A Neuro-Operant Analysis of Mnemonic Recognition

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Abstract Historically, the fields of operant selection and recognition memory have not interacted substantially with one another. However, both deal with how behavioral repertoires change over time as a function of environmental stimulation. In this article, we propose neuro-operant interpretations of behavioral phenomena occurring in recognition memory procedures based on (a) the ability to discriminate changes in the strength of responses caused by environmental stimulation and (b) the occasioning of supplementary responses by current stimulation. A neuro-operant interpretation of mnemonic behavior may further the understanding of the phenomena in place and simplify the current taxonomy of learning and memory.

Keywords Hippocampus · Mnemonic behavior · Operant selection · Perirhinal cortex · Priming · Repertoire

Competing paradigms are the norm in the social sciences (e.g., Becher & Trowler, 2001; Ritzer, 1975), and research on operant selection can either be considered one of the paradigms within psychology or an entirely independent discipline that has branched out from research on learning, closer to biology than psychology (e.g., Donahoe, 1996, 2017; Hull, Langman, & Glenn, 2001). Based on different philosophical foundations—the first typically reductionist and essentialistic, the other tending to be nonreductionist and selectionist—psychological research on cognition (and specifically memory) and research on operant selection deal with the subject matter of learning in diverging ways (e.g., Ortu & Vaidya, 2017; Palmer & Donahoe, 1992). More specifically, cognitive psychology and cognitive neuroscience are dominated by a taxonomy of learning and memory in which the storage metaphor is still widespread (e.g., Squire, 2004; Watkins, 1990); conversely, researchers interested in operant selection identify ultimate causes of learning and memory in contingencies of

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reinforcement while in the process avoiding storage metaphors (e.g., Fryling & Hayes, 2010; Palmer, 1991; Skinner, 1977). Ultimately, the most parsimonious (and technologically fertile) interpretation may prove to be more useful in creating a consistent, nonfragmented, unified account of adaptive learning that does not rely on an unnecessary multiplication of concepts and models.

In relation to mnemonic behavior specifically, memory research has produced interesting procedures and results, but a Skinnerian interpretation of those phenomena has seldom been proposed (e.g., Palmer, 1991; Wixted, 2008). Relatedly, Wixted (2008), one of the most prominent memory researchers, has argued specifically for the potential importance of Skinnerian interpretations:

How is it that, usually, people are very good at expressing an appropriate level of confidence in their memories? How did they learn to do that? That question is not often asked, and I am not sure that it has ever been considered in light of Skinner's ideas. (p. 139)

Operant researchers have described mnemonic behavior as behavior under the control of current stimulation (e.g., Donahoe, 2017; Palmer, 1991; Skinner, 1957, p. 143). Consistently, researchers interested in operant selection tend to disagree with interpretations of mnemonic behavior provided by cognitive scientists, as they are typically based on mediating, inferred, hypothetical constructs that then circularly become unobserved independent variables that *cause* behavior (e.g., Palmer, 2009b; Watkins, 1990). For example, in the cognitive literature, a participant can be described as using his or her “familiarity memory” to explain his or her performance on a recognition task. Aggleton et al. (2005) mention that “patients with selective hippocampal pathology can still *use their intact familiarity information to guide recognition* [emphasis added]” (p. 1810). However, familiarity memory is itself inferred by looking at the behavioral results, creating a circular definition. In other words, “familiarity” is never directly observed. What can be observed are the behavior and a range of activity at the brain level.

In addition to the theoretical dissimilarities, the divide between research on operant selection and research on mnemonic behavior is probably also an outcome of procedural differences predominant in the two fields. For example, if we compare the literature on free operant learning (e.g., Ferster, 1953; Ferster & Skinner, 1957; Sidman, 1958; Staddon, 2016) to the research on recognition memory (for a review of recognition memory, see Yonelinas, 2002), a free operant paradigm appears to be hard to integrate with the study–test procedures typically used in recognition experiments.¹ Also, experiments that measure operant selection do not typically report memory performance (e.g., signal detection variables as hit rate, false alarm rate, correct rejections, misses, receiver operating characteristic [ROC] curves), and vice versa.

