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Attraction and repulsion in perception and working memory as complementary outcomes of learning

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Visual perception is imperfect. Fortunately, the environment contains an incredible amount of structure that observers can learn to exploit through experience. As a result, representations of the environment that are perceived and stored in memory are often biased towards or away from other stimuli, reference points, and expectations that are acquired across varying timescales. We propose that this myriad of bias phenomena reflects a shared adaptive principle where the brain optimizes its noisy sensory representations to support behavior within its resource constraints. Under this principle, experience is stabilized through the integration of mutually informative stimuli, whilst the discriminability between stimuli is maintained through adaptation. We suggest that this principle emerges naturally from predictive and adaptive coding frameworks that can operate across multiple levels of processing and predict attraction and repulsion even within the same task or stimulus. Viewing these biases as emergent properties of a hierarchical statistical learning system offers new insight into how the brain balances stability and flexibility when shaping our perception and memory of the world.

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Introduction

Our representations of the world are rarely true to the physical stimuli that they correspond to. Instead, these representations are shaped by statistical properties of the natural environment that accumulate through experience and by the relational encoding of stimuli into mind. This produces systematic biases in perception and memory that shift our representations towards or away from other stimuli, reference points, or expectations. Traditionally, these attractive and repulsive biases have been studied separately, from tilt illusions in early perception to categorical and similarity-based biases in working memory. Here, we propose that attractive and repulsive biases reflect complementary outcomes of a shared computational framework that optimizes noisy sensory representations within existing resource constraints by stabilizing representations of mutually informative signals and maintaining discriminability between those that are distinct. This framework provides a common computational rationale for attraction and repulsion across multiple levels of processing and explains how these opposing biases can co-occur in the same task or even in the same stimulus, depending on contextual variables such as stimulus similarity, contrast, reference offset, and timescale of integration. Below, we describe how these opposing biases emerge in perception and working memory, and discuss how computational models have sought to explain them.

Perception

Rather than veridically reflecting physical stimuli, items are often perceived as more similar (*attraction*) or more distinct (*repulsion*) than they truly are. One of the most famous examples of repulsion in perception is the Tilt Effect [1]. In this phenomenon, seeing two similarly-angled line segments at once, or seeing them sequentially for an extended amount of time (i.e., several seconds or more) typically leads to repulsion between their perceived angles. This repulsive "adaptation" in stimulus perception is shown to arise from altered neural sensitivity and has been found throughout most levels of sensory coding, including color, motion, and face perception [2]. At

the same time, perception can also be biased toward recent history. This phenomenon, commonly termed serial dependence, has been observed consistently across different features and modalities [3,4]. Thus, sequential perceptual inputs can elicit attractive serial dependencies and repulsive adaptations.

The distinction between adaptation and serial dependence is not always immediately obvious. To some extent, this ambiguity stems from the choice of nomenclature. For example, while the term "serial dependence" was proposed as a shorthand for integration between sequential perceptual representations [5], its name could be interpreted more broadly as any aspect of perception that is correlated with prior perceptual experience, which would include repulsive adaptations. The distinction is further muddied by the inconsistent use of each term in the literature. Serial dependence has been used to refer to repulsive aftereffects (Figure 1a; [6,7]), and adaptation to attractive aftereffects, [8–11]. However, based on their origination in the literature, each term is most accurately used to refer to only one of the two opposing perceptual biases, with adaptation used to refer to repulsion and serial dependence to attraction, respectively.

At a mechanistic level, the likelihood of observing serial dependence or adaptation may depend on the relevance and quality of the inducer stimuli. For example, Rafiei et al. [12] demonstrated that previously-attended stimuli attract perception, consistent with serial dependence between task-relevant information, whereas previously-ignored distractors induce adaptation that maintains their discriminability from targets (Figure 1b). Moreover, low-contrast stimuli, which carry less reliable sensory information, are more susceptible to serial dependence, whereas high-contrast stimuli, which provide stronger signals, are more susceptible to adaptation [13]. The duration of stimulation also matters; brief motion exposure tends to produce spatiotopic serial dependence, while longer exposure leads to retinotopic adaptation [14]. Similar dynamics are also found in multisensory integration. In the ventriloquist illusion, auditory localization is initially biased towards visual cues, reflecting a tendency to pool across ambiguous multisensory signals [15]; however, when this discrepancy persists, perception recalibrates and shifts auditory spatial maps away from the visual reference to preserve the discriminability between distinct sensory sources [16]. In this sense, the presence and magnitude of serial dependence or adaptation in any single perceptual experience reflects the degree to which previous inducers are perceived as informative of current perception, which can be jointly shaped by top-down priority and bottom-up signal reliability.

