



The Role of Biological Significance in Human Learning and Memory

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Deeply rooted within the history of experimental psychology is the search for general laws of learning that hold across tasks and species. Central to this enterprise has been the notion of equipotentiality, that any 2 events have the same likelihood of being associated with one another as any other pair of events. Much work, generally summarized as *biological constraints on learning*, has challenged this view and demonstrates pre-existing relations between cues and outcomes, based on genes and prior experience, that influence potential associability. Learning theorists and comparative psychologists have thus recognized the need to consider how the evolutionary history as well as prior experience of the organism being studied influences its ability to learn about and navigate its environment. We suggest that current models of human memory, and human memory research in general, lack sufficient consideration of how human evolution has shaped human memory systems. We review several findings that suggest the human memory system preferentially processes information relevant to biological fitness. We suggest a simple computational amendment to existing models of learning and memory that would expand their explanatory power and discuss potential theoretical and applied benefits (and costs) afforded by adopting this functionalist perspective.

Keywords: adaptive memory, equipotentiality, learning, memory

The early days of the behaviorist tradition relied heavily on the notion of equipotentiality of stimuli. It was assumed that any two events (e.g., cue-outcome or response-outcome) had equal potential to be associated with each other, so long as they were paired in a contiguous fashion. This reasoning was one basis for theorists having little concern with respect to the species and stimuli they used to study learning. One of the first challenges to this idea, although it was not necessarily interpreted as such at the time, was Thorndike's (1911) concept of *belongingness*. In describing his renowned puzzle box experiments, he noted how there appeared to be certain responses that belonged in certain situational contexts that could be easily reinforced (e.g., pulling a chain to escape the box), while other responses that did not belong in that situational context could not be easily reinforced (e.g., grooming to escape). This finding was put aside for a half century until Breland and Breland (1961) reported their inability to effectively train nonconventional animals like pigs and raccoons on select tasks. Despite some of their animals learning to perform a task following a sequence of reinforcement, species-specific behaviors related to the motivational system engaged by the reinforcer would often drift back into the animal's repertoire, thus preventing the animal from performing the desired response and

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obtaining reinforcement. For example, by reinforcement-mediated response shaping, a pig could be taught to deposit a wooden coin into a piggy bank. Eventually, what would often occur was that the pig would begin to root the coin, so much so that these behaviors would prevent the animal from depositing the coin and obtaining reinforcement. These findings, especially coming from students of Skinner, were especially difficult to understand from a pure reinforcement perspective of behavior. Another instance of the inadequacy of the contiguous reinforcement view of learning first appeared in a highly controversial publication by Garcia and his colleagues in which they reported evidence for long-delay conditioned taste aversion. A saccharin solution was followed by nausea that was induced via radiation hours later, which produced effective aversion to the saccharin on a later test trial (Garcia, Kimeldorf, & Koelling, 1955). That learning of this magnitude could occur following a single trial with such a large temporal interval between CS and US presentation strongly challenged conventional wisdom that close temporal contiguity with reinforcement was necessary and sufficient for learning to occur.

Discovery of Selective Associations

The biggest blow to the equipotentiality assumption and general process learning models came about a decade later from Garcia's classic bright-noisy water experiment (Garcia & Koelling, 1966). Rats drank a sweetened solution from a water bottle that also elicited light and noise when licked. Thus, all rats experienced the bright-noisy and sweet water, but, for some rats, this water was paired with tactile pain (via foot shock); for other rats, it was paired with gastric malaise (via radiation). Using this double-dissociation design, Garcia and Koelling showed that rats were better able to associate the audio-visual cues with tactile pain than they were with illness. Conversely, the sweetness was more readily associated with illness than with tactile pain. Animals that rely more heavily on visual systems for feeding, like pigeons and quail, show equivalent ecologically-appropriate effects and more readily associate visual cues with post-ingestive consequences and auditory cues with tactile pain (Foree & LoLordo, 1973; Wilcoxon, Dragoin, & Kral, 1971). This suggests that the specific species being studied is also important in determining the ability to condition a behavior. Despite initial resistance, the notion of selective associations was adopted, and it fueled more wide-spread investigations of biological constraints on learning (Bolles, 1993; Domjan, 2015). A number of influential publications followed (Bolles, 1970; Rozin & Kalat, 1971; Seligman, 1970; Shettleworth, 1972), and such proponents of biological constraints would remain a thorn in the side of learning theorists' attempts to formulate future general process learning models (e.g., Rescorla & Wagner, 1972). For instance, the well-established effects of cue competition, such as overshadowing and blocking, are often attenuated when using biologically significant cues (Blaisdell, Denniston, Savastano, & Miller, 2000; Denniston, Miller, & Matute, 1996; Miller & Matute, 1996; Oberling, Bristol, Matute, & Miller, 2000). In his 2005 piece for the *Annual Review of Psychology*, Domjan (2005) did well to summarize contemporary understanding concerning biological constraints on learning:

[L]earning with ecologically relevant stimuli often proceeds differently from learning with arbitrary cues [...]. These [...] suggest that efforts to understand how

Pavlovian conditioning occurs in the natural environment have to consider the role of pre-existing relations between CSs [Conditioned Stimuli] and USs [Unconditioned Stimuli]. p.186.

Findings of selective associations have also been extensively studied in fear conditioning situations with humans. Öhman and Mineka (2001) proposed an evolved fear module that underlies the preferential acquisition and persistence of some phobias over others. For instance, pictures of snakes and spiders that signal an aversive outcome (shock) are learned more rapidly and are more resistant to extinction compared to pictures of flowers and mushrooms paired with that same aversive outcome, as measured by electrodermal skin conductance response (Öhman, Eriksson, & Olofsson, 1975; Öhman, Fredrikson, Hugdahl, & Rimmö, 1976; Öhman & Mineka, 2001). Similarly, angry faces paired with shock are more resistant to extinction than happy faces paired with shock (Öhman & Dimberg, 1978), though cultural differences in emotional perception may influence these effects (for a review, see Mallan, Lipp, & Cochrane, 2013). While evidence of greater resistance to extinction for more biologically relevant cues paired with shock has been taken as evidence of some sort of preparedness in humans, a recent meta-analysis has questioned the replicability of this effect (Åhs et al., 2018). Future studies with larger sample sizes will be needed to further understand the extent to which preparedness in humans can be observed using this basic procedure, as many of the original studies were not conducted using methodologically sound practices (e.g., in which sample size is informed by power analysis). Nevertheless, an argument can be made that images being paired with shock in a laboratory setting is a highly artificial occurrence, and evidence (reviewed below) of evolutionary influences on memory, as opposed to Pavlovian conditioning, are quite strong and well-replicated (Nairne & Pandeirada, 2016; for meta-analyses, see Scofield, Buchanan, & Kostic, 2018, and Tay, Jonason, Li, & Cheng, 2018).

Ecological Approaches to Learning

Also influential in the debates on biological constraints on learning during the 1970s was the recognition (in the form of a Nobel Prize) of European ecologists Niko Tinbergen, Karl von Frisch, and Konrad Lorenz for their efforts in describing animal behavior by observing the animals in their natural, or at least quasi-natural, environments. A central theme from their work was the view that learning serves the function of integrating an animal with its environment. This was in stark contrast with the strictly laboratory-based approach of most American psychologists, which largely ignored functional considerations of learning and behavior (save Skinner, 1953, and his followers). One of the most successful attempts to combine an ecological approach with general learning systems was William Timberlake's *Behavior Systems Approach* (Timberlake, 1993, 1994; Timberlake & Lucas, 1989). Central to this approach is the assumption that behaviors are organized into functional hierarchal systems. These systems dictate not only the temporal relationship between behaviors but also, depending on the motivational system that has been activated by the US, the dyadic associability of the specific cue and outcome and the form of the conditioned response in relation to the CS (Timberlake, 2001). The behavior systems approach has

offered much insight into a number of complex behaviors like eating, defense, play, and sexual behaviors (Akins, 2000; Domjan, 1994; Domjan & Gutiérrez, 2019; Domjan, Lyons, North, & Bruell, 1986; Fanselow, 1994; Pellis, Pellis, Pelletier, & Leca, 2019; Timberlake, 1993).

