

Multi-plasticities: Distinguishing context-specific habits from complex perseverations

Abstract

Though perseveration and habit have always been understood as distinct phenomena, they have also been closely linked throughout the history of their scientific study. Seminal work, in particular in the study of lesions and neurological disorders, has described symptomatic errors of commission as being a form of one or the other (Sandson & Albert, 1984), sometimes with disagreement among researchers. More recently, researchers have explored the idea that a formal computational framework widely used to describe the learning and dynamics of habits may also, and perhaps more accurately, be used to understand the emergence and utility of perseverative responding (Gershman, 2020). An explicit lesson from this work is that claims to measure putative habitual behavior would do well to take into account the contribution of one or more types of perseveration. Thus, it makes sense to review the current state of understanding of perseveration, both to draw distinctions of difference with habits, where they are possible, and to outline areas of potential further research. This chapter briefly summarizes the classical conception of perseveration, including conceptual underpinnings and empirical research. We then examine how this conception has been altered by both empirical observations and the popularity of new theoretical frameworks for describing action selection. We summarize these findings into a taxonomy of types of perseverative behavior, and describe recent work arguing for an adaptive role of perseveration in multiple forms of cognition. We argue that perseveration is in fact a complex set of constructs that have widespread influence on behavior, with important implications for the experimental measurement of habits and compulsive responding more broadly.

1. Introduction

Research on perseverative and habitual behaviors share a long and highly intertwined history. The distinction between these behaviors was formalized as part of the earliest modern theories of learning and conditioning. Since that time, the study of both ideas has often proceeded together, resulting in working definitions that often overlap. In this chapter we aim to disentangle the definitions of perseveration and habit, understanding both their common mechanistic basis and also their distinct expressions, and thus to outline the respective roles they play in the measurement of behavior.

Thorndike's laws of effect and exercise provided early insights into the principles governing the formation and reinforcement of behaviors (Thorndike, 1911). The law of effect posits that responses followed by satisfying consequences are more likely to be repeated in the future, while those followed by discomfort or dissatisfaction are less likely to recur. In contrast, the law of exercise posits that the mere repetition of a response can strengthen the association between a stimulus and its corresponding response. In contemporary neuroscience, two fields – classical conditioning (largely in animal models) and

computational reinforcement learning (in humans and animals) – predominantly work with these concepts to study aspects of instrumental behavior including goal-directed and habitual control, and perseveration. However, for historical and sociological reasons, these fields have tended to employ diverging mappings of control concepts to Thorndike's laws. In conditioning, the law of exercise has been linked to habits whereas, in RL, it has been linked to perseveration. As a result, the consensus contemporary working definitions of these concepts outline a number of areas of distinction as well as several commonalities. We outline them here.

Perseveration, often considered to be a universally maladaptive form of responding, is characterized by explicitly current-goal-incongruent, previous-goal-congruent, and apparently unintentional repetition of behavior. Scientists and clinical researchers have proposed that both "higher-order" prefrontal cortex-dependent processes (e.g. working memory, inhibitive control) and "lower order" processes (e.g. attention) play critical roles in subserving perseveration (Sandson & Albert, 1984). Habit, on the other hand, represents a more ingrained and automatic pattern of behavior which facilitates efficient functioning (Orbell & Verplanken, 2015), which may be considered to adaptive or maladaptive ends in a given context. Further, habitual behaviors result from the repeated pursuit of particular goals, such as following a particular procedure to get ready in the morning: Without the goal of getting out of the house, the habitual series of behaviors would not form. More generally, we can thus say that the development of a habit necessitates some binding between a response, at least one stimulus (potentially including contextual cues), and, crucially, an outcome (though once behavior enters the habitual stage, the outcome is no longer necessarily represented by the organism). Both constructs involve some level of automaticity and repetitive actions, and researchers have even posited that some perseverations may arise due to prior reinforcement, something considered fundamental to habit formation (Leicester et al., 1971). Inertia also plays a theoretically important role in both constructs as a signature of immutability – especially as perseverations become more frequent and habits get more deeply ingrained. However, the driving forces behind them, the manner in which they can manifest, as well as their functional implications, differ significantly. Habits are considered to involve repetitions that relate to the purpose around which the habit was constructed, while perseverations can involve any type of repetition (motor, semantic etc.) Habits involve automaticity in their implementation that implies rapid and inevitable response to stimulus, while perseverations, though also automatic, may be delayed in their expression (Sandson & Albert, 1984). Habits are typically cued in stable contexts, while perseverations do not have to be (Orbell & Verplanken, 2015). Finally, habits can be both task- and goal-congruent or incongruent, but perseverations are *always* incongruent with the individual's present goals.