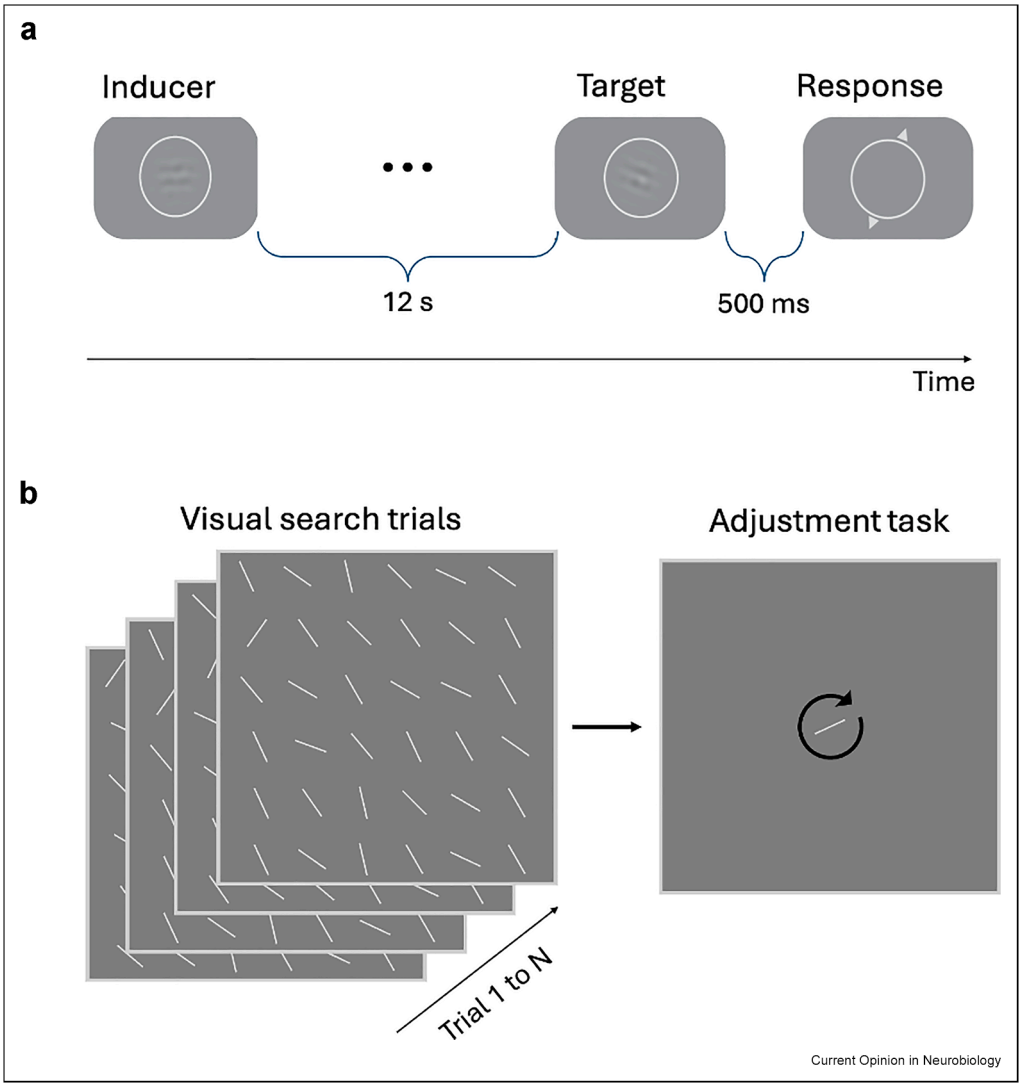
These variations in the direction of perceptual biases may also depend on the stage of visual processing. For example, several studies report repulsion from previous stimuli but attraction toward previous decisions, suggesting adaptation in lower-level sensory responses and serial dependence in higher-level cognitive processes such as decision-making [17–20]. However, other findings challenge such a strict mapping between bias and mechanism. Some have found, for example, that attractive biases can occur even in the absence of explicit prior decisions [21]. In the auditory domain, Lieder et al. [22] showed, using a two-tone pitch discrimination task, that pitch perception is attracted toward specific frequency components of a preceding tone even when perception differs from the tone's abstract pitch, indicating a low-level form of serial dependence that is frequency-specific, but not pitch-specific. All-in-all, the research suggests that attractive serial dependencies and repulsive adaptations are dynamic and that their biases can co-exist across levels of processing. As such, ongoing efforts in the field have begun to move beyond measuring biases through mean responses to better capture these dynamics as they unfold within individual perceptual experiences [7,23].