In sum, many investigators have argued that biological constraints on learning represent a serious challenge to the conventional general process learning models (e.g., Bolles, 1970; Domjan, 2005, 2008; Öhman & Mineka, 2001; Seligman, 1970; Shettleworth, 1972; Timberlake, 2001). Seemingly, there is too much environmental input for animals to come into the world as pure empiricists (Bolles, 1988). Instead, animals appear sensitive to the biological significance of a learning event, and, at the very least, pre-existing relations between CSs and USs appear to affect learning (Domjan & Krause, 2017). Despite decades of debate, empirical phenomena such as selective associations and species-specific responses are well established, and it is now commonplace for introductory learning texts and introductory courses to discuss biological constraints on learning in some detail (Domjan, 2014; Dugatkin, 2008; Nasser & Delamater, 2016; Olson & Hergenhahn, 2013).

The Challenge to Equipotentiality in Models of Human Memory

Surprisingly, in learning's sister discipline, the study of memory, such biological constraints are rarely discussed, and general process models of memory continue to dominate the field. Take for instance the older but most common memory models one might find in an introduction to memory textbook (e.g., Multi-Store [Atkinson & Shiffrin, 1968], Parallel Distributed Processing [Rumelhart & McClelland, 1986], Levels of Processing [Craik & Lockhart, 1972], Working Memory Model [Baddeley, 1992]). The first process that occurs in all of these models is that *information* or *input* enters the memory system. That information may then travel through different *pathways* and, according to the model in question, that subsequent pathway will determine the memorability of the input. What these commonly cited models imply, at least initially, is that all information is inherently neutral to an organism and has equal potential in being remembered. Absent from these models is consideration that certain stimuli and/or events may be preferentially remembered due to evolutionary biases of the human memory system. In the following section, we review a number of recent findings that support the notion that there exist systematic biases in how well different kinds of information are remembered.

Another omission of these older but still influential models is that, while they well describe how information is processed and stored, they provide little ability to make predictions about whether a given event will be strongly or poorly remembered, based specifically on a description of what that event is. Differences in functional associations between events X and Y can be explained by such models, but these explanations often appear circular. For instance, if X was better remembered than Y, it was because X yielded more rehearsal (multi-store model) or perhaps it was more semantically encoded (levels of processing). While general process learning models (e.g., Rescorla & Wagner, 1972) have their own struggles (see Miller, Barnet, & Grahame, 1995), certainly a strength is their ability to predict the extent to which

learning will occur on any given trial. For instance, consider two identical events that differ only in the saliency of the CS. A clear prediction is made about which event will be better learned about (the one with the more salient CS), and the behavioral data, more often than not, confirm these predictions. Finally, while learning models struggle with selective associations, the architecture to accommodate such could be added in principle, either by adjusting the learning rate parameter assigned to the CS (e.g., α in the Rescorla-Wagner model), the learning rate parameter to the US (e.g., β in the Rescorla-Wagner model), or by adding a new term that accounts for a pre-existing relationship between the CS and US. In fact, a parameter, say omega (Ω), that quantifies some sort of belongingness between the CS and the US or that captures the perceived fitness relevance of an event would add much predictive power to many models of learning and memory. Figure 1 describes such a parameter, whereby the perceived fitness relevance of event is linearly related to the likelihood of its being learned about and remembered. Most, if not all, of the empirical phenomena described in the following section could be captured and understood by the addition of such a parameter that scales the storage and/or retrieval strength of incoming information based on its perceived fitness value. Thus, the function of the omega scaling factor would not be to replace existing models of learning and memory but instead to scale their products by the omega value to reflect the influence of perceived biological significance on learning and memory (e.g., $\Omega \times [\text{computational learning/memory model}]$). As such, this amendment is purely for computational purposes and makes no current inferences as to whether the biological significance of an event specifically influences encoding, storage, or retrieval. On the negative side, such an addition to existing computational models is that it introduces a large number of new parameters, that is, a new omega value for each possible cue-outcome dyad.