To give a more concrete example, consider an individual who drives to a game arcade. There, she spends some time playing a car racing game where

she needs to use a steering wheel to guide the car. She realizes that the steering wheel is old and stiff, and actually needs to exert additional force when turning left to better execute the movement. Once she figures this out, she starts to win races. After playing her fill, she moves on to the next game. At the end of the evening, she gets back into her car and suddenly finds that on the first left turn she takes, she exerts far more force than necessary. This is an example of a perseverative behavior: additional force when turning left was previously optimal in the context of the arcade game but is not so in the context of driving on the road. The degree to which she may continue or cease to exert additional force when turning left may vary due to several factors. However, this repetition of a previously optimal behavior is distinct from the hangover that may result from habit, which is conceptualized as forming over the course of repeated experiences. This does not preclude behaviors attributable to habits from expressing themselves as perseveration, however. For example, consider instead that the individual in this example had a car with a faulty steering wheel that required finagling (e.g. cannot press down too forcefully) while driving. When she begins to play the racing arcade game, she may initially find herself pressing too lightly. This is *also* perseveration, though it is a perseveration due to a habit.

Through a careful examination of the distinctions between perseveration and habit, this chapter will seek to illuminate their respective neural and cognitive underpinnings, as well as their implications for learning, memory, and behavior. By synthesizing findings from various subfields of psychology, including cognitive, behavioral, and neuroscientific perspectives, we aim to provide a rich, multidimensional understanding of these constructs, enabling scholars and practitioners alike to appreciate their unique contributions to human cognition and behavior.

1.1 The distinction between perseveration and habit in timescales of expression.

Perseveration and habit operate across distinct timescales, both in the formation and in their expression. While habits are typically established over repeated experiences, this is not necessary for perseveration. The timescale of their expression also roughly corresponds to the potential adaptive and maladaptive instances of each. Perseveration typically arises on shorter timescales, from the order of seconds to minutes (and sometimes hours) and is always measured with respect to a specific situational demand (i.e. goal, task). Though perseveration cannot be identified in absence of a particular goal by definition, it can also manifest in remarkably diverse contexts and, in some cases of severe neurodegeneration, become almost ever present (Ell et al., 2010; Sombric & Torres-Oviedo, 2021). An individual with aphasia, for example, might verbally perseverate (i.e. repeat a previous utterance) anywhere they have the goal to communicate (Sandson & Albert, 1984). Similarly, an individual with a disorder affecting the basal ganglia, like parkinsons, might perseverate motor rules (i.e. making an action that is consistent with a previous goal/task) (Sandson & Albert, 1984). The goal-specific component of perseveration then makes the

timescale of its expression intuitive. Here, we are not concerned with goals with long temporal horizons (i.e. “I need to be a “healthy” person) but instead with specific and immediate goals (i.e. “I need to learn how to do this experiment properly” or “I need to communicate something to you.”). Thus, as individuals go about their day, their goals shift and subsequent perseverations typically either cease after some time or never manifest. Despite this, we can see how perseverations can bleed across contexts when the processes that are invoked during their expression support general or continually-reappearing goals, as in the previous example (drive appropriately).

Habit, on the other hand, is traditionally conceptualized as highly context-specific through the strengthening of stimulus-response associations, which persist across long spans of time. That is, once certain cues or triggers associated with the habit are present, the habit can be instantiated regardless of the last time the individual performed the habit. This is due to the specificity with which habits are developed: over longer timescales and tightly coupled with specific (verbal, motor, internal/thought) actions. This also means that habits arise on a timescale from seconds (immediately repeating the goal-associated actions) to years.

Put simply, we argue that perseverative behaviors are more general as they can occur across a range of goals/invoked processes whereas habits, often invoking the same processes and even goals, are more specific as they require certain initial conditions to be fulfilled. This specificity suggests that habits are more complex and could possibly be decomposed into repeated- or reinforced-action and value-guided components (Miller et al., 2018, 2019). There may still be overlap between the mechanisms that generate repeated action a la Thorndike’s law of exercise in both constructs, though these mechanisms may express themselves differentially.

2. Neurobiological underpinnings of perseveration and habit.

The neurobiology of perseveration and habit, though sharing some commonalities, exhibit critical differences as well. Understanding these distinctions provides clues as to the process-level distinctions between each phenomenon.

Perseveration has been primarily associated with dysfunction in or the development of the prefrontal cortex (PFC), particularly the orbitofrontal and dorsolateral regions (Milner, 1963; Stuss & Alexander, 2007). The PFC is critical for executive functions such as cognitive flexibility, decision-making, and response inhibition, which can play critical roles in perseveration, as it is traditionally conceptualized. Key putative cognitive processes therefore include working memory (Head et al., 2009; Stedron et al., 2005) inhibitory control (Head et al., 2009), and attention (Kirkham et al., 2003). Damage to the PFC or its connections to other brain areas, such as the basal ganglia and thalamus, can also lead to perseverative behaviors (Aron et al., 2004; Fuster, 1981). Indeed,

damage to basal ganglia regions themselves can lead to behaviors measured as perseveration (Sandson & Albert, 1984).

