Recognition Memory: The Role of Recollection and Familiarity

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Abstract

Recognition memory is perhaps the simplest and most widely studied measure of episodic memory. Behavioral and neural studies have examined a variety of different types of recognition tasks and shown that recognition judgments can be based on two functionally and neurally separable processes (i.e., the recollection of qualitative or relational information about the study event, and assessments of item familiarity). In the current chapter we provide a brief review of the literature by considering the different types of recognition tests commonly used in studies of humans and rodents, we show why there is a need to include multiple point measures of recognition such as receiver operating characteristics, and we consider the evidence showing the separability of the different processes underlying recognition. We then consider the progress that has been made in behavioral studies characterizing the functional nature of those processes, as well as lesion and neuroimaging studies examining the role of different medial temporal lobe regions in supporting recognition judgments. The results of these studies have been important in assessing a number of competing theoretical claims about the processes underlying recognition, in characterizing memory changes in various conditions such as aging and amnesia, and in developing neurocomputational models of recognition and the medial temporal lobes. Moreover, these findings have been useful in revealing how different recognition processes are related to other cognitive functions such as those underlying emotion, implicit memory, working memory and perception.

1. Introduction: What is recognition, why is it important, and how do we measure it?

The ability to remember episodes from our past is one of the most remarkable and mysterious cognitive abilities we possess. The importance of episodic memory becomes most obvious when it fails us, such as the awkward situation when we recognize a person as familiar but are unable to remember where or when we encountered that person before—or, even worse, when that acquaintance doesn't seem familiar at all. In this chapter, we will consider the processes that underlie episodic memory, and examine how the brain gives rise to these processes.

Our scientific understanding of episodic memory has been based, to a large extent, on studies of recognition memory. In its simplest form, sometimes referred to as "item recognition", subjects are first asked to study a list of items such as words, objects, or images. Then, after a delay, they are presented with a mixture of studied and nonstudied (i.e., new) items and are required to use their memory to indicate whether each item had been in the studied list or is new. Alternatively, in a "forced-choice" version of this task, subjects view multiple items at once and are required to determine which of those items was studied previously. These tests are said to be "episodic" in the sense that they require subjects to remember if an item occurred in a specific learning episode, which in the previous example is the studied list. The extent to which the recognition test requires memory for a specific study context, however, can vary considerably. For example, in “relational” recognition tests (sometimes called “associative” or “source” tests) the context information that the task requires is more specific than in standard item recognition tests. That is, the test may require subjects to determine if an item was studied in the first or second of two different study lists; whether it was studied in a specific location or was a specific color; or even if it was encoded in a specific way (e.g., “did you make a size judgment or pleasantness judgment about the item when it was studied?”). Additionally, there are “high-precision” recognition tasks in which the required specificity of the contextual decision can be increased even further by asking subjects to select the precise location, color, or orientation of the studied item.

The recognition memory literature is vast and we do not attempt to thoroughly review it here. Rather, we focus on a few key issues that have most strongly motivated our own work and the work of many of our colleagues, and we highlight some of the theoretical insights that have emerged from that work. We begin by considering why recognition memory has played such an important role in the science of memory. Then, we discuss the various methods that have been developed to measure it, and explore the evidence showing that recognition memory judgments can be based on two distinct memory processes: recollection and familiarity. We then briefly review behavioral studies that have been useful in testing competing theories, and finally consider neural studies examining the role of different brain regions in supporting these processes. Finally, we consider a theoretical framework emerging from the memory literature that we find to be quite useful for understanding recognition memory and integrating that literature with related work from studies of emotion, implicit memory, working memory and perception.

Why study recognition? Recognition has played a central role in the study of memory because of its simplicity, flexibility, and sensitivity. First, its relatively simple response requirements allow it to be utilized in human populations that may have difficulties with more complex memory tasks such as free recall. For example, recognition can be measured in infants—who may not have developed the verbal or executive abilities needed for a free recall test—by determining whether they preferentially look at old or new items in a set. In addition, recognition can be assessed in various nonhuman species such as rats, mice and monkeys. In a “delayed non-match to sample” task, these animals are often presented with a studied and a new item, and are rewarded for selecting the new item. Presumably, because the animal desires the food reward, they will select the new item to obtain the reward if they are able to recognize the studied item. Alternatively, animals’ innate tendency to prefer novel stimuli is leveraged in the “novel object recognition” task whereby memory is inferred when the animal prefers to explore a new item more than a previously studied item. Thus, the simplicity of recognition memory tasks has been important in allowing researchers to examine episodic memory in a wide variety of human and nonhuman groups, and therefore to utilize pharmacological, lesion and neural monitoring methodologies that may not be otherwise possible.

In addition, recognition tests are extremely flexible in the sense that they can be used to assess memory for a wide variety of materials (i.e., visual or auditory information, simple objects, complex text, etc.). Moreover, the extent to which any given recognition task measures the retrieval of specific or general episodic information can easily be manipulated by varying the nature of the contextual information that is required by the task. For example, some tasks may require retrieval of more specific contextual information such as the precise location in which an item was studied, whereas other tasks may require only general contextual information such as whether an item was studied in the top or bottom half of a screen. As described below, this has been important in separating different types of memory processes that underlie recognition. In addition, recognition lends itself well to neuromonitoring methods such as event related potentials (ERPs), and functional magnetic resonance imaging (fMRI). Because recognition tests involve presenting the items at both encoding and retrieval, one can examine the neural signals related to successful encoding, successful retrieval, and interactions between encoding and retrieval processes. This has proven useful for determining the brain regions and networks that are involved in different memory processes, as well as for characterizing the temporal dynamics of how those processes unfold over time as the items are encoded and retrieved.

Finally, recognition is quite sensitive to a large array of different experimental manipulations, making it a useful tool for researchers interested in understanding the conditions that lead to improved or impaired memory (Diana & Reder, 2006; Yonelinas, 2001b, 2002). In addition, recognition tasks have also proven useful in characterizing the specific memory deficits observed in a variety of populations such as healthy aging (Koen & Yonelinas, 2016), Alzheimer's disease (Koen & Yonelinas, 2014; Wolk, Dunfee, Dickerson, Aizenstein, & DeKosky, 2011) and schizophrenia (Libby, Yonelinas, Ranganath, & Ragland, 2013).

Recognition tests, however, are not without their limitations. For example, they are generally less sensitive to processes that allow us to mentally organize and search through our memories than are tasks such as free recall, where subjects are required to search memory and produce previously studied items without any external memory cues. Thus, the search strategies often involved in recalling past events may not be well indexed by recognition tasks. As a classic example, free recall is quite sensitive to deficits in strategic search processes that are often associated with frontal lobe pathology, and so free recall tests can provide a more sensitive index of some types of cognitive disorders (Stuss, 1994).