While the present focus has been on the older foundational models of memory, some of the more contemporary models have refined this assumption of equipotentiality, although their explanatory scopes tend to be narrower. For instance, the Glutamate Amplifies Noradrenergic Effects (GANE) model predicts enhanced attention and memory for stimuli encoded during arousing situations through the mediation of norepinephrine (Mather, Clewett, Sakaki, & Harley, 2016). Thus, the model clearly predicts that information encoded during arousing contexts will be preferentially remembered. The New Theory of Disuse nicely captures and describes the difference between storage and retrieval strength and predicts that items or events with higher retrieval strength are more likely to be remembered (Bjork & Bjork, 1992). Nevertheless, the model does not speak to potential biases in the memory system to preferentially remember some types of items/events, in particular, those relevant to evolutionary fitness. Recently, Talmi, Lohnas, and Daw (2019) proposed an Emotional Context Maintenance and Retrieval model (eCMR) that posits additional attention to high-value information that binds that information more tightly with its encoding context. This makes retrieval of those items easier in the initial context but also hinders those items from being linked to a novel context later on (Madan, Fujiwara, Gerson, & Caplan, 2012). Of course, how items are given value in these studies is often no more than ordinal (e.g., placing a number from 1-10 above a to-be-remembered word to indicate its reward value), and relatively little consideration is given to an ecological understanding of value.

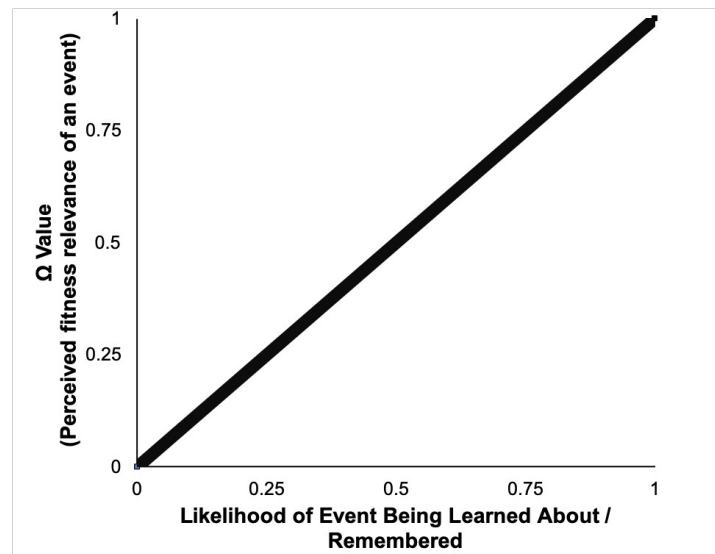


Figure 1. A graphical representation of the relationship between our hypothesized omega scaling factor and the memorability of information. The omega value is a quantification of the perceived biological significance of an event, which can then be used to scale the extent to which information has been learned about or remembered using any number of models of learning and/or memory.

Empirical Support for Selective Human Memory

The first challenge to the implicit assumption of equipotentiality in the study of human memory is a finding by Nairne, Thompson, and Pandeirada (2007) that items rated based on their relevancy to a survival-related task were much better recalled than those same items rated for their relevancy to a nonsurvival related task (moving to a foreign land). Specifically, participants were asked to imagine that they were stranded in the grasslands of a foreign land and complete various tasks related to survival (e.g., finding food and shelter). They then rated neutral concrete nouns based on their relevancy to this hypothetical situation. When these participants were subsequently given a surprise recall task of the nouns, their mnemonic performance outperformed other participants who rated those same items based on their relevancy to an imagined moving scenario in which one has simply moved to a foreign land and must complete moving-related goals (e.g., finding a home, transporting belongings) or those same words rated based on how pleasant participants perceived them to be (Figure 2). This so called *survival processing effect* has been well replicated (for recent meta-analyses, see Scofield et al., 2018; Tay et al., 2018) and results in even better recall performance than other processing tasks known to improve memory such as imagery, self-reference, generation, or simply intentional learning (Nairne & Pandeirada, 2008). Just as selective associations have been documented in one-day old rat pups (Gemberling & Domjan, 1982), the survival processing effect has similarly been documented in young children 4-12 years old (Aslan & Bäuml, 2012; Howe & Otgaar, 2013; Otgaar, Howe, Smeets, & Garner, 2014; Otgaar & Smeets, 2010). Nairne and his colleagues (2008, 2010, 2014) suggest that the survival processing effect is

evidence of evolutionary tunings that bias the human memory system to best remember fitness-related information (Cosmides & Tooby, 2013).