In contrast, habit formation is primarily linked to the basal ganglia, especially the striatum, which includes the caudate nucleus, putamen, and nucleus accumbens (Graybiel, 2008; Yin & Knowlton, 2006). The basal ganglia are involved in the gradual learning and reinforcement of habits through the modulation of cortico-striatal loops. Over time, the role of the PFC in controlling behavior diminishes, as habits become more automatic and are increasingly driven by the striatum (Doya, 2008).

Though both perseverative and habitual behaviors involve the PFC and basal ganglia, the neural processes and their interactions may differ. In perseveration, the diminished or developing ability to inhibit prepotent responses or shift cognitive sets can be attributed to dysfunctional or developing PFC-basal ganglia circuits (Ridderinkhof et al., 2014). This may lead to a failure or inability in suppressing the influence of the basal ganglia on behavior, resulting in repetitive, maladaptive responses. Inappropriate inhibition is also implicated in some theories of substance use disorder (Belin et al., 2013), of which some symptomatic behaviors are commonly associated with neural and cognitive substrates of habit-learning.

In habit formation, on the other hand, this transition from goal-directed to habitual behavior also involves a shift in the balance between the PFC and the striatum. Initially, goal-directed actions are mediated by the PFC and the associative (dorsomedial) striatum. As behavior becomes more habitual, the control gradually shifts toward the sensorimotor (dorsolateral) striatum (Yin et al., 2005). In this case, however, the influence of the basal ganglia on behavior, also resulting in relatively inflexible cue-response contingencies, is typically considered to be adaptive, reflecting a rational tradeoff of speed and accuracy (Keramati et al., 2011). Supporting this view, human studies of habit are typically more reliable when conducted under time pressure, resulting in habit-like 'slips of action' (Verhoeven & de Wit, 2018).

Taken together, these observations point to the possibility of a qualitative distinction between behaviors used to identify perseveration and those used to identify habits. Future work should examine whether behavioral expressions of insensitivity to outcome omission (perseverations) are necessarily co-extant with insensitivity to outcome degradation (habits); such finding would be an important step towards determining the distinct neural substrates supporting each behavior.

2.1 Neuropsychological evidence for perseverative behaviors arising from brain injury

The Wisconsin Card Sorting Task (WCST) is a widely used neuropsychological test that assesses cognitive flexibility, set-shifting, and the ability to adapt to changing environmental contingencies. Perseveration is a common phenomenon observed during the WCST, as participants may continue to sort cards based on

a previously relevant rule even after the rule has changed. Several studies have investigated perseveration in the WCST, with a particular focus on lesion patients and individuals with traumatic brain injuries (Ord et al., 2010). These studies provide insights into the neural basis of perseveration and its relationship to cognitive flexibility. Indeed, as we make more explicit later on, perseveration has been conceptualized as effectively the opposite of flexibility, cognitive or otherwise.

Milner (1963) conducted one of the earliest studies using the WCST in patients with prefrontal cortex lesions. Patients with lesions in the dorsolateral prefrontal cortex (DLPFC) exhibited significant difficulties in shifting between sorting rules and demonstrated perseverative errors. These findings suggested that the DLPFC plays a crucial role in cognitive flexibility, set-shifting, and inhibitory control. Patients with basal ganglia lesions, such as those with Parkinson's disease, have also been found to display perseverative behaviors on the WCST (Downes et al., 1989). These perseverative errors were attributed to impairments in the cortico-basal ganglia-thalamo-cortical loop, which is involved in the regulation of goal-directed behaviors and cognitive flexibility.

Perseveration in the WCST has also been observed in patients with lesions in other brain regions, such as the anterior cingulate cortex (ACC) and the orbitofrontal cortex (OFC) (Swainson et al., 2000). Patients with ACC lesions showed increased difficulty in adapting to changing rules and made more perseverative errors, suggesting a role for the ACC in error detection and cognitive control. In contrast, patients with OFC lesions exhibited more impulsive errors, reflecting a deficit in inhibitory control and outcome evaluation.

3. A taxonomy of perseverative behaviors

As we have seen, perseverative behaviors can be broadly observed across modality (semantic, perceptual, response), age/disorder, temporal profile, and other forms. We first taxonomize these subtypes, and then introduce a unifying perspective in which perseveration is as a computational concept, appearing across many neural circuits and cognitive processes due to its value as an adaptive affordance to a variety of constraints.