Here, we analyze developments in recent memory research by using some interpretive tools available to the operant researcher. Specifically, we will examine some of the

¹ Not all recognition memory experiments are based on a study–test paradigm. Some, in fact, use what is called a “continuous recognition” procedure (e.g., Friedman, 1990). Moreover, many experiments within the behavior–analytic field have increasingly started using experimental designs similar to the study–test procedure; see, for example, the literature on stimulus equivalence (e.g., Sidman, 1994).

vast literature on neurobiology of memory that typically interprets memory phenomena as either mediated by “familiarity” or “recollection” (e.g., Eichenbaum, Yonelinas, & Ranganath, 2007). Familiarity represents the instances of mnemonic behavior when the participant can recognize previous exposure to a stimulus but not the particular instance in which the stimulus had been originally presented. Recollection represents situations in which the participant can not only recognize previous exposure to a stimulus but can also correctly provide information about some contextual details present when the original stimulus was experienced (e.g., Cansino, Maquet, Dolan, & Rugg, 2002). More specifically, we will interpret recent studies on “familiarity memory” based on the acquired ability to discriminate changes in response strength, describe “recollection memory” based on the evocative function of current stimulation, and suggest some directions for applied research.

To understand mnemonic behavior, perhaps the most useful point to appreciate is an analysis of the procedures used in standard experimental paradigms. Recognition memory experiments typically involve a study–test procedure in which participants discriminate if an item has been previously experienced during the experimental session or during a past session (for a review, see Yonelinas, 2002). A study–test paradigm typically comprises a large number (e.g., 100) of items in both the study and the test lists and might be considered an extension of a delayed matching-to-sample (DMTS) procedure; however, in study–test procedures, there is no explicit reinforcement. Nonetheless, in both cases, there are what can be considered sample (study items) and comparison (test items) stimuli, and organisms typically respond differentially to the comparison items based on the exposure to items presented in the study list. More specifically, in a typical recognition experiment, a list of items is displayed during an initial study phase, and then in a subsequent test phase the same items are presented again, randomly intermixed with items that had not been presented in the study phase. Participants are required to discriminate the oldness or newness of each item (e.g., Mandler, 1980; Shepard, 1967; Squire, Wixted, & Clark, 2007). Both human and nonhuman participants can perform such tasks accurately (e.g., Eichenbaum, Fortin, Ergorul, Wright, & Agster, 2005).

Because no explicit reinforcement is present in study–test procedures and because “oldness” and “identity” are not physical properties of the stimuli (i.e., nothing in the stimulus itself varies between the first and subsequent presentations), a change in the way organisms respond to a stimulus may allow them to discriminate if they have already experienced the stimulus or not. Based on this possibility, we can start building an operant interpretation of what has been described in cognitive terms as “familiarity-based” recognition behavior.

Familiarity-Based Recognition

In understanding how to create an operant analysis of familiarity-based recognition behavior, let us start by considering the concepts of behavioral repertoire and response strength. Behavioral repertoire is a term used to describe operants—environment–behavior relations—selected during the lifetime of the individual (e.g., Glenn, Ellis, & Greenspoon, 1992; Palmer, 2009a). Importantly, in the account provided herein, the repertoire is not a “thing” or a collection of memory traces, and it is not represented by

changes occurring at the brain level. The brain, from an operant perspective, is a part of the physiological mechanism that supports selection and retention of environment–behavior relations (e.g., Donahoe, 2017; Donahoe, Burgos, & Palmer, 1993). Reinforcement is responsible for the selection of environment–behavior relations, and moment-to-moment stimulus control continuously alters the response strength and the probability of emission of a vast number of responses (Palmer, 2009a).²

When a response is emitted, the relative strength of other responses in the repertoire varies, as evident in priming experiments. In priming experiments (e.g., Neely, 1991), the presentation of a priming word (e.g., *coffee*) is followed by the presentation of a target word. If the target word is “related” (e.g., *milk*), the reaction time to an observing response (e.g., an emission of a textual or reading operant) to the stimulus will, on average, be shorter as compared to a response following an unrelated target stimulus (e.g., *dog*).