Another limitation of recognition tests is that it is difficult, and sometimes impossible, to separate recognition accuracy (i.e., the ability to correctly discriminate between old and new items) from response bias (i.e., the tendency to endorse both old and new items as having been studied). Thus, the proportion of studied items that is correctly recognized (i.e., hits) may increase either because of an increase in memory accuracy or because of a more liberal response bias. This issue becomes even more complicated if there is more than a single memory process that contributes to recognition, as memory accuracy itself can then increase for very different reasons. One way of separating response bias from the various memory processes that contribute to recognition memory is to examine performance as response bias is varied, and this approach is outlined next.

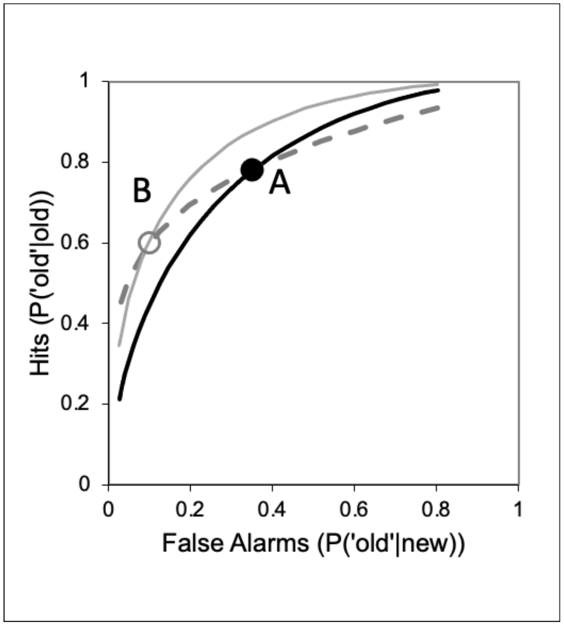
<u>The importance of measuring Receiver Operating Characteristics (ROCs) when assessing recognition accuracy {NOTE - this heading is underlined}.</u> Imagine that you have two groups of subjects (e.g., A and B), and you want to determine if recognition memory is different in the two groups (e.g., You may want to know if a new experimental drug improves memory, or if one set of encoding conditions leads to more accurate eyewitness testimony than another, or if

there are differences in memory between two different patient populations.). To assess this, you have subjects study a list of pictures, then after a delay you present them with a mixture of old pictures from the study list mixed with new pictures that were not studied, and you ask subjects to indicate if each picture is ‘old’ or ‘new’. This might produce the results illustrated in the scores in Table 1 and the two points plotted in Figure 1, where the hit rate is the probability of correctly responding ‘old’ to an old item, and the false alarm rate is the probability of incorrectly responding ‘old’ to a new item.

Table 1.

	Condition A	Condition B
Hits (P(’old’|old)	.78	.60
False Alarms (P(‘old’|new))	.35	.10

Figure 1.



How do we determine if memory is better in one condition than another? Because condition A has a higher hit rate (i.e., more of the studied pictures are recognized) than condition B, this might suggest that memory is better in condition A. However, condition A also has a higher false alarm rate (i.e., more of the new pictures are incorrectly recognized as having been studied). So memory may not be better in A, rather subjects in that condition may just have adopted a more liberal response criterion and so exhibit a greater tendency to respond ‘old’. This could happen for several different reasons. For example, B may require higher levels of memory strength than A before they are willing to respond ‘old’. Alternatively, B may respond ‘old’ only when they can remember specific details about studying the image (e.g., “I remember that this picture was the second picture in the list and it reminded me of my summer in the Sierra’s”), whereas A may respond ‘old’ even if the item is highly familiar even if they cannot recollect any specific details about the study event itself (i.e., “That picture is highly familiar so I think it was probably in the study list”). In either case, based on the data you have collected you can’t tell if the observed differences between A and B reflect differences in memory per se, or differences in the criterion that subjects used to make those memory responses.

In order to determine if memory is actually different in these two conditions, one useful approach is to examine ROCs which will allow you to determine how hits and false alarms change as response criterion is varied. So rather than just measuring memory at a single response criterion, you would measure it at several different points so that you can determine how memory changes across a range of different response criteria, and in this way you can plot the memory function (i.e., the operating characteristic) rather than just a single point on that function. You can then compare the ROC functions that are observed in condition A and B to determine if memory truly differs across these conditions as response criteria is varied. One way to plot an ROC is to ask subjects to rate their confidence of each response, and plot hits and false alarms as a function of confidence. This produces a memory function, rather than a single memory point on ROC space, where the points more to the left side of the ROC reflect higher confidence 'old' responses, and each subsequent point includes less and less confident responses.

For the two conditions in Figure 1 you would plot the observed ROC function for each condition and compare those ROCs. If they produced the same shaped ROC functions then you can conclude that memory is similar in those two conditions. For example, A and B may both produce an ROC that looks like the dashed curve in Figure 1, which indicates that when you control for differences in response criterion, memory is comparable in the two conditions. In contrast, if the shapes of the ROCs in the two conditions differ from one another this would indicate that there are differences in memory in the two conditions. For example, the observed ROCs in the two conditions might look like the two solid curves in Figure 1. In this case, you would conclude that memory is better in B than in A because the ROC is always higher for B than A. Finally, the shapes of the observed ROCs may be different, such that they may intersect one another at one level of response criterion, but then diverge as the response criterion becomes more or less strict. For example, B may produce the dashed ROC and A may produce the lower solid ROC. In this case, one would conclude that whether there is a difference in memory between the two conditions depends on the response criterion that is adopted. As described below, the shapes of the ROCs that are actually observed in different recognition memory conditions can vary in a number of different ways, and so it is essential to directly measure the ROCs in a new experiment in order to separate the effects of memory from those of response bias.

Note that another method of measuring recognition is to use a forced-choice test whereby subjects are presented with an old item along with a number of new items and are asked to select the old item. This produces a single-parameter measure of memory (i.e., probability correct). This measure is not dependent on response criterion per se, because subjects don't have to set a response criterion, rather they just have to select the strongest of the two items. Thus, this procedure could be used to determine if overall recognition discrimination is comparable across conditions in a test in which subjects don't need to set a response criterion. However, such a forced-choice test does not provide a measure of the underlying memory ROCs and so it does not in itself tell us if memory changes as response bias is varied (for a comparison of old/new and forced choice recognition tests see Kroll et al., 2002). In this way, exactly the same force-choice score could arise in two different conditions for entirely different reasons (e.g., two conditions corresponding to the two ROCs passing through point A in figure 1) and so forced-choice performance would be unable to detect this. For this reason, old/new ROC procedures are generally preferable.

The important practical take-way from the ROC results is that a single point measure of recognition memory (i.e., measuring memory at only a single level of response criterion) is not adequate to characterize recognition memory and to separate the underlying memory processes from factors like response bias. Thus, multiple-point measures of performance such as ROCs are needed in order to adequate to characterize recognition memory.

