstances, color. All this points to multiple routes to serial dependence, both via task relevance and attention and via more automatic processes.

Kim et al. (2020) used a binocular rivalry task to probe the role of stimulus awareness in serial effects. On alternate (priming) trials, they presented orthogonally orientated gratings to the two eyes—a standard rivalrous stimulus where one orientation dominates perception while the other is suppressed (**Figure 6b**). These binocular trials were alternated with non-rivalrous, monocularly presented stimuli, whose orientation was ±10° from one of the rivalrous stimuli (ideal for serial dependence) and ±80° from the other (too distant for serial effects). The monocular probe stimuli were biased toward the previous rivalrous stimuli only when the orientation of the dominant stimulus was near that of the test; when the similarly oriented stimulus was suppressed, there were no serial effects. This shows that only stimuli that reach visual awareness induce serial effects, consistent with the idea that perceptual priors are generated at high levels of analysis, although they act at low levels.
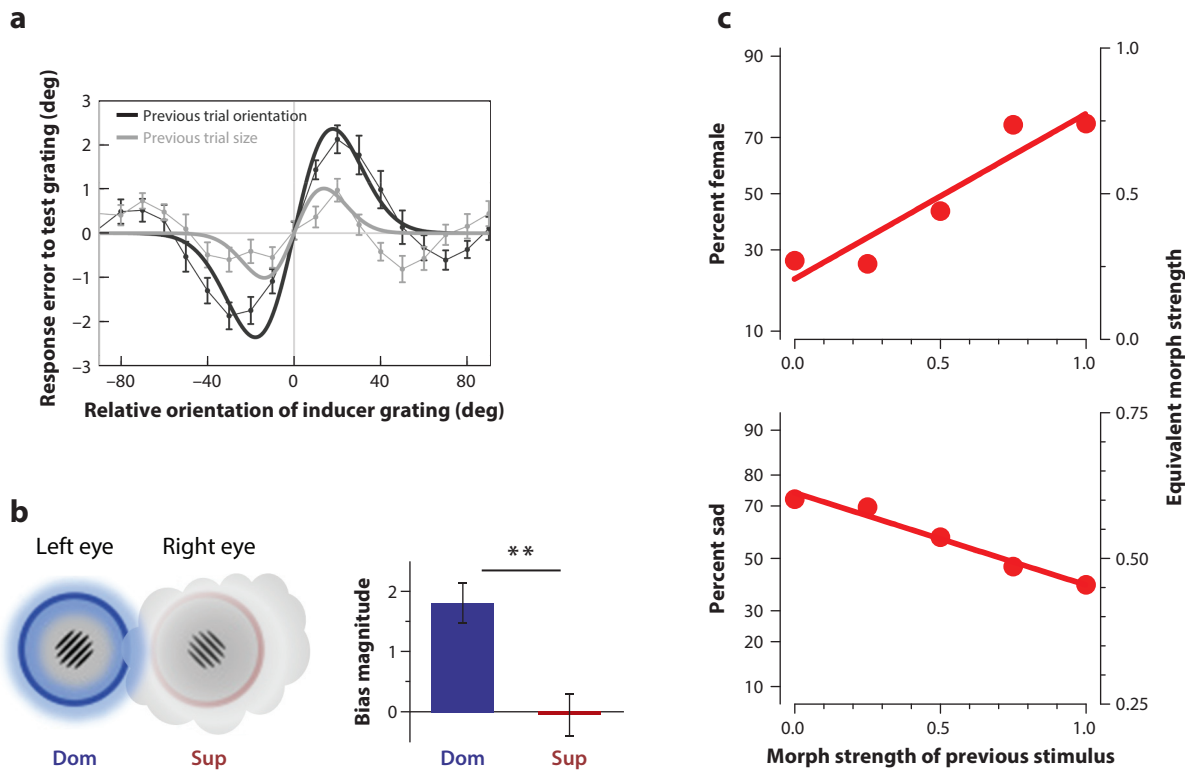
a

Response error to test grating (deg) vs Relative orientation of inducer grating (deg)