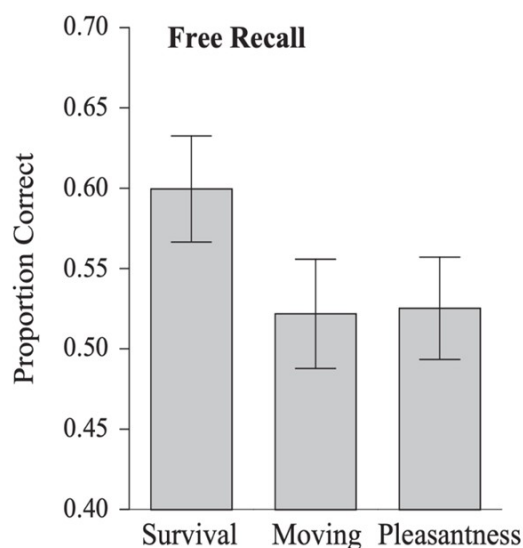


Figure 2. Proportion of items recalled depending on the encoding task. The same items were rated for scenario relevancy by all participants, but those in the survival condition were instructed to process those items based on an imagined survival scenario compared to those in the moving condition who imagined how those items would be helpful to the less evolutionarily important task of moving. Figure copied from Nairne, Thompson, and Pandeirada (2007).

Seitz, Polack, and Miller (2018) extended Nairne's approach and demonstrated that rating items based on their relevancy to an imagined parenting task similarly resulted in increased retention of those items. In fact, the memory benefit was just as large as the already robust survival processing effect (see Figure 3). What is more, manipulating the biological relatedness of the imagined child (i.e., adopted vs. biological) can also affect memory performance such that information relevant to your imagined biological child is better remembered than information relevant to an imagined adopted child (Seitz, Polack, & Miller, 2019 pre-print, but see Krause et al., 2019). Better memory has also been observed for the descriptions of individuals being evaluated as potential long-term mates compared to those same descriptions if the individual is being evaluated as a potential coworker (Pandeirada, Fernandes, Vasconcelos, & Nairne, 2017). Along similar lines, mnemonic advantages for animate versus inanimate stimuli (words or pictures) are prevalent even when those stimuli are matched for other characteristics that could influence memory performance (e.g., imaginability, meaningfulness, saliency, valence; Nairne, VanArsdall, & Cogdill, 2017; Nairne, VanArsdall, Pandeirada, Cogdill, & LeBreton, 2013). This bias towards animacy has been suggested to reflect the view that the most important aspects of our environment (e.g., potential predators, high quality food sources, mating partners) are often animate objects. Items in lists containing inanimate and neutral stimuli, such as chairs and water bottles, can be especially well remembered if they are described as being touched by someone who has a contagious disease rather than a healthy individual (Bonin, Thiebaut, Witt, & Méot, 2019; Fernandes, Pandeirada, Soares, & Nairne, 2017). Words that are paired with pictures of faces that appear sick are better

remembered than words paired with pictures of faces that appear healthy. Interestingly, this benefit is attenuated if the sick looking faces are described as actresses who are wearing makeup for a film (Fernandes et al., 2017), which highlights the importance of perceived biological significance of an event impacting future recallability. Hou and Liu (2019) recently found a mnemonic bias for faces perceived as trustworthy or untrustworthy compared to faces perceived as neutral during a scenario involving survival. Finally, New, Krasnow, Truxaw, and Gaulin, (2007) had participants walk through a farmer's market and then recall the locations of various vendors. Memory error for the locations of different food vendors was negatively associated with the number of calories in the food item, such that the locations of stands that sold items with higher caloric density were better remembered (see Figure 4).

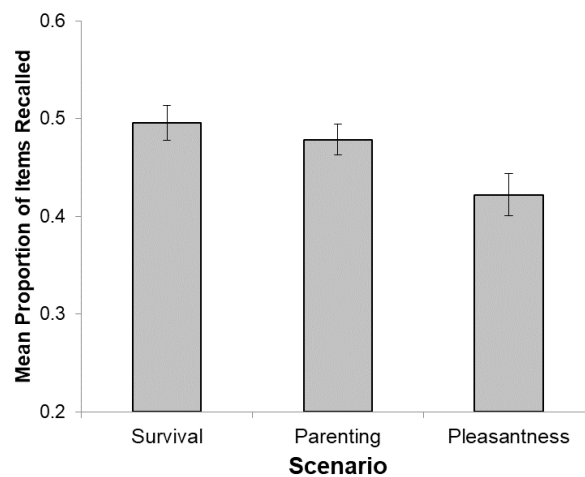


Figure 3. Words rated based on their relevancy to an imagined parenting scenario are just as well as words rated based on the survival processing scenario. Both processing scenarios elicit better recall than a pleasantness control condition. Figure adapted from Seitz, Polack, & Miller (2018).