Content

1. Semantic perseveration: This type of perseveration is characterized by the repetitive production of semantically related words, phrases, or ideas, even when the context demands a shift in focus or topic. This form of perseveration is often observed in individuals with language or cognitive impairments, such as those with aphasia, and can also manifest in healthy individuals under conditions of high cognitive demand or stress.
2. Perceptual perseveration: Perceptual perseveration occurs when an individual persistently perceives or interprets stimuli based on prior experiences, despite the availability of new information that should modify their perception. This phenomenon can be observed in various perceptual

tasks, such as visual search or pattern recognition, where individuals may continue to perceive an object or pattern in a certain way even after receiving contradictory evidence.

3. Response perseveration: This subtype involves the repetitive execution of a specific motor or cognitive response (e.g. words), even when it is no longer appropriate or effective in the current context. Response perseveration is commonly observed in individuals with frontal lobe damage, as well as in certain developmental disorders, such as autism spectrum disorder. In these cases, individuals may have difficulty inhibiting previously learned responses or adapting to changes in environmental demands.

Disorder

4. As highlighted in the previous sub-section, pathology can often play a causal role in how perseveration manifests. These pathologies or injuries lead to reduced information transmission or retention capacities in the participant (e.g. are associated with lower working memory capacity or reduced fidelity of recall), the severity of which corresponds to the frequency and temporal duration of perseverative behaviors.

Temporal Profile

5. A seminal paper by Sandson and Albert highlighted three different temporal profiles of perseveration: stuck-in-set, recurrent, and continuous perseveration (Sandson & Albert, 1984). Stuck-in-set perseveration refers to when individuals deploy previously appropriate rules. For example, a child that focuses on a previously rewarding but now not rewarding stimulus behavior to guide choice behavior, or a patient when previously drawing a human face, began to incorporate human features onto the current drawing of a cat (Sandson & Albert, 1984). Recurrent perseveration is defined as the repetition of responses: from saying the same word twice in a row during free recall, to repeating the same word over a larger temporal lag (Fischer-Baum et al., 2016). Finally, continuous perseveration, the most “extreme” is typically only present in pathological cases: the unbroken repetition of some action (e.g. drawing increasingly numerous petals of a flower; (Sandson & Albert, 1984).

Others

6. Other forms of perseveration: Beyond the primary types mentioned above, perseveration can also manifest in other forms, such as affective perseveration (the persistent experience of an emotion despite changes in context), and thought perseveration (the repetitive occurrence of a particular thought or cognitive schema, which can be observed in clinical conditions like obsessive-compulsive disorder). An open question is whether such forms are also expressed as habits.

Interestingly, much of the literature studying the neurobiology and pathology of perseveration appears to be capped at the semantic. That is, the

content of perseveration spans from lower-order (motor) to higher-order (semantic). We propose that there is a heretofore-underexplored dimension of higher order perseveration: the computational. We define computational perseveration as the (partial) reuse of recently performed (complex) mental calculations. Our recent work (Banavar & Bornstein, 2023) empirically explores this idea in experiments that typically require some sort of computation. Specifically, we consider standard behavioral economics experiments aimed at characterizing how individuals behave under different types of uncertainty. These experiments typically deploy a randomized task design: previous choice options seen and choices made have no influence on the current choice option presented and critically should have no bearing on the current decision. This type of experiment can be contrasted with other experiments that have inbuilt trial-trial dependencies, like those that explicitly involve learning. To make their choice on each trial, subjects may behave normatively (e.g. calculate Expected Value) or perform some sort of heuristic-driven comparison between the [numerical] options presented on a screen. Importantly, these are experiments that do not provide feedback (i.e. only one trial's outcome at the end of the experiment is realized.) We demonstrated that, across three qualitatively different types of uncertainty, young adults with no known impairments do indeed demonstrate trial-trial sensitivities. These sensitivities manifest in a range of manners, for example, if successive choices are similar enough, individuals from an effort-minimizing perspective are incentivized to redeploy the same computations. Theories of intertemporal choice suggest that choice can be guided by simulating the future, and that the product of these simulations would be represented with greater uncertainty the further out in time they are. When the individuals in our sample make decisions under immediate uncertainty (i.e. choosing between lotteries vs. fixed amounts), we find that relative decision difficulty (is the current decision harder or easier than the previous?) plays a critical role. This suggests that these types of choices are resource intensive and that computational redundancy could be avoided by reusing previous simulations, or more generally assessing the present relative to the past. This type of behavior is deemed perseverative as it is task-incongruent. While we demonstrate such perseveration in randomized experiments, there is no reason to believe that it should not be present even in experiments with explicit sequential dependencies (e.g. bandit problems). Indeed, "choice stickiness" is often modeled as an effect of no interest in such tasks (Lau & Glimcher, 2005).