— Previous trial orientation
— Previous trial size

b

Left eye   Right eye

Dom   Sup

Bias magnitude

**

Dom   Sup

c

Percent female / Equivalent morph strength

Percent sad / Equivalent morph strength

Morph strength of previous stimulus

Figure 6

Adaptation, attention, and awareness. (*a*) Results of Fritsche & de Lange (2019) on feature attention. Observers either made an orientation judgment in all trials or alternated size judgments with orientation judgments. Serial dependence was stronger when successive trials both required orientation judgments (*black symbols and curve*), but it was still present, if reduced, for the alternating-size orientation judgments. (*b*) Kim et al. (2020) tested whether serial effects for orientation depend on conscious awareness. They interspersed a binocular rivalry stimulus (orthogonal gratings to each eye) with a monocular probe of orientation near that of one of the previous gratings. The bias occurred only when the test trial probed the orientation that dominated (Dom), indicating that no information from the suppressed (Sup) stimulus affects the prior. (*c*) Taubert et al. (2016a) showed sequences of faces that varied over both gender and expression and asked observers to rate both features. Whereas previous gender affected positively successive gender judgments (*top*), previous expression affected in a repulsive way expression judgments (*bottom*), showing that the task affected not only the magnitude of serial dependence but also the sign.

6. RELATIONSHIP TO OTHER SERIAL PHENOMENA

Serial dependence is not the only phenomenon in which previous experience affects current perception. Perhaps the best-known serial phenomenon is adaptation, which occurs in nearly every sensory domain: After prolonged exposure to a certain stimulus, subsequent stimuli will be perceived as more different from the adapter than they really are. For example, adaptation to a clockwise-tilted grating will cause a vertical stimulus to appear tilted counterclockwise (Gibson & Radner 1937).

Adaptation has the exact opposite effect to serial dependence, causing biases against the adapting stimulus rather than assimilation toward it, as it occurs with serial dependence. How can these two phenomena coexist? What are the circumstances under which one prevails over the other, and how do the two opposing mechanisms interact? One factor is certainly stimulus conditions: Strong, salient, high-contrast, long-duration stimuli tend to lead to negative aftereffects, while

brief, less salient, low-contrast stimuli lead to assimilative aftereffects (Daelli et al. 2010, Kanai & Verstraten 2005, Pantle et al. 2000, Yoshimoto & Takeuchi 2013). Chopin & Mamassian (2012) reported that stimuli in the recent past caused negative aftereffects, while those in the remote past had a positive effect. Fritsche et al. (2017) also reported evidence interpreted as demonstrating negative aftereffects on sensory processes and positive effects on decisions; but as argued in Section 4, this interpretation has been questioned.

An interesting study has shown that the same stimuli can simultaneously cause both positive and negative aftereffects, depending on the task. Taubert et al. (2016a) displayed a series of face images varying in both gender (male/female) and expression (happy/sad), and they had participants judge simultaneously gender and expression on a two-by-two response box (**Figure 6c**). They found positive serial dependence for gender, whereby previous male faces biased perception of androgynous faces toward male and vice versa, but negative effects for expression, with previous happy faces biasing perception toward sad and vice versa. They argued that the direction of the effect depends on whether the feature is permanent or transient. Serial dependencies can lead to efficient vision by integrating past with present stimuli to improve signal-to-noise ratios, but this strategy relies strongly on the items of interest remaining constant, at least over the short term. Gender is, of course, a relatively permanent attribute of a face. However, expression is changeable and therefore less amenable to integration over time; on the contrary, differentiation (negative aftereffects) can be more appropriate to exaggerate the change, which can be important to detect the sensory update quickly and with high sensitivity (such as the onset of anger). Thus, serial dependencies can not only vary in magnitude to optimize performance but also change sign and become negative, even within the same stimulus.

More generally, perceptual systems are often faced with conflicting demands: to integrate (over time and space) to improve signal strength, or to differentiate to detect change (Braddick 1993). The best strategy depends both on the stimulus and on the task. So far, this variable strategy has been demonstrated only with faces, but it would be very interesting if the principle generalized to other stimuli, with permanent or changeable attributes.

Another phenomenon where history strongly affects perception is termed central tendency or regression to the mean: Estimation of almost all stimulus attributes, including size, color, and weight, shows a systematic bias toward the mean of the sequence (Hollingworth 1910). Like serial dependence, this effect has been couched in Bayesian terms, where the mean is the Bayesian prior built up over time (Cicchini et al. 2012, Jazayeri & Shadlen 2010). While there are clear similarities between central tendency and serial dependence, in that both show a bias toward previous stimuli (and an improvement in efficiency), there are also important differences. Serial dependence looks mainly at the effects of the immediate past, while central tendency averages over a longer period. A few studies have attempted to separate the contribution of recent trials from that of remote ones. Gekas et al. (2019) reported that very recent items have an attractive effect, while items further in the past have a repulsive effect, and those in the remote history have yet again a positive influence (see also Chopin & Mamassian 2012). Perhaps the clearest example showing that they are not identical is that strong central tendency effects (on a spatial number line) have been reported even on the first trial, before serial dependence has a chance to act (Cicchini et al. 2022a). So, while both phenomena illustrate the importance of spatial and temporal context on shaping perception, they are not identical and are not to be confused with each other.