Priming effects indicate that environment–behavior relations are not independent of each other, showing instead that a single stimulus alters the strength of a variety of related responses (Ortu, 2012; Palmer, 2009a), possibly due to the fact that fluctuations in the strength of a particular response alter the strength of other responses as well. The implication is that ongoing stimulus control has complex (possibly nonlinear) effects on the strength and probability of emission of a multitude of responses.³ If organisms are able to learn to discriminate changes in response strength based on recent stimulus control, it would be possible to make sense of experiments that have been described in the wider memory literature as “memory illusions”:

People can be fooled into confidently believing that they remember something when they clearly do not. In the Deese-Roediger-McDermott procedure (Roediger & McDermott, 1995), for example, subjects are presented with a list of words that are all related to another word that was not presented (e.g., they are all related to the word *sleep*, which did not itself appear on the list). On a subsequent recognition test in which subjects are asked to discriminate between targets that appeared on the list and lures that did not, the word *sleep* is very likely to be endorsed (often with high confidence) as having appeared on the list. Results like these show that memory researchers can create memory illusions in the same way that vision researchers can create visual illusions. (Wixted, 2008, p. 139)

² Skinner (1948) explicitly discussed response strength and probability of emission in the William James lectures, noting that

we recognize... that some responses are more likely to occur than others and that, in fact, every response may be conceived of as having at any moment an assignable probability of emission... A latent response with a certain probability of emission is not directly observed. It is a scientific construct. But it can be given a respectable status, and it enormously increases our analytical power. (p. 25)

³ When multiple responses are competing for emission (as is probably the case in most situations) a “winner takes all” selection process, centered at the brain level on the thalamocortical–striatal loop, eventually leads the strongest response to inhibit competing responses and their emission (e.g., Redgrave, Prescott, & Gurney, 1999). Palmer (2009a) has given a fully behavioral account of response competition, stating that

in any one response system, most responses are mutually incompatible. We can walk to the left of a tree or to the right of the tree, but we cannot do both. We can say, “Hello,” or “Hi there,” but not both, at least not at the same time. Response competition is an important concept. If we tried to engage in every response that had some strength, our behavior would be chaotic. If two incompatible responses are roughly equipotent, only one will actually be emitted. The competing response appears to be inhibited. (p. 56)

This memory illusion might be interpreted as a case of response strengthening through thematic verbal control (Palmer, 2016; Skinner, 1957). Related words are selected, even though they have not been previously seen, quite possibly because they are “members of a group of responses strengthened by a single variable” (Skinner, 1957, p. 263; e.g., those responses strengthened by the word *sleep*; see also Michael, Palmer, & Sundberg, 2011, and Palmer, 2016). More generally, discriminating changes in response strength may be a key component in being able to accurately perform a variety of tasks, including recognition memory tasks. Palmer (1991) mentioned that “the strength of a response to its controlling variables is often discriminable” (p. 276). What we ask here is *What are some plausible neurobehavioral mechanisms that might allow organisms to learn how to discriminate moment-to-moment changes in response strength?* We suggest that previous research on discriminating interoceptive responses offers a solid foundation for an alternative account of familiarity-based recognition memory.

A classic example of familiarity-based recognition involves what has been described as the “butcher-on-the-bus phenomenon” (e.g., Gimbel, Brewer, & Maril, 2017; Yonelinas, 2002; Yovel & Paller, 2004)—when seeing the familiar face of the butcher in an entirely different context, such as a bus, an individual may be able to discriminate that that particular person had been seen before, but responses about any other contextual detail are not evoked by the current stimulation (e.g., the individual is not able to describe in which other contexts that face was seen on previous occasions). From a strictly behavioral perspective, the organism can describe (i.e., emit an “old” response in the case of a nonhuman subject) that a stimulus has been seen before but is not able to say where or when. In other words, the stimulus does not evoke supplementary responses about the spatiotemporal environment to which the organism had been initially exposed. When an organism is responding to a particular stimulus for the second time, it may discriminate that the response to the stimulus experienced the second time differs from responses to stimuli that have been presented for the first time. Another way to phrase such a phenomenon is that the strength of the response varies based on current and past stimulus control.

The fact that participants can discriminate between different degrees of strength of responses in mnemonic behavior is presented here in a way that is qualitatively consistent with the ability organisms acquire early on in life to respond to proprioceptive and interoceptive stimulation (e.g., Benoit & Davidson, 1996). More specifically, together with exteroceptive stimulation, proprioceptive and interoceptive responses can also acquire discriminative stimulus function. For instance, Benoit and Davidson (1996) have shown how organisms can learn to respond differentially between different degrees of interoceptive stimulation specifically due to various food deprivation durations. We propose here that the ability organisms acquire to discriminate between varying degrees of response strength (e.g., interoceptive responses that acquire differential stimulus function) may be useful to explain what has been called familiarity-based recognition memory.