2. The processes underlying recognition: recollection and familiarity.

Since the time of Aristotle, it has been apparent that not all recognition memory judgments are the same. In some cases, recognition can be based on *recollection*, which is the retrieval of qualitative details about the specific study event, such as remembering when or where you met someone before. In other cases, however, recognition can be based on a sense of *familiarity* in the absence of recollective detail; for example, when you recognize someone as familiar but are unable to remember anything about the circumstances of how you know them. The distinction between recollection and familiarity-based recognition has long been discussed by philosophers such as Aristotle and William James, and has been examined by a host of modern human memory researchers including Richard Atkinson, George Mandler, Larry Jacoby, Lynn Reder, and Endel Tulving, as well as a number of neurobiological and animal learning researchers such as Malcolm Brown, John Aggleton, Magdalena Sauvage, Howard Eichenbaum, Daniela Montaldi and Andrew Mayes — to name just a few (Aggleton & Brown, 1999; Diana & Reder, 2006; Eichenbaum, Yonelinas, & Ranganath, 2007a; Montaldi & Mayes, 2010; Rugg & Yonelinas, 2003; Yonelinas, 2002). The term 'familiarity' here refers to the strength of contextually-mediated episodic information rather than semantic/perceptual information. For instance, I may know that the animal in front of me is a dog, and it is thus familiar in the colloquial sense of the term, but this is distinct from *episodic* familiarity in which I know that this specific dog was previously encountered.

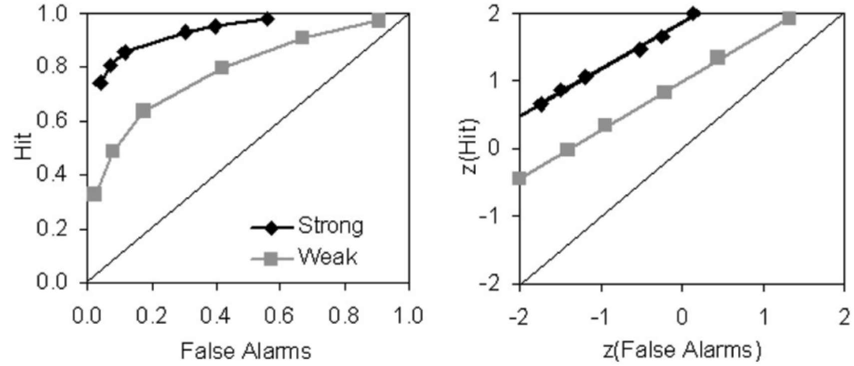
One potential account of the recollection/familiarity distinction is that recollection simply reflects stronger memories than familiarity, which is consistent with a variety of *strength*, or *single process*, theories of recognition (Dede, Wixted, Hopkins, & Squire, 2014; Donaldson, 1996; Dunn, 2004; Egan, 1958; Wixted & Squire, 2010, 2011). So by this account the recollection and familiarity distinction simply reflects stronger and weaker memories rather than reflecting a meaningful behavior or neural distinction. If recollection and familiarity reflect the same underlying form of memory then they should in general behave in similar ways and reflect the same underlying memory mechanisms. There are in fact experimental manipulations that do have similar effects on both recollection and familiarity (e.g., Dunn, 2004; Yonelinas 2002). However, an extensive body of research has indicated that recollection is not simply strong familiarity; rather, they reflect two functionally and neurally distinct memory processes. That is, recollection and familiarity are found to be behaviorally dissociable and to rely on separable brain networks. For example, some experimental manipulations are found to impact recollection, but not familiarity, whereas others are found to impact familiarity but not recollection (e.g., for reviews See Yonelinas, 2001, 2002; Diana & Reder, 2006; Eichenbaum et al., 2007; Brown, Warburton & Aggleton, 2010). Early behavioral examples came from studies showing that response speed deadlines disrupt relational recognition more than item recognition (Hintzman, Caulton, & Levin, 1998; Gronlund, & Ratcliff, 1989); that is, when one has very little time to make a recognition decision, relational recognition is especially impaired. In contrast, over short delays, item recognition deteriorates more rapidly than relational recognition, suggesting that item familiarity decreases more rapidly over brief periods of time (Hockley, 1992; Yonelinas & Levy, 2002). These dissociations, as well as numerous other behavioral and neural dissociations discussed below support the notion that recognition memory involves at least two separable underlying processes or forms of memory, and single-process models cannot easily account for these types of systematic dissociations.

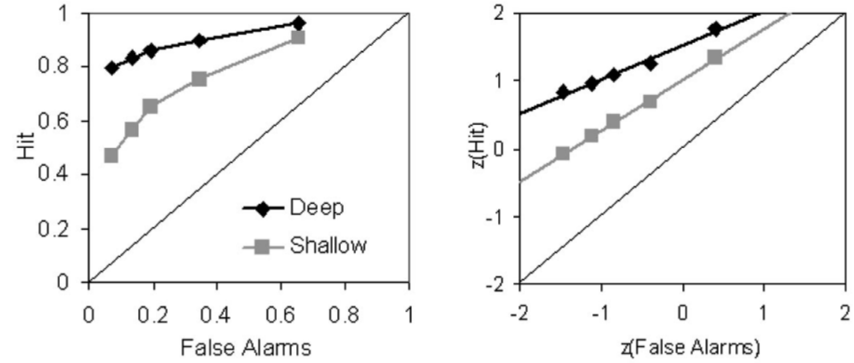
Although there is little doubt that more than one memory process is needed to account for the observed dissociations between item and relational recognition tests, it has been suggested that in tests of item recognition, subjects may rely, at least sometimes, solely on familiarity (e.g., Donaldson, 1996; Dunn, 2004; Wixted & Squire, 2010, 2011). Thus, item recognition might provide a process-pure measure of familiarity (for an early critique of this possibility see Jacoby, 1991). However as described in Box 1, ROC studies of item and associative recognition show evidence of both recollection and familiarity, and they reveal why single point measures of recognition are inadequate in characterizing recognition memory.

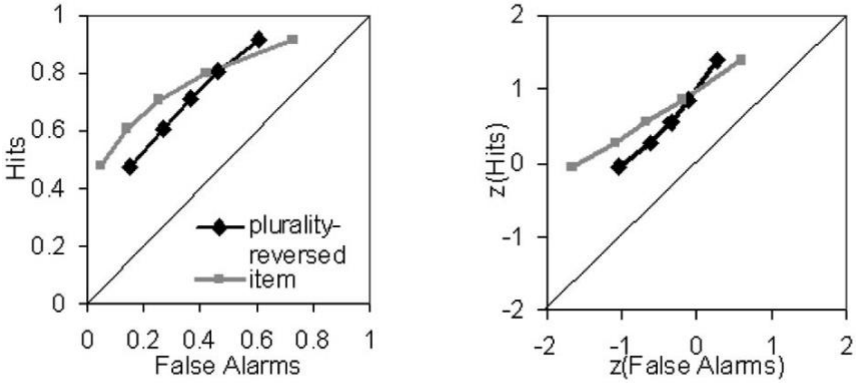
Box 1. An examination of ROCs shows that single factor models and single-point measures of memory are inadequate to characterize item recognition and associative recognition {NOTE – this heading is underlined}.