Working memory

Working memory (WM) also exhibits attractive and repulsive biases that emerge under different conditions. Much like perception, these opposing effects can be thought to reflect the same fundamental tension between stability and discriminability: attraction integrates consistent information under uncertainty, while repulsion maintains the individuation between distinct representations (e.g., [24]).

When multiple items are held in WM, similar items tend to attract each other under high memory load or when representations are weak [25]. This manifests most clearly in hierarchical encoding effects, where individual items are biased toward the summary statistics of their perceptual group [26–28]. For instance, the remembered size of a red circle tends to be pulled toward the average size of other red circles present in the visual display (Figure 2). This attractive bias appears to reflect an optimal integration strategy—when individual representations are uncertain, incorporating group information can improve accuracy on average [29]. Critically, this attraction occurs toward the group average rather than through swapping of representations [30], suggesting an organizing principle of memory representations. By contrast, when memory load is low and items can be represented with high fidelity, similar items often repel each other instead [31,32]. This repulsion bears similarities to adaptation in perception where the simultaneous presentation of similar stimuli leads to exaggerated differences between their features. For example, the strength of repulsion is continuously modulated by factors like item similarity and memory strength [24,25]. Thus, with less demand on

Figure 1

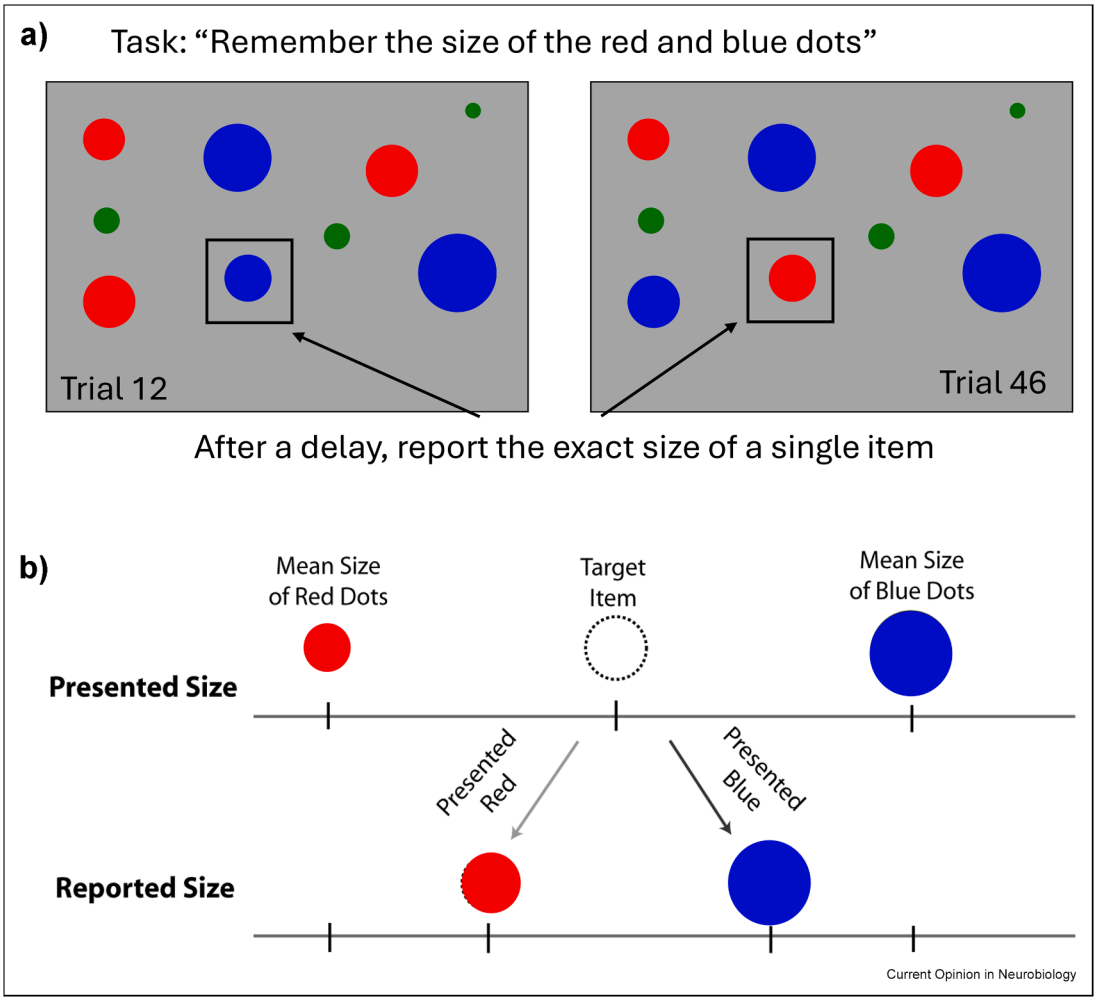


Schematic illustration of task structures from two studies demonstrating task-dependent direction of serial bias. **a.** In Ceylan & Pascucci [6], participants viewed a sequence of one to three oriented Gabor stimuli (inducers), followed by a target Gabor, each presented for 500 ms. The number of inducers determined the interstimulus interval (ISI): 12 s for one inducer, 6 s for two, and 4 s for three. After a 500 ms delay, a response tool appeared, and participants reproduced the target's orientation by rotating the tool with the mouse. The intertrial interval ranged from 1000 to 2000 ms. Panel A illustrates a trial with a single inducer. The experiment included 208 trials. Reproduced orientations were attracted toward the previous trial's target and repelled from inducers within the current trial. **b.