Neuroscientific research may, in this case, inform the behavioral level of analysis by showing how repeated stimulus presentation often leads to a weakening of neural responses (e.g., Henson & Rugg, 2003). Many neuroscientific measures have in fact shown what has been described as “repetition suppression” (Horner & Henson, 2008). Specifically, measures from functional magnetic resonance imaging (fMRI) to single-unit recordings indicate that the magnitude of neural responses decreases with repeated

stimulus presentation. This reliable effect has been interpreted in a variety of ways, including “fatigue” of neural responses (Grill-Spector & Malach, 2001) and “sharpening” (Wiggs & Martin, 1998). Repetition suppression has been linked to the “behavioral facilitation” effects described earlier as *priming* (e.g., Henson, 2003). It is possible that participants can discriminate the change in the way they respond to stimuli and can accurately differentiate between “old” and “new” items.⁴ Gonsalves, Kahani, Curran, Norman, and Wagner (2005) described repetition suppression in the following manner:

Firing rate decreases, termed “repetition suppression” . . . can emerge as early as 75 ms after stimulus onset, occur after a single encounter with an item, and can be long lasting . . . consistent with the hypothesis that they might support recognition discrimination based on item memory strength. (p. 751)

If we had to characterize repetition suppression as a behavioral process, we could perhaps describe it as a form of habituation (e.g., Fischer et al., 2003). Habituation is the decrease in the magnitude of a behavioral response through repeated presentations of a stimulus. A vast number of response topographies have been shown to habituate (e.g., Harris, 1943; Rankin et al., 2009; Thompson & Spencer, 1966), and in some cases neural responses have been explicitly described as habituating (e.g., Breiter et al., 1996). A relatively straightforward way to describe recognition between old and new items, then, might be based on the possibility that organisms learn to discriminate the habituation of neural responses and that some brain areas such as the perirhinal cortex support long-term habituation in responding to stimuli.⁵

The perirhinal cortex appears to be one of the key brain areas involved in the way organisms discriminate changes in their responses to stimuli. More specifically, neurons in the perirhinal cortex have been found to be sensitive to the recency of stimulus presentation and the overall novelty of stimuli given the individual’s history (Xiang & Brown, 1998). Importantly for the current discussion, cells in the perirhinal cortex have shown relatively long-lasting sensitivity to stimulus repetition and priming in general (e.g., Wang, Ranganath, & Yonelinas, 2014). More precisely, neurons in sensory or perceptual cortices (e.g., the inferotemporal [IT] visual cortex) show a repetition effect that is short lived, and the perirhinal cortex shows repetition effects that can be long-lasting. For example, Baylis and Rolls (1987) stated that

neurons in the inferior temporal cortex have responses which would be useful for a short term visual memory for stimuli, but would not be useful in recency

⁴ The possibility that organisms learn to discriminate weakening of neural responses through repeated presentation of stimuli is a hypothesis that requires empirical validation. However, from a logical perspective, organisms need to be able to learn to discriminate *some* kind of change in the way they respond to repeated presentation of identical stimuli if they are to adapt to the contingencies intrinsic in recognition procedures.

⁵ The discussion of the role of the perirhinal cortex (and of the hippocampus in subsequent parts of the paper) in mnemonic recognition should not be interpreted as a reductionist argument in which recognition behavior is considered to be caused by or equated with activation of the perirhinal cortex. Instead, the role of the perirhinal cortex needs to be understood within a systems perspective in which the perirhinal cortex is one of many interactive parts embedded within an adaptive neural network (Bussey & Saksida, 2007; Carlesimo, Lombardi, Caltagirone, & Barban, 2015; Ortu & Vaidya, 2017). In turn, neural activity in general needs to be considered within the context of the behavior of the whole organism in relation to environmental variables.

memory tasks in which more than one stimulus intervenes between the first and second presentations of a stimulus. (p. 614)