Figure 2 A & B illustrates the types of ROCs that have been observed in studies of item recognition memory (i.e., subjects must discriminate between studied items and novel items, and indicate their response confidence). Importantly, the ROCs are generally curved downward, and in addition, they can vary with respect to how high they are (i.e., how good memory is), and they can vary in the degree to which they are asymmetrical (i.e., the ROCs appear to be pushed up on the left side, rather than being symmetrical along the diagonal). To characterize the shape of the ROCs it is traditional to re-plot the ROCs in z-space which leads the ROCs to be approximately linear (right side of Figure 2). Plotted in this way, the intercept of the linear function reflects the height of the ROC, and the slope of the function reflects the degree of asymmetry such that symmetrical ROCs have a slope of 1 and the asymmetrical ROCs like those in Figure 2 have slopes less than 1.

Generally, item recognition ROCs have slopes less than 1 when performance is above chance, but in addition, different experimental manipulations impact ROC slope quite differently (e.g., Yonelinas, 1994). For example, as illustrated in Figure 2 with simple strength-based encoding manipulations like increasing study duration or number of repetitions, the ROCs shift upward, but the ROC slope remains constant (e.g., Ratcliff, et al., 1994; for a review see Yonelinas & Parks, 2007). In contrast, with more elaborative encoding manipulations such as semantic compared to perceptual encoding instructions (e.g., during encoding, participants are asked to answer questions about either semantic or visual features of each word) the ROCs shift upward while the slope decreases (e.g., Yonelinas 2001; for a review see Yonelinas & Park, 2007). The finding that ROC height and ROC asymmetry are functionally dissociable indicates that there is no single-parameter model of item recognition that can adequately describe performance. Essentially, one needs two separable factors or processes to account for the observed dissociations.







But what are those two factors? One account of these results described the main text is that they reflect the effects of recollection and familiarity (Yonelinas, 1994; Yonelinas et al., 2001). That is, familiarity is assumed to be a signal detection process (Swets, 1962) whereby familiarity strength is used to make recognition judgments. Familiarity strength is assumed to have some variability from one item to the next and so forms two normal distributions where the studied item distribution is more familiar on average than the new item distribution. The distance between the two distributions reflects familiarity strength and is typically measured as a d' value. If familiarity strength is used to make confidence judgments this results in a perfectly symmetrical ROC (when plotted in z-space the function would be perfectly linear and the intercept would be d'). In addition, however, if subjects can recollection specific information about the study event for some of the studied items this will support relatively high confidence responses compared to familiarity, and would effectively push the ROC up, producing the observed ROC asymmetry. In this way, the dissociations observed in ROC studies of item recognition can be explained as reflecting the differential effects of different manipulations on recollection and familiarity. That is, recollection will impact the degree of ROC asymmetry whereas familiarity will impact how curved the resulting ROC is.

Another approach is to adopt a 2-parameter signal detection account referred to as the unequal variance signal detection model, whereby one parameter (i.e., d') reflects overall memory strength (i.e., how much stronger the old items are compared to the new items), and a second memory parameter reflects how much more or less variance there is in the memory strength of the old compared to the new items. For example, it has been proposed that because there is variability in how well each studied item is encoded this can lead the old item variance to be greater than that of the new items (Wixted, 2007). Because strength and variance are separate parameters they can be independently manipulated and so could account for the two factors seen in recognition memory. However, the unequal variance model has been criticized on a theoretical basis because it leads to some knotty theoretical problems (Green & Swets, 1966; DeCarlo, 2002) such as predicting below chance performance as old item variance increases. In addition, studies designed to increase encoding variability have failed to provide any evidence that the greater old item variance is due to encoding variability (Koen & Yonelinas 2010; Starns, Rotello & Ratcliff, 2012; Koen, Aly & Wang, 2013; Koen & Yonelinas, 2013: Spanton & Berry, 2020). Rather they suggest that the increased old item variance is due to the fact that there are two process (namely recollection and familiarity) that contribute to old item strength (e.g., Koen, Aly & Wang, 2013). Additional evidence against the unequal variance account and in direct support of the dual process account comes from parameter validation studies showing that the asymmetry observed in item recognition ROC is accurately predicted by subjective reports of recollection and as well as by objective measures of recollection such as the ability to accurately retrieve source and associative information - a relationship that is not predicted on the basis of the unequal variance signal detection approach (for reviews see Yonelinas, 2001; Yonelinas, Aly, Wang & Koen, 2010; for a discussion of modifications and alternative modelling approaches see Parks & Yonelinas, 2007).

Perhaps the strongest evidence against the unequal variance model and in favor of the dual process model comes from studies designed to directly pit the *a priori* predictions of those models against one another. For example, although in item recognition the two models can produce ROCs that are almost identical, according to the dual process model, under conditions in which performance is expected to rely more heavily on recollection the ROCs should become more linear (and U-shaped in z-space). In contrast, according to the unequal variance model the ROCs should always be curved and perfectly linear in z-space. This prediction was initially tested in studies of associative recognition where subjects discriminated between intact and rearranged word pairs (Yonelinas, 1997), in source memory tests where subjects discriminated between items from differences sources (Yonelinas, 1999; e.g., left or right side of the screen, or spoken by male or female), and in plurality tests where they discriminated between words studied in either singular or plural forms (Rotello et al., 2000). As illustrated in Figure 2C, whereas item recognition judgements produce ROCs that are curved (and linear in z-space), relational ROCs are linear (and markedly U-shaped in z-space). These results support the predictions of dual process model and contradict those of the unequal variance model.

We note that an important weakness of the dual process signal detection model is that it is an overly simplistic 'measurement models' and it cannot be expected to capture all of the processes or factors that can influence recognition memory. It is useful in the sense that it can provide a way of characterizing recognition using only a small number of free parameters, and so it allows researchers to begin to separate the effects of response bias from the different underlying memory processes. However, in order to do this it needs to make simplifying assumptions. For example, the model assumes that familiarity can be measured as a d' value and that recollection can be measured as a simple probability. Moreover, the model in itself says nothing about the neural substrates of these underlying processes. We and many others have taken up the task of addressing these issues by developing more complex models that incorporate other important aspects of performance such as providing a more complete characterization of the shape and the functional nature of the recollection strength distributions (Elfman, Aly & Yonelinas, 2014; Harlow & Yonelinas, 2016; Rotello, Macmillan, & Reeder, 2004; Sherman, Atri, Hasselmo, Stern, & Howard, 2003), and that consider alternative ways in which recollection and familiarity information may be combined such as summing and mixing models (Rotello, Macmillan, & Reeder, 2004; Weidemann & Kahana, 2019; Wixted & Mickes, 2010; Cha & Dobbins, 2021), as well as by developing computational and neurobiological models that consider the role that different brain regions play in supporting the neurocomputations underlying these recognition processes (Bogacz & Brown, 2003; Elfman, Aly & Yonelinas, 2014; Norman & O'Reilly, 1993). The extent to which each of these different approaches provide better accounts of memory than the simple measurement models, and how they compare to one another is yet to be fully determined. Future studies that directly compare the different models across a wide range of different recognition tests, experimental conditions and in different subject populations will be critical (for an early review and a more extensive consideration of other alternative models see Yonelinas & Park, 2007).