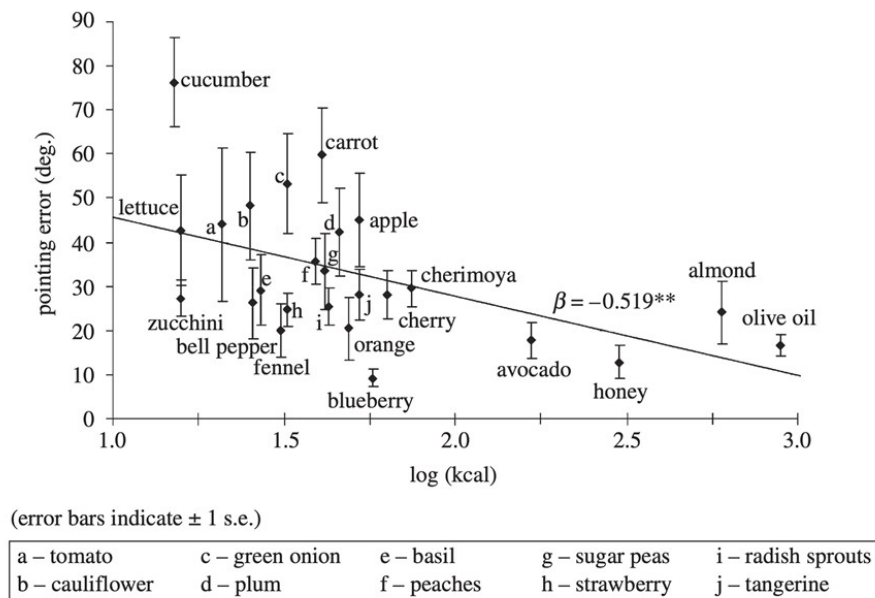


Figure 4. Error in the spatial location of food stands at a farmer’s market is negatively associated with the caloric density of the food item being sold at the food stands. This suggests better spatial memory performance for items of higher evolutionary fitness value. Figure copied from New, Krasnow, Truxaw, and Gaulin (2007).

That fitness-relevant information receives privileged processing is not an a priori assumption of the basic memory models mentioned earlier. More generally, these models make no assumptions that some information may be intrinsically better remembered than others (e.g., animate stimuli compared to inanimate, high-calorie vs. low-calorie food items) or that, given some circumstances (e.g., an item being touched by a sick rather than healthy individual), information may be consequently better remembered. That said, the omega parameter that scales the potential retrieval and/or storage strength of information based on its perceived fitness value should be able to predict all of these findings. While claims of evolutionary predispositions to any behavioral or physiological trait are often criticized as invoking “just so stories,” the studies mentioned above are decidedly a priori. Instead of observing a difference and then providing an evolutionarily oriented justification, researchers have hypothesized conditions under which mnemonic performance might have evolved to be potentiated and then test retention in that situation compared to an appropriate control (Nairne, 2014; Nairne & Pandeirada, 2010; but see Krause, 2015b, for important methodological considerations and discussion of issues of circular reasoning in understanding adaptive specialization). The omega scaling factor, while offering explanations to many existing phenomena, also seemingly provides straightforward and testable predictions about the potential memorability of described events.

Since Nairne and colleagues’ (2007) original publication on survival processing, a number of researchers have investigated potential proximate explanations of this effect (for reviews, see Kazanas & Altarriba, 2015; Nairne, Pandeirada, & Fernandes, 2017; Nairne, 2014). Some have argued that this effect is due to enhanced self-

referential processing (Erdfelder & Kroneisen, 2014; Howe & Otgaar, 2013; Klein, 2012; but see Weinstein, Bugg, & Roediger, 2008). That is, the survival processing scenario better promotes self-referential processing than relevant controls, which, in turn, results in superior recall. Others have made similar arguments in terms of the survival processing scenario putatively yielding more elaborative processing (Burns, Hart, Griffith, & Burns, 2013; Kroneisen & Erdfelder, 2011; Kroneisen, Erdfelder, & Buchner, 2013). Another interpretation of the survival processing effect is that the survival scenario produced better recall through enhanced arousal, potentially via some activation of norepinephrine as the GANE model suggests, but a number of studies have demonstrated the survival processing effect cannot simply be explained by heightened arousal induced by the scenario (Kang, McDermott, & Cohen, 2008; Smeets, Otgaar, Raymaekers, Peters, & Merckelbach, 2012).