As mentioned previously, the first serial phenomenon to be systematically studied was priming, usually measured as shorter reaction times to repeatedly presented stimuli. Although serial dependence measures response bias rather than speed or accuracy (which in signal detection theory terms can be thought of as criterion rather than sensitivity), the two may share common neural mechanisms. However, when this possibility was investigated, the evidence was not consistent with

common mechanisms. Galluzzi et al. (2022) measured both priming of pop-out and serial dependence in the same paradigm. They used Maljkovic & Nakayama's (1994) technique of odd-ball priming (where repetition of the cuing color leads to faster identification) together with an orientation reproduction task like that of Fischer & Whitney (2014). The pattern of results for the two effects differed in their dependence on the priming color and in the extent that the effects accumulated over trials. Most notably, the magnitudes of the two effects did not correlate with each other across participants. All this pointed to independent rather than shared neural mechanisms for priming and serial dependence.

7. NEURAL MECHANISMS OF SERIAL DEPENDENCE: OSCILLATIONS?

The evidence presented so far suggests that serial dependence acts directly on sensory mechanisms, most probably at very early stages in the processing stream, affecting the perceptive fields of early visual analysis. It is therefore reasonable to expect that serial dependence should leave neural signatures detectable by modern neurophysiological techniques, which should further help identify and localize the underlying mechanisms.

The first clear physiological evidence of serial dependence in humans was probably an fMRI classification study by St. John-Saaltink et al. (2016). The researchers required participants to identify the orientation of a cued grating, presented left or right of fixation. The reported orientation ($\pm45°$) was strongly influenced by that of the previous stimulus in that location, showing serial dependence. With standard classification techniques they could classify the orientation of the current stimulus from the distribution of blood-oxygen-level-dependent (BOLD) activity in area V1; but more impressively, they were able to classify the orientation of the previous stimulus in that position with high accuracy (**Figure 7a**). This is very clear evidence for the presence of serial dependence signals in the brain, and it proves that these affect the response of very early visual processing, as early as V1.

Bae & Luck (2019) similarly applied classification techniques to detect the memory trace of the previous stimulus in human electroencephalogram (EEG) responses to the current trial. Fornaciai & Park (2019a) used similar techniques to classify the neural representation of numerosity. Their study showed a clear neural signature of numerosity, and the numerosity magnitude incorporated the serial dependence effect of the previous stimulus. The signal emerged early, soon after stimulus onset, and continued for up to two seconds, showing that the biased neural representation of a stimulus induced by serial dependence is preserved throughout a relatively long period. However, none of the above studies shows evidence that the neural signatures are directly connected with serial dependence measured psychophysically.