** In Rafiei et al. [12], participants first performed a series of visual search trials (N = 4–5 per block), identifying an oddly oriented line among 35 distractors arranged in a 6 × 6 grid. On each search trial, they pressed the E key if the target appeared in the upper three rows and the D key if in the lower three; incorrect responses triggered an "Error" message displayed for 1 s. Following the search trials, participants adjusted the orientation of a single randomly oriented line to match the target from the last search trial. Panel B illustrates one full block. The experiment included 264 blocks. Reproduced orientations were attracted toward the last target and repelled from the distractors.

representational resources, the brain tries to preserve the individuation between potentially confusable memoranda.

Here too, the transition between attractive and repulsive effects is mediated by task relevance. Items that are actively maintained for a task show different interaction patterns compared to task-irrelevant information [31,34,35], mirroring the influence of attention in perceptual biases. Moreover, attraction and repulsion biases can occur simultaneously for the same memoranda, with a given item showing attraction towards task-relevant items and repulsion away from task-irrelevant distractors [36]. Like perceptual biases, WM

Figure 2



Schematic of Brady and Alvarez [26] (replicated by [33]). **a.** Participants must remember the exact sizes of many dots, and reproduce a randomly chosen dot's size after a brief delay. The task is designed such that unbeknownst to participants, there are two trials that feature identical size dots, and the same target is probed on these trials, with the only difference being that the color of the target item is swapped with another item. Thus, on one trial the target groups with the red dots; on another it groups with the blue dots. **b.** Brady and Alvarez [26] found that participants reports of the size of the target dot were reliably biased toward the other items in the same group (attraction); and to a degree consistent with the 'standard' Bayesian integration model, which treats the group the items are drawn from as the 'prior'. They use this to argue for hierarchically structured WM representations.

biases may similarly reflect a combination of mechanisms that reduce uncertainty by integrating across mutually informative inputs (e.g., encoding items as groups or "ensembles", [26]) or adapting neural sensitivity (e.g., repulsion from cardinal axes in orientation, [37]).