Consistently, Xiang and Brown (1998) mentioned that

there are far more neurones with short latencies in area TE⁶ than in Perirhinal cortex and far more neurones with long memory spans in the perirhinal cortex than in area TE: Accordingly, the contributions of the two regions to recognition memory are unlikely to be equivalent. (p. 672)

Response strength fluctuations in the behavioral repertoire determined by current stimulus control are presumably a function of both proximal and distal history. It follows that the described ensemble of cells in the perirhinal cortex—sensitive to repetition at both short and long intervals—seems to be potentially adequate to support differential responding based on exposure to a stimulus in the recent or distant past. Consistently, organisms with damage localized at the perirhinal cortex level typically have trouble discriminating if a stimulus is old or new unless the stimulus evokes supplementary responses (e.g., Bowles et al., 2007). An interpretation of this phenomenon could be that current stimulus control determines a discriminable fluctuation of response intensity, supported by sensitivity to stimulus repetition at the perirhinal cortex level, to which the participant has learned to respond by describing the change. Examples of this could be in the case of humans emitting the sentence “I have seen that face before” or in the case of nonhumans performing correctly in a study–test recognition procedure.

It is difficult to determine how both humans and nonhumans could perform so well in study–test recognition memory procedures without the ability to discriminate changes in the strength of sensory–perceptual responses. There has to be a plausible mechanism to discriminate between old and new items in case of physical identity of the stimuli. A plausible interpretation is that the first instance in which the stimulus is presented yields a sensory–perceptual response of a particular magnitude. The second instance then produces a response of magnitude that varies compared to the first one, possibly due to a relatively straightforward habituation process that is conceivably supported by the perirhinal cortex. Through differential reinforcement, then, the organism can learn to discriminate between old and new items. Importantly, nonhuman research carried out with rats using olfactory stimulation has shown ROC results similar to those typically seen in humans (Eichenbaum et al., 2005; see also Wright, 2007), suggesting that rats may be able to discriminate changes in response strength. Interestingly, when rats undergo hippocampal excision, they seem to be able to perform memory tasks based exclusively on their ability to discriminate changes in the way they respond to changes in response strength. Intact rats, however, appear to use a combination of discriminations of response strength and recollecting behavior (i.e., current stimulation is directly evoking target responses or responses that in turn will evoke target responses). The next section discusses recollecting behavior from a neuro-*operant* perspective.

⁶ The TE area is a visual area located in the inferior temporal cortex (e.g., Muñoz-López, Insausti, Mohedano-Moriano, Mishkin, & Saunders, 2015).

Recollecting Behavior

When responses (both perceptual and motor) that were evoked during an original event are evoked again by some subset of the initial stimulus configuration, cognitive scientists typically speak of “recollection” (e.g., Yonelinas, 2002). Recollection can be summarized as the second presentation of Stimulus A occasioning Response A' *together with* a particular constellation of responses B'C'D'E'F' that had temporally co-occurred during the original episode as responses to the original stimulus configuration ABCDEF. The participant might in turn describe the evoked perceptual or motor behavior.

From a procedural perspective, experiments investigating recollection in humans typically involve presenting a stimulus during a first phase—called the “study phase”—embedded in a particular context—for instance, a picture displayed on one of the four corners of a screen (e.g., the top left corner). Subsequently, in what is typically described as the “source memory” test phase, the same stimulus is presented again, this time in the center of the screen. The participant is asked to remember in which of the four corners the stimulus was presented during the first phase. The target response (the response scheduled for reinforcement), therefore, involves being able to describe the unique configuration of stimuli presented during the first phase (e.g., Cansino et al., 2002).

Skinner (1974) proposed an interpretation of the phenomenon of recollection, suggesting that a

stimulus may “remind” us of a person, place, or event if it has some resemblance to that person, place, or event. Being reminded means being made likely to respond, possibly perceptually. A name may remind us of a person in the sense that we now see him. This does not mean conjuring up a copy of the person that we then look at; it simply means behaving as we behaved in his presence upon some earlier occasion. (p. 121)

Consistently, Palmer (1991) describes the phenomenon as automatic—

that is, it is directly under the control of environmental variables and does not require intermediate responses on the part of the organism. We experience memories of this sort as “spontaneous.” A strain of music will often elicit emotional responses, and covert verbal and perceptual behavior appropriate to an earlier context, as it did so forcefully for Humphrey Bogart in the film, *Casablanca*. The taste of a madeleine will “summon up remembrance of things past.” We name objects with ease, and with somewhat less ease recall the names of friends and acquaintances when we see them. We never forget how to ride a bicycle or how to swim. In each case, the behavior in question is directly controlled by a particular stimulus or set of stimuli. (p. 265)