By examining a type of behavioral perseveration that is demonstrated to exist in healthy young adults already, we argue that computational perseveration presents a fine grained opportunity to see how the systems supporting both computations (heavily PFC dependent) and perseveration (also PFC dependent, but traditionally different regions) may degrade over age.

4. Perseveration in cognitive aging and age-related cognitive decline

Perseverative behaviors can manifest differently across various stages of development and normal cognitive aging and age-related cognitive decline (Noh et al., 10/2023; Sombric & Torres-Oviedo, 2021). As a result, several studies have examined how different types of perseverative behaviors differ over time, providing insights into the underlying cognitive and neural mechanisms. Interestingly, perseverative errors in “healthy aging” tend to follow a U shaped trajectory across the lifespan: initially present in early childhood (as early as 8 months old; (Carroll et al., 2016), stabilizing to a minimal level over young adulthood, to finally presenting again in older adults. We note that perseveration in young children is one of the rare instances in extant literature where it can be considered to be a sign of growth: in some experiments children of very young ages (5 month old, 2 years old) demonstrated random responding, slightly older children perseverated (8 month old, 3 years old), and even older children overcame perseveration (12 months old, 4 years old) (Carroll et al., 2016). Thus, perseveration here demonstrates the ability to maintain some previously task-optimal or relevant information: be it as simple as grasping in the previously correct direction (recurrent perseveration) or as complicated as learning a rule (stuck in set perseveration).

While much literature examining the notion of perseveration talks about the fundamental, yet putative, role of working memory, the fact that such young infants demonstrate perseverative behaviors casts doubt on both the necessity and sufficiency of working memory but perhaps not its constituents. As perseveration manifests differently due to task demands, the differential recruitment of cognitive processes is but natural. The two processes that seem to be present – barring some rudimentary memory function – across all known types of perseveration are a) focused attention (i.e. the individual is drawing on *specific* previously task-relevant information) and b) impaired inhibition (i.e. the individual is unable to suppress or resolve the conflict involving said previously relevant information, though researchers have argued that this impaired inhibition is via working memory; (Head et al., 2009). This is an oversimplification as there are many other mechanistic explanations for perseveration. Another key distinction between perseveration in early development and that present as a function of pathology is that there are several instances of adults verbalizing their intention to perform a task congruent action but actually performing the previously congruent action (Sandson & Albert, 1984). On the contrary, researchers showed that 6 year olds (whose working memory capacity is still developing but substantially better than at infancy) who successfully switched had stronger working memory representations than those that perseverated (Cepeda & Munakata, 2007). That is, the researchers have demonstrated evidence suggesting that faulty inhibition is not in itself enough to elicit perseveration; working memory also plays a critical role.

Agnostic on the development of working memory, there is significant evidence for these more “complex” (requiring learning and accessible internal representation) stuck in set and/or recurrent perseveration in children as young

as 8 months old (reaching errors), perhaps most famously demonstrated in Piaget's A-not-B task (Piaget, 2013). In this task, infants had two options: to grasp to the left or to the right. On trial 1, an attractive object was placed on the left hand side, and therefore the reward-motivated infant should (and does) make a grasping notion to the left. However, on subsequent trials when the attractive object is now placed on the right, infants still continue to grasp to the left. In their review paper, Carroll et al argue that much of the putatively perseverative behavior observed in children is a function of task design and choice availability (Carroll et al., 2016). Indeed, young children cease to perseverate when they are presented with an increased number of choices. Further, they do not tend to perseverate indiscriminately, typically when faced with previously task-relevant distracting information. This showcases that even at a very young age, perseveration is not only present, but likely manifests as a function of neurobiological development, and is also very sensitive to context.

Normal cognitive aging is associated with certain declines in cognitive functions, such as processing speed, working memory, and executive functioning (Salthouse, 2009). These declines can lead to an increase in perseverative behaviors, particularly in tasks that require cognitive flexibility and inhibitory control (Andrés et al., 2008; Hasher & Zacks, 1988). For example, older adults may exhibit increased difficulty in switching between tasks or inhibiting irrelevant information, which can result in perseveration (May et al., 1999). Further, older adults without impairments are demonstrated to show more response (recurrent) perseveration than their younger counterparts (Foldi et al., 2003). Finally, recent work has shown that individuals in the most severe stages of Alzheimer's tend to respond randomly (Westfall & Lee, 2021).

In summary, the literature suggests that different types of perseverative behaviors can change with normal development and cognitive aging and age-related cognitive decline. While both development and normal cognitive aging may lead to a general increase in perseveration, due to the establishment of / declines in cognitive flexibility and inhibitory control respectively, age-related cognitive decline can result in more pronounced and diverse perseverative behaviors, reflecting the deterioration of various cognitive domains and neural systems.