While there are likely a number of proximate mechanisms that underlie the survival processing effect (see Krause, 2015a), it should be emphasized that proximate explanations do not negate ultimate explanations. Rather, proximate explanations (the immediate cognitive or physiological mechanism responsible for behavior) and ultimate explanations (the long-term function value of a behavior) should complement each other and provide a more holistic understanding of the factors that influence said behavior (Scott-Phillips, Dickins, & West, 2011; Tinbergen, 1963). Thus, the survival processing effect or parent processing effect cannot be explained per se simply by finding that such scenarios yield more elaborative processing (Nairne & Pandeirada, 2016). Why fitness relevant scenarios result in more elaborative processing compared to otherwise matched control scenarios is at the heart of the ultimate explanations provided by Nairne and his colleagues and Seitz et al., (2018). More conceptually, a scaling parameter that influences retrievability of incoming information based on its perceived fitness value may derive this value from the inputs of many different systems, each of which could be conceived as a proximate explanation to why fitness relevant information is better remembered. Nevertheless, the existence of these combined inputs affecting retrievability, such that fitness relevant information is better remembered, reflects the ultimate function of the system(s).

Applying an Ecological Approach to Human Memory

While ecologically-valid approaches to learning are often discussed and considered by learning theorists, current models of human memory frequently fall prey to similar issues of equipotentiality that confronted early learning theorists who attempted to construct models of general laws of learning. In arguing for ecologically-inspired learning theories, Timberlake (1994) discussed their potential utility well, especially compared to a more general process approach:

The general success of models of learning based on connections between simple elements has been bought at the cost of some uncertainty as to their generalizability to situations that have not been tuned by experimenters to isolate the determinants and effects of interest.

Although the isolation of phenomena for the purposes of study is a powerful technique dating back at least to the study of spinal reflexes (Sherrington, 1906), it is ultimately an incomplete venture that must be embedded within a larger framework to account for behavior (Fearing, 1930; Sherrington, 1906; Timberlake, 1993). p.418

General process memory models have shed light on many phenomena, such as spacing effects, benefits of encoding-retrieval match, serial position effects, and separate pathways for visual and auditory processing. Nevertheless, we have argued that these models are often insufficient to help us understand determinants of memory in situations not tuned by the experimenter. More troubling, the mounting evidence that fitness-relevant stimuli are better remembered than fitness-irrelevant stimuli is largely ignored in the field and is excluded from many introductory memory textbooks (e.g., Baddeley, Eysenck, & Anderson, 2014; but see Schwartz, 2011). There was much pushback in accepting the phenomena of belongingness, long-delay conditioned taste aversion, and selective associations, as they were incongruent with a simple model of contiguity learning. Similar resistance to adequately acknowledging these examples of privileged memory for perceived fitness relevant information may originate with the phenomena being similarly incongruent with iconic models of memory. Nevertheless, much has been gained from adopting ecologically inspired accounts of learning (e.g., behavior systems theory), and similar success may also come from exploring more functional perspectives of memory (Nairne, 2014; Sherry & Schacter, 1987).

Inspired by this reasoning, that evolutionary relevant information and events typically result in superior memory performance compared to relevant controls, we were interested in how memories for eating events differ, if at all, from those of other similar but non-eating related events (Seitz, Blaisdell, & Tomiyama, 2019 pre-print). This behavior was chosen because, for mammals, eating is one of the most frequently occurring tasks an animal must perform to ensure its survival, and animals of all phyla have evolved specialized physiological features to advantage themselves in obtaining food. In fact, some species of birds (e.g., Clark's nutcrackers & black-capped chickadees) have evolved astonishing mnemonic capabilities (via hippocampal enlargement and specialization) that allow them to remember the location of cached food over several weeks or months (Balda & Kamil, 1992; Sherry, Jacobs, & Gaulin, 1992; Shettleworth, 1990). Thus, our proposed omega scaling factor predicts enhanced memory for eating events due to their elevated fitness value, compared to a relevant procedural behavior that does not involve eating.