In other words, recollection is mnemonic behavior triggered directly by stimulus control that, different from what has been described as familiarity-based remembering, involves recalling some of the unique combinations of features of an episode when a subset of those features is presented again to the individual. For instance, hearing a song can remind us of a particular time and place when we first heard the song. Similar to the discrimination of changes in strength, recollecting behavior has been investigated

in memory research with rats. Results showed asymmetrical ROC curves—analogue to human participants—and rats have been shown to remember not only spatial but also temporal configuration of stimuli, with those abilities severely impaired by hippocampal excision (Eichenbaum et al., 2005).

The selection of co-occurring responses in sensory–perceptual cortices can be considered one of the primary functions of the hippocampus (e.g., Donahoe et al., 1993; Ortu & Vaidya, 2013). More specifically, mnemonic behavior directly triggered by stimulus control is considered to be supported by hippocampal *pattern completion activity* (e.g., Horner, Bisby, Bush, Lin, & Burgess, 2015; Rudy & O'Reilly, 1999). When, by way of the hippocampus, the organism learns a configural discrimination (involving, for example, pressing a button when a specific color is presented on a screen together with a sound and a particular word shown in the center of the screen), presentation of a subset of the original stimulation during the test phase (just the specific word) may allow the complex perceptual response to recur even if only part of the study stimulation is presented again (e.g., Kesner, Lee, & Gilbert, 2004). This pattern completion operation is considered to be possible because the hippocampus not only receives sensory–perceptual responses from a large number of unimodal and polymodal areas in temporal, parietal, and occipital cortices but also projects back to the same areas (e.g., Lavenex & Amaral, 2000). The described neuroanatomical arrangement allows the possibility of reactivating the matching ensemble of sensory–perceptual responses that were activated in the original episode. In other words, as mentioned earlier, responses that had been evoked during an initial event are evoked again by some subset of the original stimulus configuration.

The hippocampus has such high internal connectivity (e.g., Buzsaki, 2006, p. 285) within a relatively small area (compared to the neocortex) that it has the capability of creating a response network uniquely matching the particular configuration of stimuli that were experienced during an episode based on current stimulus control received from sensory–perceptual areas. Importantly, the hippocampus receives (among others) both dopaminergic (Otmakhova, Duzel, Deutch, & Lisman, 2013; Scatton, Simon, Le Moal, & Bischoff, 1980) and noradrenergic (Berridge & Waterhouse, 2003) real-time feedback signaling the current reinforcing and punishing value of the experienced stimulation, effectively modulating the selective function that the hippocampus has over current sensory–perceptual responses. Specifically, this increases the probability that a particular stimulus configuration is selected and therefore remembered on future occasions when a subset of the original stimuli is presented again (e.g., Ortu, 2015). To sum up, the mechanism of pattern completion occurs via the hippocampus and supports recollecting behavior (i.e., when starting from a fragment of the stimulation present during the original episode [for example, a picture taken at the beach during childhood], we can remember contextual details [the smell of the sea, the wind, the heat, what we ate for lunch shortly after the picture was taken, etc.]). The hippocampus allows the perceptual responses active during the first episode to be subsequently reactivated.

As a final consideration, it is relevant to mention that recollection is often described in relation to salient, “surprising” events. For example, humans are typically more likely to be able to describe the unique configuration of stimuli in the environments surrounding them when finding out about President Kennedy’s assassination or learning of the 9/11 attacks compared to relatively “neutral” events (e.g., Kensinger, 2009; Murty & Adcock, 2013). Palmer (1991) interpreted the concept of surprising

stimulation based on the phenomenon of blocking described within the classical conditioning literature (Kamin, 1969), suggesting that

the conditioning of a response can be blocked if the reinforcer has been “predicted” by antecedent stimuli. Technically speaking, reinforcement only occurs when there is a discrepancy between responses elicited by the putative reinforcing stimulus and responses elicited by other stimuli present. . . . Anthropomorphizing, we say that reinforcement is effective only if it “surprises” the organism. As this has been shown to be relevant to the acquisition of stimulus control, we would expect it to be relevant to the retention of stimulus control. (p. 270)