Ranieri et al. (2022) also used EEG classification to study serial dependence signals while observers judged the orientation of peripherally displayed gratings. The upper panel of **Figure 7b** plots the evolution of decoding accuracy of the current stimulus, showing that decoding was possible over a long interval. The topographical maps associated with each decoding instance show how the relevance of each electrode in the classification (the activation pattern) evolved over time, involving both occipital and more frontal regions. The lower panel of **Figure 7b** shows the decoding accuracy of the previous stimulus (using current EEG activity), demonstrating several interesting facts. First, the topographical maps show a strong activation pattern in parietal and occipital areas, pointing to activation of perceptual rather than decision-making areas. Second, the signal of the previous stimulus could not be decoded before the current stimulus had been displayed for about 700 ms, suggesting that perceptual history is communicated through activity-silent signals that are not observable before the current stimulus is presented. Silent reactivation seems to be a general principle in serial dependence, brought out even more clearly in a more recent auditory decoding
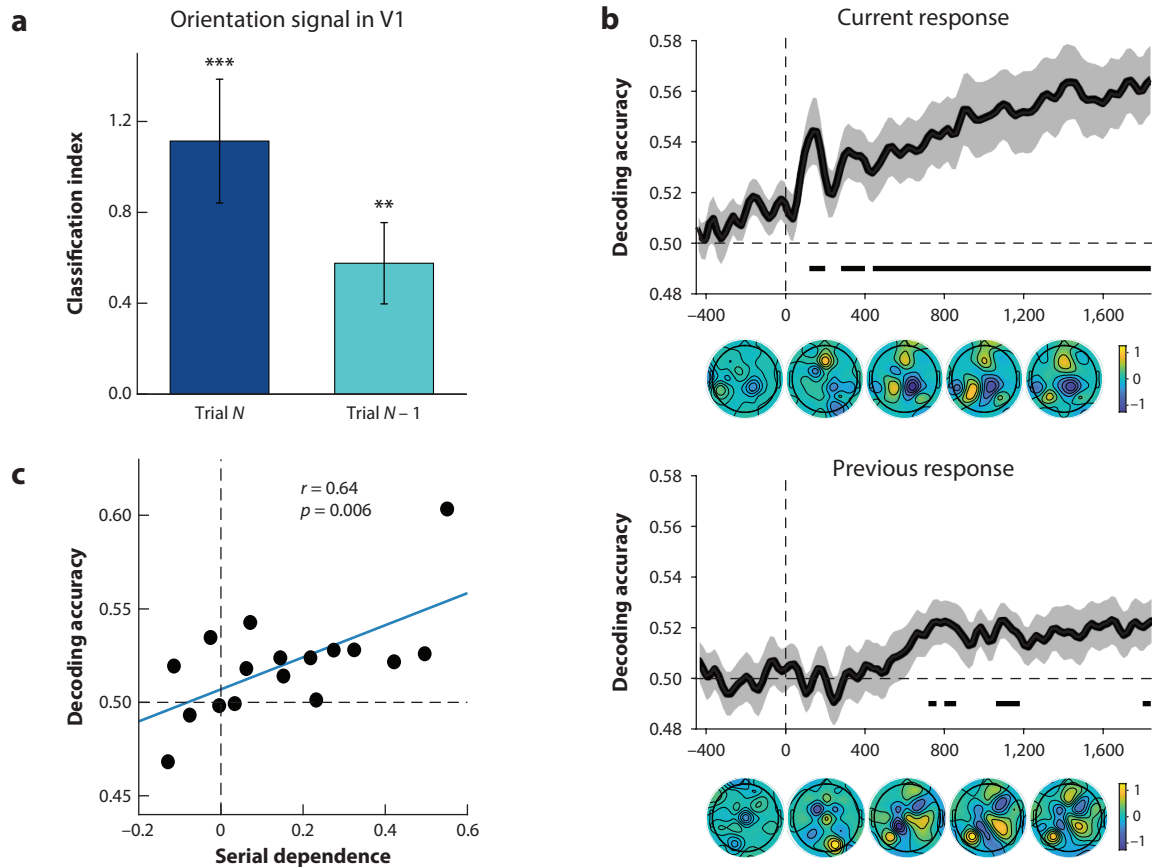
Figure 7

Neural correlates of serial dependence. (*a*) Output of algorithm classifying the orientation of the currently cued stimulus (*dark blue*) or previously cued stimulus (*light blue*) from the distribution of V1 blood-oxygen-level-dependent (BOLD) activity. Error bars indicate standard error of measurement. Panel adapted from St. John-Saaltink et al. (2016). (*b*) Accuracy of decoding current (*top*) and previous (*bottom*) stimuli from EEG distributions as a function of time after onset of the current stimulus. The topographies indicate the relevance of electrodes for classifications (tested samples weighted based on model coefficients); both bright yellow and deep blue indicate reliable electrodes. Panel adapted from Ranieri et al. (2022). (*c*) Accuracy of decoding the previous stimuli from current EEG after training on current stimuli, as a function of the strength of serial dependence, for each participant. *r* indicates the regression coefficient, *p* is the *p*-value.

study of Zhang & Luo (2023), where they show that activation of the previous stimuli not only depended on the presentation of the current stimulus but also was specific to the features being measured.

Ranieri et al. (2022) investigated further the coexistence of past and present neural representations in the EEG scalp potential by training the classifier on the current response and testing on the previous one. Average cross-condition coding accuracies for all participants are shown on the ordinate of **Figure 7c**: They are almost all above chance. These measures of decoding capacity are plotted against the strength of serial dependence for each observer, showing that the two correlate positively: the stronger the serial dependence, the stronger the decoding accuracy of past stimuli. This is an important connection, showing that the neural trace revealed by this technique relates to the perceptual effects of serial dependence measured by psychophysical means.