5. Relationship of perseveration to theoretical frameworks of habit

"Plasticity, then, in the wide sense of the word, means the possession of a structure weak enough to yield to an influence, but strong enough not to yield all at once. Each relatively stable phase of equilibrium in such a structure is marked by what we may call a new set of habits." ~ William James (1890)

Recent computational frameworks have formalized the idea that habits and perseveration are distinct manifestations of plasticity. Value-free habits, as proposed by Miller, Shenhav, and Ludvig (Miller et al., 2019), share similarities with perseveration in that they both involve the repetition of actions. However, while value-free habits arise from the mere repetition of actions in stable contexts, perseveration is characterized by the persistent repetition of a behavior, thought, or emotion, despite changes in context or negative consequences (Dajani & Uddin, 2015).

Gershman (Gershman, 2020) offers a complementary perspective that can be related to the concept of value-free habits, proposing that perseveration can be seen as a consequence of a trade-off between reward and complexity, with the brain minimizing the complexity of the internal model used for decision-making. In this framework, the brain favors simple, low-complexity models that reduce cognitive demands, even at the expense of potential rewards. When the environment changes, the brain may be slow to update its internal model, leading to perseveration as a result of this inertia.

This perspective aligns with the value-free habits hypothesis in that both emphasize the role of the brain's propensity to minimize cognitive demands by forming reliable stimulus-response associations. In the case of value-free habits, this propensity leads to the formation of habits based on action repetition and context stability, rather than reinforcement or outcome value. In Gershman's view of perseveration, the brain's preference for low-complexity policies contributes to the persistence of repetitive behaviors, even when they may no longer be appropriate or rewarding. These behaviors are, however, still *rational*, in the sense that they minimize the metabolic cost of cognition in support of action, at minimal detriment to long-run rewards.

Thus, both value-free habits and Gershman's account of perseveration highlight the importance of the brain's drive to minimize cognitive demands and efficiently process information, which can manifest in the formation of habits and/or perseverative behaviors. Gu and colleagues (2017) investigated the neural network dynamics underlying habit formation and emphasized the role of efficient metabolic activity control in this process. They found that during habit learning, the brain's large-scale networks transition between different network states, and the activation required for these transitions decreases as habits form.

In light of these findings, one could hypothesize a continuum linking habits and perseveration based on the activation required for transitioning between network states. At one end of the continuum, efficient habit learning is characterized by a low threshold for network state transitions, reflecting the formation of specialized and modular neural circuits that enable efficient cognitive processing and automatic behavioral control.

At the other end of the continuum, perseveration, as described by Gershman (2020), might be associated with higher demands on the activation needed to transition between network states. This could result from the brain's preference for low-complexity models to reduce cognitive and representational

demands, leading to the persistence of repetitive behaviors even when they are no longer adaptive. The increased metabolic requirements for network state transitions in this case could reflect the brain's resistance to updating its internal model when the context changes, ultimately leading to perseveration.

While this hypothetical continuum is based on the metabolic requirements for network state transitions, it aligns with the common theme in Gershman's work on perseveration and Gu et al.'s work on habit learning, which is the brain's inclination to optimize cognitive processing. This optimization can manifest in both adaptive (habit learning) and maladaptive (perseveration) behaviors, specific to the context of optimizing repetitive behaviors, depending on the underlying mechanisms and energy efficiency involved in controlling network dynamics.

Cognitive and Computational mechanisms of adaptive, higher-order perseveration

As described above, the potential adaptiveness of perseveration arises from the brain's preference for cognitive efficiency, which can be achieved through the simplification of complex internal models or by relying on previously learned patterns (Gershman, 2020). In this section, we explore possible mechanisms of higher-order perseveration, focusing on cognitive and computational aspects.

Policy Compression

Lai, Huang, and Gershman (2022) explore how various forms of complex repetitive behaviors may arise from policy compression, which posits that the brain compresses complex policies into simpler representations to reduce cognitive demands. This simplification allows for more efficient decision-making but can lead to suboptimal choices or perseverative behaviors when the environment changes. Policy compression can be viewed as an adaptive mechanism that enables efficient cognitive processing at the expense of potential rewards.

Amortization

Dasgupta and Gershman (2021) proposed that *amortization*, the reuse of previously computed information to reduce the cognitive cost of future computations, can underlie some apparently perseverative behaviors. Amortization can be adaptive, as it allows for more efficient cognitive processing by leveraging prior knowledge. However, it can also lead to perseverative behaviors when the environment changes, as the brain may rely on outdated information. This mechanism highlights the tension between cognitive efficiency and adaptiveness, suggesting that perseveration may arise as a byproduct of the brain's attempt to optimize cognitive resources.