There are also additional and perhaps alternative theoretical reasons that predict eating behavior to be particularly well remembered. For instance, that conditioned taste aversions can be learned so quickly with such a large temporal trace favors the view that eating-related events might be governed by unique learning processes that operate on different terms than those underlying how noningestive events are learned and/or remembered (Garcia et al., 1955). There is also now a large body of evidence supporting the causal role that memory of a recent meal plays in moderating future food consumption. Amnesiacs, such as the well-known patient H.M.,

will continue to eat the same meal served to them over and over again, and their reported hunger levels do not appear to be correlated with time since last meal (Rozin, Dow, Moscovitch, & Rajaram, 1998). Along similar lines, Hannapel et al. (2019) optogenetically inhibited either the dorsal or ventral hippocampus immediately after rats consumed a meal, thereby preventing the consolidation of the meal memory (but see Ryan, Roy, Pignatelli, Arons, & Tonegawa, 2015). Inactivation of either region led to decreased latency until the next meal and greater consumption of food during the next meal compared to rats that had the inactivation of the hippocampus before or during the eating event. Thus, what motivated when and how much rats ate in this experiment was not related to nutrient deficiencies (all rats consumed the same amount of food) but rather memory for the most recent eating event. In humans, interfering with memory of a meal by having participants watch television while eating results in increased future snacking. Alternatively, enhancing memory by having participants focus on sensory aspects of the meal decreases snacking relative to participants who ate the meal without any explicit instructions to focus on the sensory aspects of the meal (Higgs & Spetter, 2018; Higgs, Williamson, & Attwood, 2008; Mittal, Stevenson, Oaten, & Miller, 2011; Robinson et al., 2013).

Given the important role that memory of a recent meal plays in moderating future food intake and the evolutionary importance of eating, we set out to test how memory of an eating event compares to a similar but non-eating related task. We created a novel paradigm in which participants watched a film while being cued to either eat M&Ms or move M&Ms from one bowl to an opaque container. We found that eating 30 M&Ms was more accurately recalled than moving 30 M&Ms from a bowl to an opaque container (a behavior chosen to mimic eating except for the act of consumption), and that this effect could not be explained by consumed glucose from the M&Ms enhancing task memory (Seitz et al., 2019 pre-print). Thus, memory for the behavior of eating appears to be particularly strong compared to a nearly identical behavior that does not involve eating. Critically, this hypothesis was informed by adopting a functional perspective of memory but was formulated a priori and then confirmed by subsequent testing. That memory for an ingestive behavior might differ from memory of other procedurally similar behaviors is not something predicted by most models of memory but is congruent with our account of a scaling factor that potentiates the memorability of information based on its apparent fitness value. Additionally, adopting this functionalist perspective of memory allows one to ask novel questions regarding memory of eating behaviors. In a series of planned experiments, we intend to explore how the food item consumed during eating affects its being remembered. Dominant models of memory do not predict differences in memory for eating 30 salted peanuts compared to 30 pieces of popcorn, but something like our omega scaling factor does because the two food items differ in their caloric density and thus fitness relevance. Ultimately, the empirical data will either confirm or deny the feasibility of such a parameter.

Conclusions

In sum, the debate surrounding biological constraints on learning have offered much insight into the factors that influence learning and behavioral processes and, at

the very least, can be viewed as good circumstantial evidence against a singular learning system functioning in all species in all situations. While current models of memory do not claim to have the same sort of omnipotent explanatory capabilities that some behaviorist models ascribed (e.g., Hull, 1952; Spence, 1956), their inability to quantitatively differentiate between how any two events will be remembered represents a serious shortcoming. As ideas of equipotentiality certainly delayed discovery of a number of interesting learning phenomena (e.g., conditioned taste aversion, selective associations, cue-outcome temporal gradients, species differences in learning abilities), it remains unclear what memory phenomena have gone unnoticed by placing emphasis on general process memory models. We have briefly reviewed a number of findings that provided evidence in support of biological constraints on memory, suggested a simple amendment to existing models of learning and memory that would expand their explanatory power, and described a promising line of research inspired by a more functionalistic perspective of memory. It is our hope that others will find similar utility in this functional approach to memory.

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Financial conflict of interest: No stated conflicts.

Conflict of interest: No stated conflicts.

Submitted: June 2nd, 2019
Resubmitted: August 26th, 2019
Accepted: August 27th, 2019