3. Measuring recollection and familiarity.

Given that recognition can rely on recollection and familiarity, a number of procedures have been developed to separate the contributions of these different processes to overall performance (Yonelinas, 2002). One common approach is to utilize "task dissociation" methods, which take advantage of the fact that different types of tests can differentially rely on recollection and familiarity. For example, because relational recognition tests require subjects to remember specific details about the study event, these tests likely rely heavily on recollection. In contrast, familiarity should be more useful for item recognition tests in which subjects are asked to discriminate between studied and nonstudied items. Various dissociations have been observed across item and relational recognition tasks, indicating that that this task dissociation approach can be useful in separating recollection and familiarity. However, as mentioned earlier a potential shortcoming of this approach is that because recollection can contribute to both relational and item recognition tests (i.e., item recognition does not provide a "process pure" measure of familiarity), the task dissociation method cannot be relied on to always separate the contribution of these two processes (Jacoby, 1991; Yonelinas & Jacoby, 2012).

Another approach is to use “process estimation methods” designed to provide quantitative parameter estimates of recollection and familiarity. One such approach is based on Endel Tulving’s remember/know procedure ((Tulving, 1985); also see (Yonelinas & Jacoby, 1995), in which subjects are required to introspect about the basis of their memory judgments and report whether they recognize each item on the basis of remembering (i.e., recollection of episodic information about the study event) or knowing (i.e., the item is familiar in the absence of recollection). Because subjects are instructed to respond “remember” whenever they recollect a test item, the probability of a remember response can be used as an index of recollection. In contrast, because subjects are instructed to respond “know” whenever an item is familiar and not recollected, the probability that an item is familiar will be equal to the probability that it received a “know” response given it was not recollected. Another approach is to use Larry Jacoby’s process dissociation procedure (Jacoby, 1991); also see (Yonelinas & Jacoby, 2012) in which one measures recollection as the ability to retrieve where or when an item was studied, and familiarity as the ability to recognize an item given that it was not recollected. This approach takes advantage of the fact that the episodic details accompanying recollection could allow one to remember when or where an item was studied, whereas familiarity-based memory would lack these details. Another method is to examine receiver operating characteristics (ROCs), which are typically derived by requiring subjects to rate the confidence of their recognition responses and then plotting hits (i.e., proportion of old items endorsed as old) against the false alarms (i.e., the proportion of new items endorsed as old) as a function of response confidence. Similar ROCs can also be derived by varying the payoffs or rewards for different responses and plotting performance across these conditions – a procedure that has been used effectively with both humans, rodents and nonhuman primates (Guderian, Brigham, & Mishkin, 2011; (Eichenbaum, Fortin, Sauvage, Robitsek, & Farovik, 2010; Koen & Yonelinas, 2011). The observed ROC is then quantified by fitting a nonlinear function to the observed data to derive estimates of recollection and familiarity (Yonelinas, 1994, 2001a). The approach is similar to the way in which a regression analysis can be used to estimate the slope and intercept of a line (for a review of the ROC literature see (Yonelinas & Parks, 2007), and for software for fitting ROC data see (Koen, Barrett, Harlow, & Yonelinas, 2017)).

Each of the measurement methods assesses recollection and familiarity in different ways, and each has its advantages and disadvantages. For example, each method relies on important assumptions (e.g., the extent to which tasks are process pure, the nature of the functional relationship between the two processes, the extent to which the processes are available to subjective awareness, and the nature of the underlying familiarity and recollection strength signals), and when these assumptions are violated, it can bias the derived parameter estimates (for earlier discussions of potential measurement issues and the best practices to minimize these concerns, see (Mayes et al., 2019; Parks, Murray, Elfman, & Yonelinas, 2011; Yonelinas, 2002; Yonelinas & Parks, 2007). However, under conditions designed to avoid these measurement issues, studies that have directly contrasted the methods described above have indicated that they typically lead to convergent conclusions (Chan & McDermott, 2007; Koen & Yonelinas, 2016; Yonelinas, 2001c, 2002; Yonelinas & Jacoby, 1995; Yonelinas, Kroll, Dobbins, Lazzara, & Knight, 1998); but see (Prull, Dawes, Martin, Rosenberg, & Light, 2006). The convergence of results across these diverse measurement methods attests to the construct validity of the recollection/familiarity distinction, and suggests that the various task dissociation and process estimation methods provide a relatively unbiased view of these processes. Nonetheless, an approach that we endorse is to look for convergence in any given effect across a variety of measurement methods in order to avoid potential biasing effects that may impact any individual method. This approach is also useful because there may be conditions in which the different measures of recollection do not fully agree, and the sources of these discrepancies can be particularly informative. For example, as described in more detail below, negative emotional items compared to neutral items are associated with greater recollection for specific details of study items, but not greater recollection of the encoding context (Yonelinas & Ritchey, 2015a), suggesting that different types of recollection may be dissociable.

4. Behavioral Properties: Testing Alternative Dual Process Accounts of Recognition.

An extensive literature has focused on determining the behavioral characteristics of recollection and familiarity by assessing the effects of different experimental variables on these two types of recognition (Table 1 summarizes key findings). These studies have indicated that whereas some manipulations only impact recollection, others only impact familiarity. Such double dissociations have not only called into question single-process accounts; they have also been essential in developing and testing competing models of recollection and familiarity.

Retrieval manipulations. The differences between recollection and familiarity have been most obvious in studies examining manipulations during memory retrieval. For example, studies have shown that either speeding recognition responses or dividing subjects' attention during retrieval reduces recollection, but leaves familiarity relatively unaffected (Benjamin & Craik, 2001; Gruppuso, Lindsay, & Kelley, 1997; Toth, 1996; Yonelinas & Jacoby, 1994). These findings support models that have proposed that familiarity is a relatively automatic memory process, whereas recollection is a slower, more controlled search process (Jacoby, 1991; Mandler, 1980). In contrast, manipulations that increase the processing fluency of the test items, such as subliminal priming of the test items, increases the likelihood that items will be judged as familiar but does not generally impact recollection (Lecompte, 1995; Rajaram & Geraci, 2000). Similarly, manipulations encouraging a more relaxed response criterion—that is, encouraging participants to endorse items as old even when they are not highly confident that they are old—are found to increase the proportion of items that are judged as familiar, but to have little effect on recollection (Yonelinas, 1994, 2001c). These criterion manipulation results support models proposing that familiarity reflects a signal-detection-like process whereby both studied and nonstudied items are associated with some level of familiarity, but studied items are generally more familiar than nonstudied items; whereas recollection reflects a threshold process whereby relational or contextual information is retrieved for some test items, but fails to be retrieved for other test items (Atkinson, 1974; Norman & O'Reilly, 2003; Yonelinas, 1994).