In recent years, several groups have suggested that predictive perceptual processes like serial dependence should give rise to neural oscillations, particularly in the alpha range, the most prominent frequency in the human brain (Friston et al. 2015, Sherman et al. 2016). Several studies have provided empirical support for this idea. Ho et al. (2019) reported alpha oscillations in auditory judgments that are clearly linked to serial dependence. Participants identified the ear of origin of brief sound sources embedded within a burst of random noise. Plotting responses as a function of time after noise onset revealed clear oscillations in response bias at 9.5 Hz (**Figure 8*a***). However,
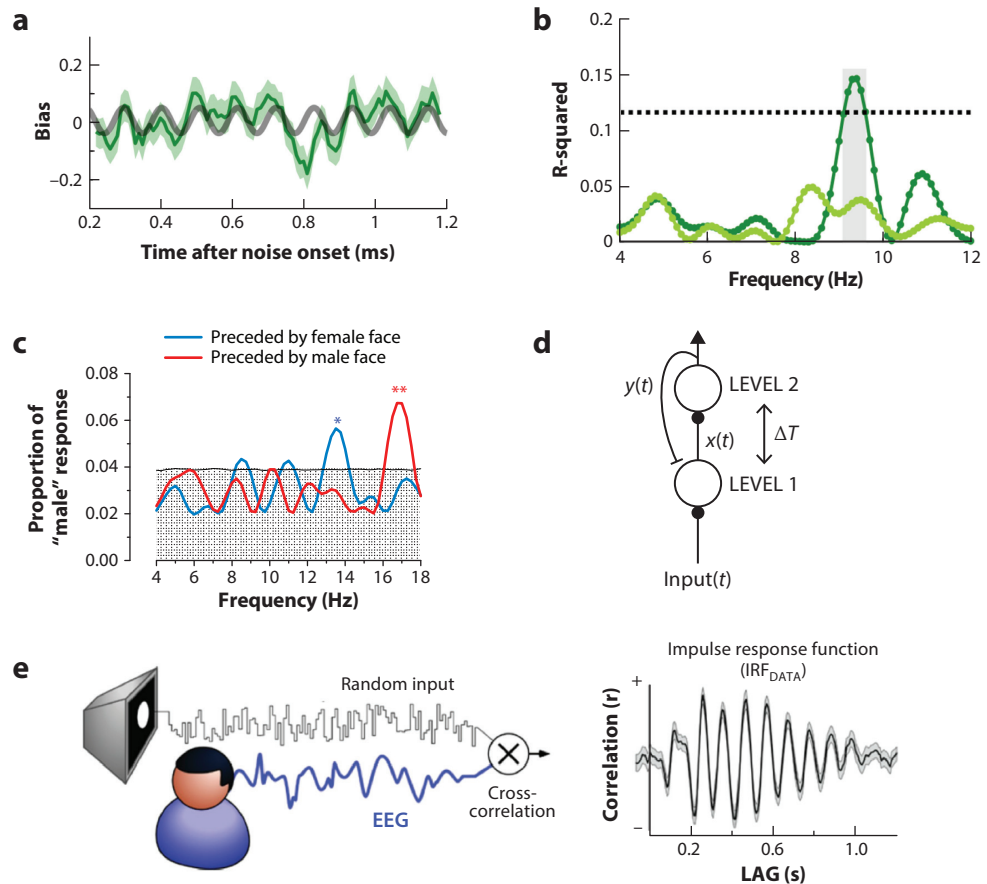

Figure 8

Behavioral oscillations. (*a*) Changes in response bias as participants detect the ear of origin of a weak sound played in noise as a function of time after noise onset. Bias is not constant but oscillates at about 10 Hz. Panel adapted from Ho et al. (2019). (*b*) Goodness of fit of best-fitting sinusoidal gratings as a function of temporal frequency. The dark green curve shows trials preceded by a tone to the same ear (congruent), the light green curve shows trials preceded by a tone to the other ear (incongruent). Only the congruent trials showed significant oscillation (significance shown by the dotted line). (*c*) Fourier transform of biases in judging the gender of androgynous faces preceded by female faces (*blue curve*) or male faces (*red curve*). Stars indicate statistically significant oscillations ($p = 0.05$ or 0.001). Panel adapted from Bell et al. (2020). (*d*) Simple predictive model of Alamia & VanRullen (2019); $x(t)$ indicates the input, $y(t)$ the feedback, and ΔT the processing time. (*e*) Cross-correlation of white-noise sequence with simultaneously recorded electroencephalogram (EEG) produces an impulse response function, which reverberates in the alpha range. Panel adapted from Alamia & VanRullen (2019).

the oscillations were not always present but only on trials in which the previous stimulus had been presented to the same ear (congruent trials); when the stimulus had been presented to the other ear (incongruent trials), there was no measurable oscillation (**Figure 8b**). That the oscillation occurred only for coherent trials clearly implicates serial dependence. The results further point to a sensory site of action, as the previous stimulus generated oscillations only if presented to the same ear. If the oscillation were at the level of decision criterion, then the oscillation should occur in both ears, irrespective of where the previous stimulus has been presented. The fact that it depends on the ear of stimulus presentation strongly implicates sensory processes.