Attention also appears to modulate integration that occurs across memory and perception. For example, when observers must attend to a newly-presented stimulus that is encountered during memory maintenance, memory biases toward perception grow larger [38,39] and are more likely to persist into long-term memory [40]. Conversely, perceptual biases towards working memories are not strongly influenced by attention to memoranda [41], perhaps reflecting a relatively low demand for integration, given the high fidelity of perceptual representations. These asymmetrical patterns of integration between memory and perception are consistent with the idea that integration exists primarily to offset the cost of target uncertainty, with attention playing a secondary role in determining the relative weighting of representations during integration.

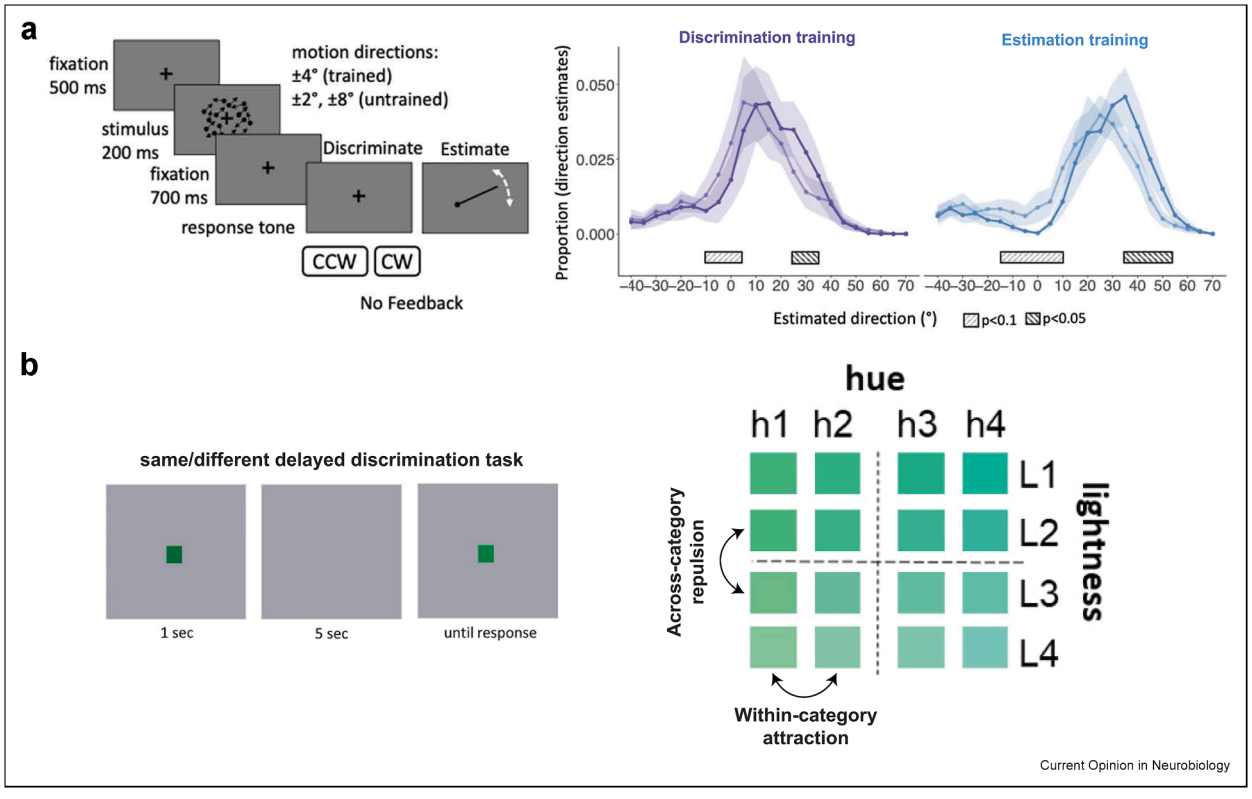
Learning shapes biases

Evidence suggests that attraction and repulsion in perception and memory are shaped by expectations—both implicit and explicit—that are learned through prior experience. In the short-term, the brain develops expectations that are specific to local task context. For example,