Encoding manipulations. The extent to which recollection and familiarity benefit from different encoding manipulations can also differ, but in general, encoding conditions that improve recollection also tend to improve familiarity. For example, increasing study duration or the number of times an item is repeated leads to similar increases in both recollection and familiarity (Gardiner & Radomski, 1999; Yonelinas, 1994). Moreover, elaborative encoding manipulations such as semantic compared to perceptual encoding, generating compared to reading words (e.g., thinking of an antonym of a presented word rather than just reading the word and its antonym), and fully focused compared to divided attention during encoding tends to increase both recollection and familiarity—but they have much larger effects on recollection than familiarity (for review see (Yonelinas, 2002)). These results provide partial support for early models that treated recollection and familiarity as reflecting semantic compared to perceptual forms of memory, respectively (Mandler, 1980), but indicate that familiarity is not limited to supporting only perceptual information. Rather, we interpret the encoding results to indicate that increased processing time benefits both recollection and familiarity, but that elaborative processing is particularly important in further increasing recollection.

Activation vs novel learning. A number of early models of recognition assumed that recollection was necessary for learning about new items and forming new associations, whereas familiarity supported the activation of existing items in semantic memory or of existing semantic associations (Atkinson, 1974; Mandler, 1980). Although it is clear that recollection is particularly important in forming new associations, it has become apparent that familiarity can also support novel learning. For example, both recollection and familiarity can support memory for novel items (e.g., nonwords, geometric shapes, novel faces), suggesting that familiarity does not simply reflect an increase in the activation of existing items in semantic memory. Moreover, although familiarity does not typically support memory for new associations such as random word pairs or random pairings of objects with colors or locations, it can do so when the

Table 1. The effects of various retrieval and encoding manipulations on recollection and familiarity. Each manipulation is described in more detail in the main text. The size of the arrow indicates the magnitude of the effect and the direction indicates whether the manipulation increases or decreased the process.

	Recollection	**Familiarity**
Retrieval		
Speeding Responses	↓	–
Divided Attention	↓	–
Increase Fluency	–	↑
Relax Response Bias	–	↑
Encoding		
Increase Duration/Repetition	↑	↑
Semantic vs Perceptual	↑	↑
Generation vs Read	↑	↑
Divided Attention	↓	↓

associations are ‘unitized’ and thus treated as single items rather than as arbitrary associations. For example, memory for arbitrary word pairs can be supported by familiarity if they are encoded as new compound words (e.g., the word pair ‘cloud-lawn’ is encoded as ‘a yard used for sky gazing’; (J. Quamme & Yonelinas, 2005; J. R. Quamme, Yonelinas, & Norman, 2007) or when colors are encoded as an integral part of the object (e.g., ‘the elephant is red because it is embarrassed’, (Diana, Van den Boom, Yonelinas, & Ranganath, 2011; Diana, Yonelinas, & Ranganath, 2008a); also see (Parks & Yonelinas, 2015; Yonelinas, Kroll, Dobbins, & Soltani, 1999). Although recollection is more effective than familiarity at supporting memory for the various associations that make up an event, these results indicate that familiarity can also support rapid learning of new associations when those associations are encoded as single items or units.

Additional dissociations. Recollection and familiarity have also been found to differ in other important ways. For example, recollection tends to be selectively disrupted by changes in context between study and test (Diana, Yonelinas, & Ranganath, 2013; Koen, Aly, Wang, & Yonelinas, 2013; Macken, 2002). This is consistent with the notion that recollection supports memory for specific contextual details, whereas familiarity is more dependent on item-related information. In addition, familiarity shows much more rapid forgetting across short retention intervals than does recollection (Hockley, 1992; Yonelinas & Levy, 2002), whereas recollection is more disrupted by learning interfering information (Norman, 2002; Yonelinas & Jacoby, 1994). These results have been interpreted as suggesting that recollection and familiarity are differentially sensitive to interference and decay processes ((Sadeh, Ozubko, Winocur, & Moscovitch, 2014, 2016); but also see (Norman & O'Reilly, 2003)). Related work has indicated that increases in similarity between retrieval cues and studied items lead to relatively linear increases in familiarity but lead to steeper and more thresholded increases in recollection, such that recollection can be said to have a sharper similarity gradient than familiarity (Elfman & Yonelinas, 2015). The results are consistent with other studies indicating that recollection is particularly important in providing ‘high-resolution’ associative information (Yonelinas, 2013), and that it may support highly precise spatial memory for item locations (Ramey, Yonelinas, & Henderson, 2019).

The two processes also have unique temporal trends across the lifespan, such that recollection develops more slowly than familiarity across infancy (Ghetti & Angelini, 2008), 2008), and shows more rapid decline in old age (Koen & Yonelinas, 2014, 2016). The electrophysiological signals related to recollection and familiarity are also found to be distinct: Scalp Event-Related Potentials (ERPs) related to familiarity are observed earlier and exhibit distinct scalp topographies compared to those related to recollection (Addante, Ranganath, & Yonelinas, 2012; Curran, 2000; Jaeger, Mecklinger, & Kipp, 2006; Rugg & Yonelinas, 2003). Similarly, oscillatory scalp activity appears to be quite different for recollection and familiarity-based recognition responses (Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011; Burgess & Ali, 2002; Gruber, Tsivilis, Giabbiconi, & Muller, 2008; Klimesch et al., 2001); but also see Weidmann & Kahana, 2019). These results are consistent with prior behavioral work showing that familiarity is available earlier than recollection. An extensive literature on recognition memory in rodents supports similar conclusions (for review see Atucha, Kitsukawa & Sauvage, 2017; (Brown & Aggleton, 2001) Brown & Banks 2015;). Also see Basile & Hampton, 2013).

Complementary Memory Processes. Why do we need to have two functionally distinct recognition processes, rather than just one? And how could these processes be implemented in the brain? Neurocomputational work has suggested that we may need two complementary learning systems to efficiently capture two different—and potentially competing—aspects of memory. That is, it has been suggested that we need to remember the details of specific events (i.e., recollection), as well as learn about the statistical regularities of the environment (i.e., familiarity or general knowledge of the world), and these two functions may be difficult to implement in a single system (McClelland, McNaughton, & O'Reilly, 1995); for similar ideas see (Marr, 1971; O'keefe, 1978; Sherry & Schacter, 1987). To overcome this problem, Jay McClelland, Randy O'Reilly and Ken Norman developed the Complementary Learning Systems (CLS) model which is based on known neuroanatomical properties of the medial temporal lobes (see top panel of Figure 3; (Norman & O'Reilly, 2003); also see (Elfman, Aly, & Yonelinas, 2014; Elfman, Parks, & Yonelinas, 2008; Elfman & Yonelinas, 2015)). The model is consistent with many of the earlier dual process theories of recognition, but it more directly links these processes to different brain regions and it provides a neurocomputational level of description not provided by most earlier models. As we hope to illustrate below, this approach is useful because it generates a number of novel testable predictions, and it provides principled explanations for some earlier findings—such as the work pointing to the threshold nature of the recollection process—that might seem particularly surprising from other theoretical perspectives.