Similar results have been reported for vision, but at higher frequencies: Bell et al. (2020) measured gender perception in faces morphed along a male/female continuum. Gender judgements of androgynous faces were strongly influenced by the gender of the previous face [agreeing with Liberman et al. (2014)]. However, the biases in the gender judgements were not constant but oscillated in the high-alpha, low-beta range (**Figure 8c**). Interestingly, two separate frequencies could be identified: one around 17 Hz for responses to androgynous stimuli preceded by a male face, and another around 14 Hz when the stimuli were preceded by a female face. Why the oscillation frequency is higher than for audition not clear, nor is the dependence on the gender of the previous stimulus. One interesting possibility is that perceptual history is communicated via a frequency code in a form of frequency tagging, but at present there is no evidence for this idea.

At this stage we can only speculate on the role oscillations play in serial dependence. One possibility is that they serve to facilitate communication and bind the previous with the current stimuli. Another, not mutually exclusive, idea is that they derive from the recursive nature of the prediction/verification cycle inherent to predictive perception (**Figure 8d**). In all predictive models, higher processing levels generate predictions, or priors, which are fed back to early levels to be tested against sensory input, which in turn transmits an error signal to correct the prior, in a recursive loop. Given that each stage will have a characteristic delay (shown as ΔT in **Figure 8d**), the loop will tend to reverberate at a certain frequency. Modeling shows that physiologically plausible delays will lead to oscillations around 10 Hz (Alamia & VanRullen 2019, Friston 2019, Friston et al. 2015).

Oscillations around this frequency have been demonstrated experimentally by VanRullen & Macdonald (2012). They stimulated the visual system with randomly fluctuating luminance input while recording EEG (**Figure 8e**). Cross-correlating the random input with the EEG output yields the impulse response function of the system, which clearly oscillated around 10 Hz. This oscillation could reflect the so-called perceptual echoes associated with memory for the past stimuli.

8. SERIAL DEPENDENCE-LIKE EFFECTS OVER SPACE, RATHER THAN TIME?

The work summarized so far shows that although serial dependencies lead to strong biases in perception, their overall action may be beneficial to the system. The effects are unconscious and obligatory, but they are also flexible, adapting to stimulus reliability and task demands to optimize performance. Serial dependence effects occur over time; but it is reasonable to ask whether similar obligatory integration may occur over space. A candidate phenomenon is visual crowding.

Visual crowding is the inability to recognize peripheral objects in clutter, usually considered a fundamental low-level bottleneck to object recognition (Levi 2008). However, it is possible that crowding is not so much a bottleneck in processing as an undesired consequence of optimizing strategies that exploit the spatial (rather than temporal) redundancies in natural scenes. This idea was recently tested by Cicchini et al. (2022b) with an orientation paradigm similar to that
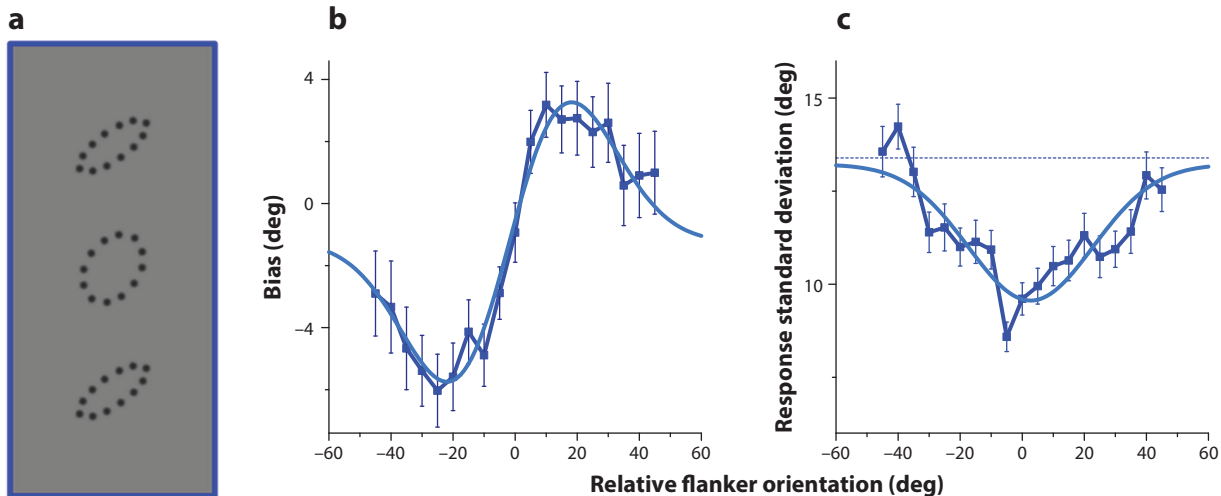
Figure 9