in perceptual training tasks, participants' reports tend to be attracted towards features that are presented more frequently [42]. When the environment is predictable, biasing perception towards what is most likely to occur is rational and can reduce errors on average. However, with continued exposure, these contextual expectations can evolve into structural expectations that reflect long-term changes in the tuning of the perceptual system. One such example is the slow-speed expectation, which arises from long-term exposure to the statistics of natural motion [43]. While structural expectations generalize well across different task contexts, their influence on behavior can still be superseded by strong contextual expectations [44,45]. Moreover, it is not the case that perception and memory are universally attracted towards these learned expectations. For example, even when observers elicit measurable improvements in perceptual discrimination after training, repulsion biases sometimes persist or even increase (Figure 3, [46]). Thus, behavior is likely the result of interactions between multiple learned expectations, each capable of producing a combination of attraction and repulsion [47,48].

In some cases, regularities in the natural environment form perceptual categories that can bias perception and memory. When two stimuli are perceived as belonging to the same category, attraction tends to occur, whereas when they are perceived as belonging to different categories, repulsion tends to occur [50]. Unlike structural expectations, which may be formed by the absolute frequency of certain feature values, category expectations tend to reflect the organizational structure that is imposed by task demands. For example, Martinovic [49] found that the same two stimuli showed opposite patterns of bias between observers that were trained on orthogonal dimensions within color space (i.e., hue, lightness). Critically, these opposing patterns of bias improved discrimination performance within the task where the category boundary was acquired. Similarly, Printzlau et al. [51] found that WM reports showed different patterns of bias when prior category training entailed the overrepresentation of stimuli at the center of the category than those at the boundary between categories. These findings suggest that category learning adaptively reshapes the perceptual similarity