5.1 Working memory maintenance from long-term memory

Hoskin and colleagues (2019) explored the role of working memory refreshes from episodic memory in the context of perseveration. According to their work, the brain periodically refreshes working memory representations by accessing related episodic memory traces. This process can be adaptive, as it allows for the maintenance of relevant information in working memory (Ritter et al., 2018) and in selecting proper contexts for cognitive control (Egner, 2023). However, inappropriate selection of past episodic information can also result in perseveration, as the brain may retrieve and reinforce outdated or irrelevant memory traces, leading to the persistence of maladaptive behaviors or thoughts.

5.2 Age-related perseveration as an adaptive response to declining information processing capacity.

Age-related increases in perseverative behaviors can also be understood within this framework. According to this perspective, the brain prefers simple, low-complexity models to minimize cognitive demands, even at the expense of potential rewards. This predisposition towards simplicity can lead to the persistence of repetitive behaviors, as the brain may be slow to update its internal model when the environment changes, resulting in perseveration.

As individuals age, cognitive and neural changes occur that can influence this trade-off between reward and policy complexity. Normal cognitive aging is associated with declines in processing speed, working memory, and executive functioning (Salthouse, 2009). These declines can lead to a reduced capacity for neural information processing and representational capacity, which in turn may cause the brain to rely more heavily on simpler models to manage cognitive demands efficiently.

In the context of age-related cognitive decline, such as mild cognitive impairment (MCI) or Alzheimer's disease (AD), the trade-off between reward and policy complexity becomes even more pronounced. The deterioration of various cognitive domains and neural systems (e.g., prefrontal cortex and basal ganglia) can further constrain the brain's ability to process and represent complex information (Stuss & Alexander, 2007). As a result, the brain may prioritize low-complexity models to maintain cognitive functioning, leading to an increased propensity for perseverative behaviors.

Older adults' tendency to block their learning in multi-option choice tasks can be viewed as one manifestation of adaptive perseveration. This behavior may emerge as a strategy to make maximal use of reduced cognitive processing resources while preserving overall learning capacity. As individuals age, cognitive changes occur, such as declines in processing speed, working memory, and executive functioning (Salthouse, 2009). These changes can impose constraints on the brain's ability to process complex information efficiently.

By blocking learning in multi-option choice tasks, older adults may simplify the decision-making process and reduce the cognitive demands associated with processing multiple options simultaneously (Noh et al., 2023). This strategy can be viewed as a form of perseveration because it involves the persistent

engagement with a single option or a subset of options, even when other options may be available or more advantageous. However, in the context of reduced cognitive resources, this form of perseveration may be adaptive, as it enables older adults to maintain overall learning capacity by focusing their limited cognitive resources on a smaller set of options.

Moreover, this adaptive perseveration can also be seen as a manifestation of the trade-off between reward and policy complexity introduced by Gershman (2020). In the face of age-related cognitive decline, the brain may prioritize low-complexity models to preserve cognitive functioning, leading to an increased propensity for perseverative behaviors. By selectively attending to a smaller set of options, older adults can effectively reduce policy complexity, thereby optimizing the use of their cognitive resources.

6. Perseveration in practice

The expansive treatment of perseveration illustrated to this point in the chapter suggests a refinement to contemporary practices for identifying perseverative behaviors within a single experimental task. Usually, in computational reinforcement learning-inspired studies of serial or sequential choice, perseveration is typically treated as a nuisance variable to be modeled out or controlled for, in order to identify behavioral and neural signatures of task-specific value-guided habits (which, in this literature, tends to be defined according to their sensitivity to consistent reinforcement, as originally given by the law of effect). This takes the form of, e.g., simultaneous logistic regression specifying the influence on action of previous actions alongside previous action-contingent reinforcements (Corrado et al., 2005; Lau & Glimcher, 2005), or as a 1-back action-dependent shift term in a logistic choice rule (Daw et al., 2006). This operationalization of perseveration only accounts for repeated motor responding, while, as we have shown, other more high-level forms of adaptation may be instrumental - e.g. amortization of complex computations. Accounting for these multiple levels of perseveration requires identifying which task-specific variables may yield adaptive affordances in the form of computational repetition (Dasgupta et al., 2018). As a result, modeling their influence on a trial-by-trial basis requires accounting for the relative similarity of successive trials along task-relevant dimensions (Banavar & Bornstein, 2023) - and, perhaps, task-irrelevant ones as well (Bornstein et al., 2017). We therefore suggest that the decision-making field adopt the more flexible conceptions of trial-trial dependencies more commonly seen in other areas of study, e.g., working memory (Kiyonaga et al., 2017) and attention (Fischer & Whitney, 2014). We have above described how this approach can reveal systematic influences on the estimation of key decision parameters in standard decision profiling instruments, where, because no trial-wise reinforcement is provided, value-guided habits are unlikely to obtain. However, near-identical decision problems are routinely used in laboratory experiments where trial-by-trial feedback is provided to the participant (Brooks & Sokol-Hessner, 2020; Mei et al., 2023), especially in

situations where the interaction of learning and decision processes are the main object of study (Erev et al., 2008; Spektor et al., 2019). Future work should systematically examine the degree to which estimates of value-guided habits in these situations are confounded by the presence of computational perseveration.