Visual crowding follows similar rules to serial dependence. (*a*) Sample stimuli used in the study of Cicchini et al. (2022b). Here a peripherally presented, broad ellipse is flanked by two narrower (more reliably discriminated) ellipses. (*b*) Bias errors as a function of the orientation difference of flankers and target. Continuous lines are the fits of an optimal model based on Equations 1 and 2. (*c*) Response scatter in the same task as a function of the orientation difference of flankers and target. There is a strong reduction in response scatter from baseline (*dashed line*) as the two are most similar.

used for serial dependence studies. Observers judged the orientation of target ellipses flanked by two vertically positioned flanker ellipses of different orientation (**Figure 9a**). The perceived orientation of the target ellipse was strongly biased toward that of the flankers, a clear sign of crowding. However, the pattern of results also followed closely the same rules governing serial dependence. First, crowding was greatest for unreliable targets with reliable flankers, as predicted from Equation 2. Second, crowding-induced biases were maximal when target and flankers had similar orientations, falling off for differences larger than 20° (**Figure 9b**), following the pattern of serial dependence for orientation (**Figure 2a**) predicted again from Equation 2. Finally, and most convincingly, while the flankers caused a strong bias in target judgments, the normal signature of crowding, they actually reduced response variance (**Figure 9c**), leading to lower overall error rate. All this suggests that crowding may be an undesired by-product of strategic, compulsory integration mechanisms, very akin to serial dependence. While crowding can have a strong impact on object recognition, it is best understood not as a processing bottleneck but as a consequence of efficient exploitation of the spatial redundancies of the natural world.

This finding suggests that serial dependence may be a subcase of a larger family of optimizing phenomena happening in the brain, whereby current weak sensory input is integrated and supplemented by relevant information obtained either in time or across space.

9. AN ADAPTIVE STRATEGY IN A STABLE ENVIRONMENT

This review has discussed some of the more relevant studies addressing the recently described phenomenon of serial dependencies. While their immediate and obvious effect is to bias perception away from veridicality, their overall action serves to improve the efficiency of perceptual systems. The improvement comes from appropriately weighted integration of the previous with current

views, exploiting the temporal—and possibly also spatial—redundancies of natural ecological viewing conditions.

Like the dalmatian dog and hollow mask of **Figure 1**, serial dependence is not under voluntary control. Although, like most perceptual mechanisms, it may be modulated by attention and task demands, serial dependence is largely automatic, compulsory, and outside conscious awareness. This contrasts sharply with other purported top-down effects, such as beliefs, emotions, or linguistic representations supposedly exerting direct top-down influences on what we see. As Firestone & Scholl (2015) elegantly discuss in their influential review, despite the recent popularity of the idea of cognitive penetrability, the evidence in favor of it is at best extremely weak, often explained away simply by (very small) response biases. Serial dependence, on the other hand, is a robust phenomenon that seems to operate outside the realm of conscious awareness, and it is an intricate part of the perceptual apparatus that serves to improve efficiency.

While not under voluntary control, serial dependence is, however, flexible and adaptive and not simply a temporal low-pass filter or a rolling average of recent events. Integration occurs only when advantageous, and it follows a set pattern of rules summarized by the simple Equations 1 and 2. Basically it is maximal when the current stimulus is unreliable (and needs improving by integration), when the previous stimulus is reasonably reliable (worth integrating with), and when the two are not too dissimilar, so they are likely both representations of the same object. Rather than being thought of as a low-pass filter, serial dependence is better considered to be an intelligent Kalman filter (Burr & Cicchini 2014).

The integration pattern is probably even more intelligent than simple up- or down-regulation by the rules of Equation 2. Perceptual systems need to integrate across space and time to increase signal-to-noise levels; but they may also need to differentiate over time to accentuate change. Serial dependence aids integration but could, in principle, dampen sensitivity to change. When viewing faces to glean information about gender and expression, it seems that the system can do both simultaneously: integrate the information of the permanent attribute, gender, and differentiate information about the changeable expression (Taubert et al. 2016a). At present this flexibility is not incorporated in our model or equations, but future research will hopefully lead to a fuller understanding of the interplay between attractive and repulsive serial effects.