Figure 3



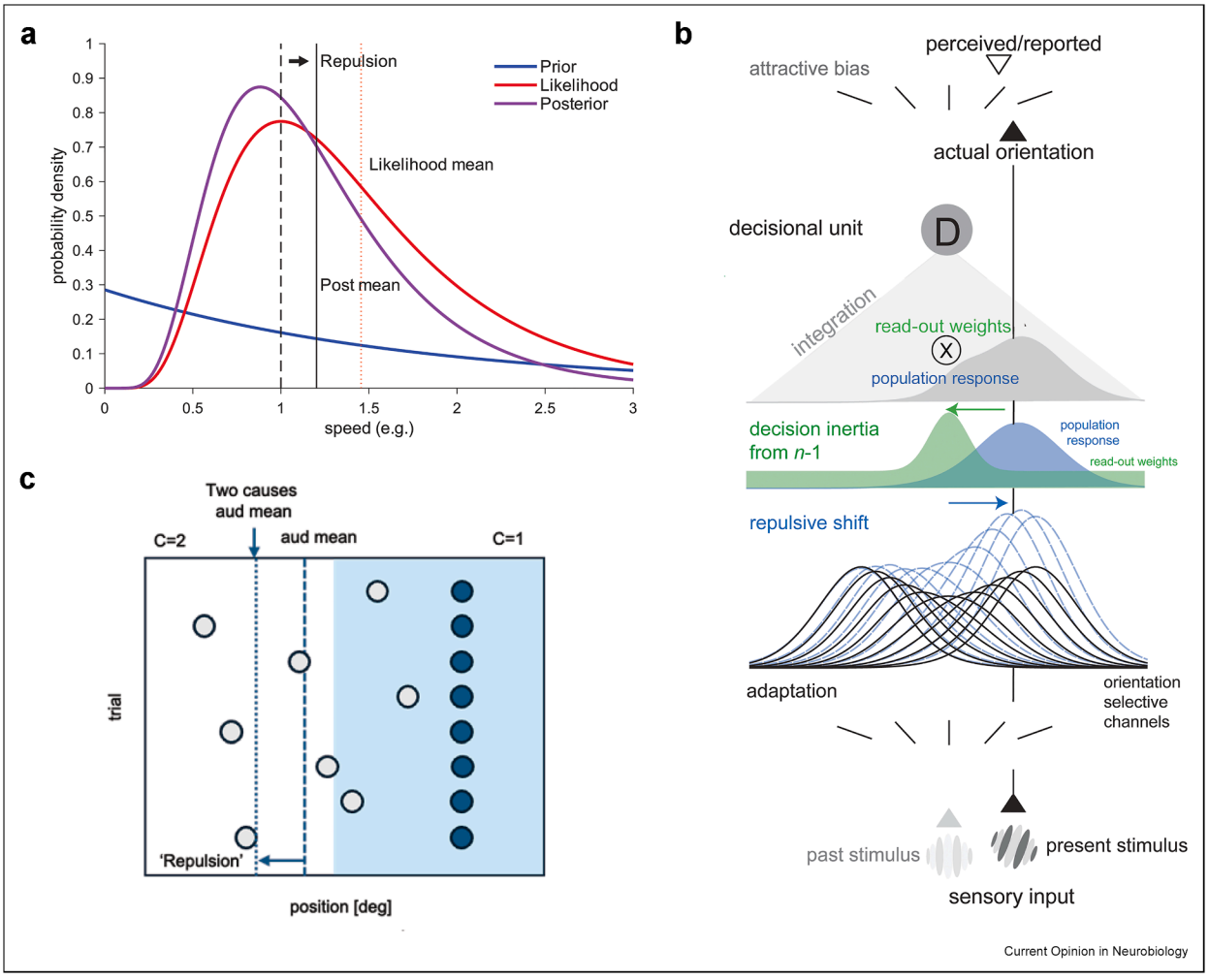
Learning-induced attraction and repulsion from perceptual and categorical training. **a**. Perceptual learning improves discrimination by increasing representational precision but does not necessarily reduce appearance distortions. Szpiro et al. [46] showed that repulsive biases away from the horizontal direction persist or even increase after both discrimination and estimation training. Mean estimate proportions were biased away from the horizontal directions both pre- (unsaturated) and post-training (saturated lines) for both types of training. **b**. Category learning reshapes perceptual similarity along the trained dimension [49]. Learning induces attraction within categories (reducing discriminability, e.g. between h1 and h2) and repulsion across category boundaries (enhancing discriminability, e.g. between L2 and L3).

space to produce biases that enhance the discriminability along feature dimensions that are deemed most informative for ongoing behavior.

A unifying computational architecture

Standard Bayesian observer models most straightforwardly predict that perception should be biased toward expectations (or "priors"), resulting in attraction to expected or frequent stimuli [52]. Yet, as noted, many empirical findings reveal repulsive biases that are not easily explained by assuming a fixed likelihood function that is integrated with a fixed prior. One way to explain these discrepancies within the Bayesian framework is to introduce an efficient coding mechanism. In the case of attraction and repulsion from reference points (e.g., cardinal axes in orientation perception), efficient coding proposes that the perceptual system has an overrepresentation of neurons that encode more frequent stimuli, which results in peakier (i.e., more precise) likelihoods for frequent stimuli and asymmetric likelihoods for those nearby in feature space. Attraction toward the reference is therefore already expected within the Bayesian framework, and repulsion results from the long, asymmetric tail in the likelihood function away from the reference which, when combined with the prior, creates repulsion away from the peak of the likelihood function ([53]; see Figure 4a).

Figure 4



Models of attraction and repulsion. **a.** Efficient encoding leads to asymmetric likelihoods and explains repulsion in a Bayesian framework. A likelihood function (red) that is right-skewed due to efficient coding can shift a response (e.g. mean estimate) away from the prior (blue). Although the prior attracts the estimate leftward, the resulting posterior (purple) is skewed such that its mean shifts away from the prior—producing a repulsive bias. **b.** Two process models (like [19]) explain attraction and repulsion without asymmetric likelihoods, but, importantly, they are not necessarily modeling the same 'type' of repulsion, i.e., the dynamics of short-term adaptation are different than asymmetric likelihoods. **c.** In causal inference tasks involving spatial localization of audiovisual stimuli, where experimental trials (e.g., stimuli of audio in gray, visual in dark blue) are split based on whether participants perceived one common cause ($C = 1$) or two independent causes ($C = 2$), an apparent repulsive bias can be observed specifically when examining trials where subjects reported two causes ($C = 2$ sampling bias), as trials that are more attracted have been classified as one cause ($C = 1$ light blue shading).