Conclusions

The two mechanisms described as being involved in recognition memory performance can co-occur: A change in response strength may be discriminated while additional perceptual or motor responses are evoked after the presentation of a subset of stimuli that were presented during an original event. Familiarity and recollection are, however, considered to be independent, in principle, from one another. For example, a person without a hippocampus may still be able to discriminate changes in response strength (e.g., Fortin, Wright, & Eichenbaum, 2004), yet a person without the perirhinal cortex may be able to discriminate additional perceptual responses without discriminating variations in response strength relative to the specific stimulus presented (Bowles et al., 2007). The relative independence of the two mechanisms involved in recognition memory performance is proposed by dual process theories of recognition (e.g., Yonelinas, 2002). Even if dual process theories tend to ascribe familiarity to the perirhinal cortex and recollection to the hippocampus, some researchers (e.g., Wais, Wixted, Hopkins, & Squire, 2006) argue that both structures are involved in expressing strength of a response (familiarity) and in allowing reactivation of complex perceptual responses (recollection).

From this analysis, there are a number of possibilities for applied behavior–analytic research that explores the mechanisms involved in mnemonic behavior from a neuro-operant standpoint through stimulus control manipulations. One interesting analysis relates to how the repertoires of interest in mnemonic behavior (i.e., response strength and/or perceptual responses) come under stimulus control. Research in this area would involve carefully constructing histories of reinforcement with stimuli under systematically varied conditions with corresponding test conditions. This might aid researchers in discovering the variables in one’s reinforcement history that bring changes in the discriminability of response strength or perceptual responses after a period of time without practice. In addition, alterations in test condition variables may give insight into different experimental conditions that either strengthen or weaken the probability of these discriminations. Numerous variations of stimulus features in isolation or in combination could be systematically varied in such studies. Results of such investigations, combined with neuro-operant measures, may help us to gain a better understanding of mnemonic behavior-related phenomena such as Alzheimer’s disease (AD) and posttraumatic stress disorder (PTSD).

From a neural perspective, research on AD has already pointed to an early deterioration of the neural circuitry in cornu ammonis 1 (CA1) of the hippocampus and the

entorhinal cortex within the broader medial temporal lobe (e.g., Neuman et al., 2015; Price et al., 2001). Given the looped structure of the hippocampal formation, disruption of one area may be enough to impair the role of the hippocampus in allowing supplementary sensory–perceptual responses to be evoked by the current environment. In other words, stimulus control–based remembering, or recollection, is expected to be impaired in AD. A neurobehavioral intervention may be based on devising a specific procedure to selectively increase the portion of gray matter in vulnerable areas of the hippocampus, as structural changes have been found to be strongly related to experience-dependent plasticity. For example, participants can be trained to accurately perform DMTS tasks with a progressively increasing delay and then can be slowly introduced to study–test procedures with a large number of items (more closely resembling the moment-to-moment richness and complexity of natural environments) embedded within specific contexts. In the test phase, the resemblance of the context in which items are presented could be manipulated while keeping accuracy constant, thereby training participants to recollect in situations that are progressively dissimilar from the original context. Practice with this kind of “progressive recollection” task may allow patients within a vulnerable population to preserve key hippocampal substructures such as CA1 and potentially delay the onset of full-blown AD. Perhaps opposite to AD in relation to recollecting behavior, PTSD is characterized by maladaptive remembering (e.g., Ortu, 2015; i.e., remembering that occurs repeatedly and in a disruptive fashion, even in environments that are apparently completely unrelated to the traumatic context). In this case, the progressive recollection task could be aimed at selecting (by reinforcement) the occurrence of supplementary sensory–perceptual responses only when the test environment is closely related to the study context, but not when the two contexts are dissimilar.

Finally, the attempts provided here and elsewhere (e.g., Donahoe, 2017; Palmer, 1991; Skinner, 1974) to reinterpret portions of mnemonic behavior from a neuro-operand perspective may help to eventually simplify the current taxonomy of learning and memory and further a collaboration between fields that have so far proceeded independently while both dealing with the difficulties of understanding complex behavioral phenomena.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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