While still subject to debate, most evidence suggests that serial dependence acts on sensory systems, affecting them directly. Apart from the psychophysical evidence pointing to early action on perception rather than decision, there is clear evidence from classification studies (of psychophysical, EEG, and fMRI signals) for a neural trace of the previous stimulus in early visual cortex (probably V1). This means that serial dependence signals are incorporated within the sensory representation of the world in a way that is indistinguishable from a response to a physical stimulus. Thus, it is impossible to understand perception without understanding the recursive feedback loops driving serial dependence and similar phenomena. It is difficult not to draw parallels with other examples of distorted representations, such as memory, where fragmentary recollections can be supplemented by Bayesian inference processes that can be strongly influenced by post-event contextual information (Loftus & Pickrell 1995). These processes have important potential legal consequences, which have been explored at length (Loftus 1996). Similarly, the influence of contextual information on perceptual processes may need to be considered more seriously, perhaps also in a legal context.

It is particularly interesting that serial dependence–like phenomena may occur in space as well as in time, potentially explaining the clinically important phenomenon of visual crowding. Like serial dependence, crowding is not just automatic spatial pooling; rather, the integration (although obligatory) follows clear rules that would for many tasks lead to increased efficiency.

Understanding the nature and functional role of the adaptable integration process should lead to new understandings of this classic phenomenon.

Since the introduction of serial dependence a decade ago, much very useful work has been done to characterize this phenomenon. What direction may future research take? Prediction (about prediction) is difficult, but a very promising test bed for serial dependence is saccadic eye movements—the large, ballistic movements that serve to reposition items of interest on the retina. Under natural conditions, eye movements are the principal mechanism by which humans actively explore the world, bringing the high-resolution fovea to bear on areas of interest. Each new fixation needs to be verified against predictions, which in turn need to be updated, before initiating further exploratory movements. Most importantly, these sequences of operations need to be seamless, merging into each other without the observers being aware that their retinal images are continually changing—or, indeed, even that their eyes have moved. Saccadic stability has of course been intensely studied for decades (Ross et al. 2001), with several authors considering Bayesian, generative ideas (Niemeier et al. 2003). However, there are probably many revealing studies than can be done within the framework of serial dependence. Serial dependence is strong during saccades (Xie et al. 2023), and there are clear signs of oscillations that may mediate some effects (Terzo et al. 2022). Serial dependence could prove key in binding the successive fixations inherent in active vision into a single, seamless stream of visual experience.

That vision is an active process is not a new idea, dating back at least to Helmholtz, and probably to much earlier philosophical writings. Most of us are impressed by the demonstrations of **Figure 1**, and few would deny the modulatory role of top-down processes. However, mainstream physiological research is still driven primarily by a bottom-up approach, considering the system to be a strict hierarchy, with metaphors like "upstream" and "downstream" reinforcing these conceptualizations. In part this may be due to the nonquantitative approach often associated with demonstrations of top-down action. That the new approach of serial dependence is theoretically grounded, intrinsically quantitative, and based on firm physiological and psychophysical evidence will hopefully pave a way forward, championing new studies on the generative processes that are essential for a complete understanding of perception.

SUMMARY POINTS

1. Perception is biased toward previously viewed items appearing in similar spatial locations.

2. The effects are particularly conspicuous for stimuli of high sensory uncertainty, which are similar to the previous stimuli along the dimension of interest.

3. Serial dependence is potentiated by attention and task demands, but it is largely automatic, compulsory, and outside conscious awareness.

4. Memory of the previous stimuli includes contextual information but acts at low levels, implicating feedback loops from high to low levels to facilitate prediction.

5. Behavioral oscillations may reflect the existence of these feedback loops.

6. Serial dependence is flexible: It is stronger for stable than for labile attributes, facilitating temporal continuity.

7. Overall, this could be a canonical neural computation set in place to improve sensory representation at all levels of sensory functions.

FUTURE ISSUES

1. Saccadic eye movements provide an ideal ecological test bed for serial dependence.

2. What are the mechanisms underlying the complementary roles of serial dependence and adaptation in integration and differentiation, aimed at optimizing signal to noise levels as well as sensitivity to change?

3. To what extent does serial dependence affect perception in real-life conditions?

4. Serial effects can improve sensory reliability; but does this also result in increased confidence in the response?

5. How general and abstract is the information inherited from the previous trial?

6. Are serial effects immune from reward and feedback?

7. How much does serial dependence rely on the observer's appreciation that the world is stable?

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