6.1 Potential implications of a computational account of perseveration for substance use disorder.

We close with an examination of some of the potential ramifications for computational perseveration on interpretations of the decision-making literature, in particular the illustrative domain of substance use disorders.

Perseverative, rather than habitual, behaviors in substance use disorder

The conception of perseveration as a computationally adaptive phenomenon with cognitive underpinnings may offer novel insights and directions of investigation for behaviors that have traditionally been characterized as maladaptive habits, such as in the context of substance use disorder. By reinterpreting certain aspects of addiction through the lens of perseveration, researchers may be better equipped to understand the complex interplay between cognitive, computational, and neural mechanisms underlying these behaviors.

Substance use disorder is often characterized by compulsive drug-seeking and drug-taking behaviors, which can persist despite negative consequences and declining hedonic rewards (Everitt & Robbins, 2005). These behaviors share some similarities with perseveration, as they both involve the persistent repetition of behaviors that may no longer be adaptive or rewarding.

One possible direction for investigation could be to explore the long timescales involved in several aspects of SUD outside of the lab, especially in the phenomenon of relapse after long periods of abstinence (Bornstein & Pickard, 2020; Hogarth, 2020), versus the more immediate cycling observed in "binges" or repeated use of drugs despite declining hedonic rewards. These may be indicative of reinstatement of "inappropriate" control contexts from long-term memory (Bornstein & Pickard, 2020; Egner, 2023). Recent research has highlighted the importance of temporal dynamics in understanding the development and maintenance of compulsive behaviors (Robbins et al., 2019). By examining the timescales of repeated drug use with respect to computational perseveration, researchers may be able to uncover potential computational similarities that can inform the development of more targeted interventions for substance use disorder.

Furthermore, the idea of perseveration as a computationally adaptive phenomenon may help explain why certain individuals are more susceptible to developing substance use disorders. For example, individuals with a predisposition towards perseverative behaviors might be more likely to engage in the compulsive aspects of drug use due to an underlying cognitive bias towards maintaining low-complexity models, as proposed by Gershman (2020). However the same neural and cognitive factors that give rise to this predisposition to

perseveration may not, *on their own*, predispose the same individuals to developing habits of long-term use - though they could provide opportunity for such habits to develop (Robbins et al., 2012). Indeed, the very existence of long-term habits may mitigate the possibility of producing policy-complexity-reducing perseverations, since the presence of habits already simplifies the policy. This perspective could provide a more nuanced understanding of the cognitive vulnerabilities associated with the development and maintenance of substance use disorders, and perhaps explain confounding results in experiments that seek to identify trait-level markers of a putative individual tendency substance use disorder.

7. Habit and perseveration: Endpoints of the continuum of plasticity.

In sum, we have offered an examination of perseveration with the goal of both complexifying it and also refining its experimental measurement as distinct from habit. In this treatment we have identified many commonalities between perseveration and habit: Both can be understood as trade-offs between simplicity and optimization under resource constraints (temporal and computational), and both can be viewed as suboptimal depending on the degree to which context-sensitivity is a necessary feature of the external demands of the task. In terms of timescale of formation and expression, perseveration can be said to differ from habit largely in a matter of degree; the main categorical difference being that habits can re-emerge after long periods of expressive dormancy. What, then, truly distinguishes perseveration from habit, in the domains where it matters for the contemporary study of value-based learning and decision-making, is in the timescale of goal to which these behaviors can be considered adaptive. One way of summarizing the current scientific treatment of value-guided habits is as “the process whereby the contingent becomes essential” (Malabou, 2022) – behaviors which had been the result of volitional choice are now instead compulsive. In this view, perhaps the strongest distinction between habit and perseveration can be to understand the latter as an ephemeral, but adaptive, response to *inessential* contingency. That is, perseverative behaviors arise when aspects of the environment exhibit sufficient regularity as to make fine-grained adjustment unimportant. As a result, they may free up attentional and effort resources, affording the agent the computational capacity to identify, and act upon, distinctions that have more extended or emphatic consequences. A key contribution of this view of perseveration is that, despite largely being understood as a maladaptive by-product of neural injury or mental illness, perseverative behaviors may instead be better understood as a rational affordance, not just to capacities limited by injury but to demands arising from the dynamic interplay of inconsistency and regularity in everyday life.

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