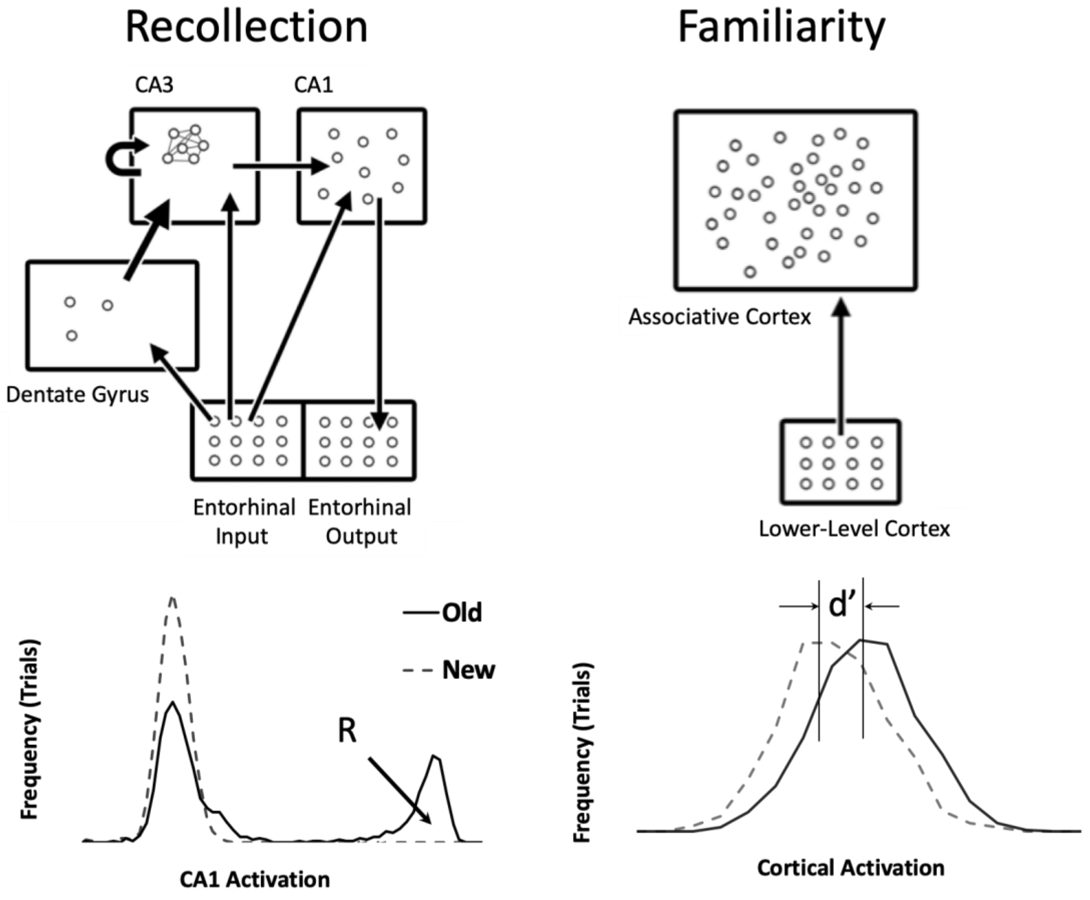
In the CLS model (see Figure 3), recollection is assumed to depend on the hippocampus, which supports a pattern completion process whereby qualitative information about a study event is retrieved. For example, when a study episode occurs, the hippocampus receives information about the item and the encoding context via the entorhinal cortex, and assigns each episode a relatively nonoverlapping representation in the Dentate Gyrus (DG) and region CA3 (the nonoverlapping representations arise because of the sparse levels of activity in the DG and high levels of lateral inhibition in CA3). Active units in CA3 are linked to one another and to a copy of the input pattern in CA1. In this way, at time of test, if a partial version of the study episode is presented as a retrieval cue, this leads to the reconstruction (i.e., pattern completion) of the original memory. For example, an object may be presented as a retrieval cue, and the hippocampus would pattern complete the details of the original study event which includes information about the item and the encoding context.

In contrast, familiarity is assumed to depend on cortical associative networks that are reliant on Hebbian learning and inhibitory competition. The idea is that units or networks of cells in the cortex surrounding the hippocampus compete to encode (via Hebbian learning) regularities that are present in the study events by altering the connectivity between units. In this way, at time of test, items that have been previously encoded will tend to have sharper representations than new items (i.e., new items will weakly activate many units whereas studied items will strongly activate a relatively small number of units). Thus, unlike the hippocampus which leads to the pattern completion of associated episodic details, the cortex provides a signal of stimulus familiarity.

The CLS model accounts for many of the behavioral results reported in studies of recollection and familiarity (Norman & O'Reilly, 2003). CLS has also generated several novel predictions that have subsequently been verified (Elfman et al., 2014; Elfman et al., 2008;

Elfman & Yonelinas, 2015). For example, one emergent property of the model that arises because of the known connectivity of the hippocampus and surrounding cortex is that the familiarity process produces a signal-detection-like signal (i.e., highly overlapping Gaussian strength distributions; see bottom right panel in Figure 1). In contrast, because the hippocampus will successfully pattern complete for some studied items but fail to pattern complete for others, it produces bimodal strength signals indicative of a threshold process. These results are in agreement with the behavioral studies indicating that recollection occurs for some studied items and fails to occur for others, whereas familiarity is well-described as a signal detection process (Parks & Yonelinas, 2009; Yonelinas, 2001b; Yonelinas & Parks, 2007). In addition, as will become clear below, the model is consistent with the evidence linking recollection and familiarity to the hippocampus and regions in the surrounding medial temporal cortex, respectively.