A recent extension of this theory proposed that attraction is proportional to the slope of the prior and becomes more pronounced in regions with low encoding precision, while repulsion emerges in areas of high encoding precision [54]. This results in a simple predictive rule: the direction of perceptual bias for a given stimulus depends on whether encoding precision or prior density varies more rapidly in the vicinity of the stimulus. This theoretical framework has successfully accounted for empirical findings of repulsion and attraction in orientation perception [55,56]. Other modeling work describes how these biases might arise through distinct stages of processing. For example, Pascucci et al. [19], Figure 4b) proposes that sensory adaptation initially repels perception away from recent stimuli, while decisional processes later attract current reports towards recent decisions (see also [13]). Indeed, recent empirical work has shown that these opposing forces across hierarchical processing stages may jointly account for the net-attractive aftereffects of serial dependence [57–59].

Another computational perspective comes from Bayesian causal inference models, which are more appropriate for understanding attraction and repulsion amongst multiple simultaneous stimuli. In essence, these models state that observers integrate or segregate information signals based on their inferences about the causal locus of those signals. For example, participants' reports about the location of two auditory stimuli tend to be closer together or farther apart when they are perceived as coming from the same or different visual stimuli, respectively (Figure 4c, [60]). A similar phenomenon is found in motion perception, where participants' continuous reports of motion direction show biases that are consistent with binary left/right responses that were given beforehand [61]. Like Bayesian observer models, causal inference models show that opposing biases can emerge organically from the rational weighting of sensory signals and other knowledge about the environment.

These Bayesian observer models and causal inference frameworks are both normative accounts of bias, meaning that they define what an ideal observer should do to optimally process information under the constraints of their perceptual and memory systems. However, there are also non-normative ways to explain these phenomena without the presumption of an intrinsically rational observer, such as biologically-inspired neural networks. For example, Ritvo et al. [62] showed how a neural network trained with non-monotonic synaptic plasticity can explain memory effects including attraction and repulsion. The basic assumption is that intermediate levels of activation for a given representation should weaken its synaptic connections, leading to different patterns of bias based on the strength of the inducer. While moderate activity from an inducer should lead to differentiation (i.e., a repulsion), strong activity should lead to integration (i.e., attraction). Of course, these process-level explanations are not necessarily at odds with normative models. For example, process models could simply reflect *how* the system implements bias, while normative models explain *why* the system does this (e.g., [63]).

Conclusion

The brain is constantly trying to make sense of a changing world, stabilizing its representations to maintain continuity, while also keeping them distinct enough to detect change. We propose that across perception and WM, attraction and repulsion biases emerge from a shared adaptive principle where the brain optimizes its noisy representations within inherent resource constraints by flexibly integrating and segregating stimulus features depending on context, timescale, and uncertainty. Within this framework, attraction and repulsion do not differ qualitatively; they are both context-dependent outcomes of the same underlying optimization process. Therefore, it may be most useful to ask when and why one outcome comes to dominate the other. Future research should examine how these biases co-occur and interact across modalities and how attention and learning dynamically shift their balance. Gaining a better understanding of this interplay will bring us closer to explaining how the brain builds a perceptual world that is both stable and sensitive to change.

Declaration of competing interest

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Data availability

No data was used for the research described in the article.

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This study investigated how stimulus task relevance, elapsed time, and the number of intervening stimuli shape serial dependence in orientation reproduction. The authors report attractive biases toward previously reported targets and repulsive biases from non-reported inducers. Attraction increased when more inducers were presented closer in time. These findings challenge the view that serial dependence arises from a single mechanism or a fixed temporal tuning window.

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In a recent example of the influence of distractors on visual working memory, this study examined the effect of similarity, relevance and reliability. Attractive effects were seen for distractors shown either

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