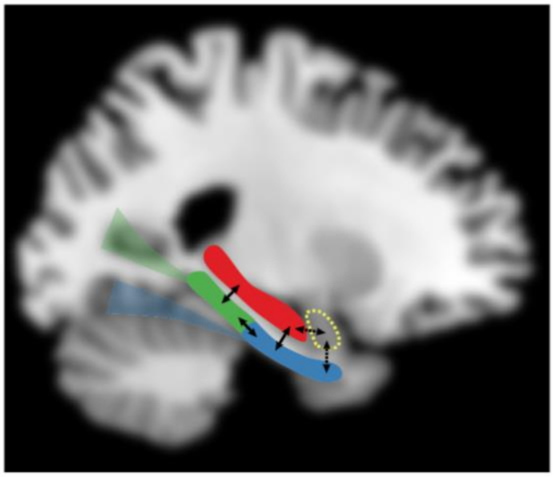
Figure 3. Hippocampal and cortical networks thought to underlie recollection and familiarity (Norman & O'Reilly, 1993; also see Elfman, Aly & Yonelinas, 2014). The hippocampus, which includes the dentate gyrus and CA3-CA1, is thought to form complex representations that bind together the various aspects of the study event that it receives from the cortex via the entorhinal cortex. At time of test, a partial retrieval cue is presented and either leads to successful pattern completion or it fails. This produces a thresholded bimodal recollection strength output in CA1 and the entorhinal cortex, with some proportion of old items leading to recollection (R in bottom left panel), and the remainder producing only very low levels of activity. In contrast, familiarity is dependent on cortical networks that are thought to associate the different aspects that make up a study event leading to a shift in the activation for old compared to new items (measured as d' in the bottom right panel).



5. The Role of the Medial Temporal Lobes.

Since the seminal studies of patient HM (Scoville & Milner, 1957) who became densely amnesic after a surgical resection of his medial temporal lobes (MTLs), it has become clear that the MTLs are essential for episodic memory. The MTL includes the hippocampus, the amygdala, the entorhinal cortex, the perirhinal cortex and the parahippocampal cortex (see Figure 4). Subsequent studies showed that patients with MTL damage are often able to discriminate between studied and non-studied items; however, they have particular difficulty discriminating

Figure 4. Regions in the medial temporal lobes involved in recollection and familiarity (i.e., the hippocampus (red), the amygdala (dotted yellow), the perirhinal cortex (blue) and the parahippocampal cortex (green)). The region between the hippocampus and the peri- and para-hippocampal regions is the entorhinal cortex.

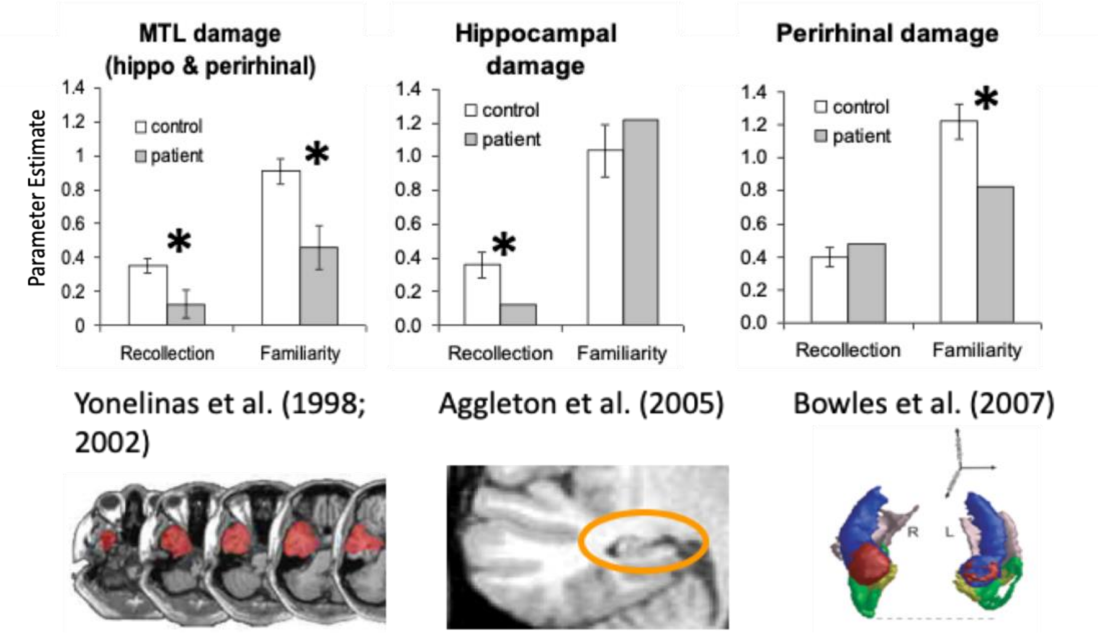


between recently and frequently presented items, suggested that the MTL may be particularly important for recollection compared to familiarity (Huppert & Piercy, 1978). The results, however, are not conclusive as to whether familiarity is completely preserved in these patients, because direct measures of recollection and familiarity were not obtained. Furthermore, they do not reveal which regions within the MTL might be involved in these processes, as the locations of the patients' lesions were often not clearly identified.

Subsequent studies using task dissociation as well as process estimation procedures including remember/know, process dissociation, and ROC methods showed that recollection is dependent on the hippocampus whereas familiarity is dependent on the perirhinal cortex. For example, results from ROC studies examining the effects of different types of MTL lesions on recollection and familiarity are illustrated in Figure 5. These studies demonstrated that patients with extensive MTL damage—similar to patient HM in that the hippocampus and the surrounding MTL cortex were damaged—were impaired in both recollection and familiarity (e.g., left panel of Figure 2; for similar results from a variety of different estimation methods see (Blaxton & Theodore, 1997; Knowlton & Squire, 1995; Verfaellie, 1993; Yonelinas et al., 1998; Yonelinas et al., 2002)). In contrast, patients with selective damage to the hippocampus exhibited selective deficits in recollection (e.g., middle panel in Figure 2; for similar results see (Aggleton et al., 2005; Bastin et al., 2004; Brandt, Gardiner, Vargha-Khadem, Baddeley, & Mishkin, 2008; Jager et al., 2009; J. R. Quamme, Yonelinas, Widaman, Kroll, & Sauve, 2004; Turriziani, Serra, Fadda, Caltagirone, & Carlesimo, 2008; Yonelinas et al., 2002). Finally, a patient with an intact hippocampus but partial damage to the perirhinal cortex was impaired in familiarity, but not recollection (e.g., right panel in Figure 2; (Bowles et al., 2007); also see (Brandt, Eysenck, Nielsen, & von Oertzen, 2016)).

Additional evidence linking the hippocampus to recollection came from studies examining the effects of damage to the fornix: a major fiber tract connecting the hippocampus to the thalamus, which may be key for processes drawing on the hippocampus. Several studies examining patients with fornix lesions have indicated that these patients exhibit selective deficits in recollection (Carlesimo et al., 2007; Vann et al., 2009); for similar results in rodents see (Easton, Zinkivskay, & Eacott, 2009). In fact, fornix damage appears to lead to selective recollection impairments in both anterograde amnesia (i.e., the inability to encode new memories) and retrograde amnesia (i.e., the inability to retrieve memories formed long prior to the lesion), (Gilboa et al., 2006). Moreover, neuroimaging evidence indicates that the white matter microstructural integrity of the fornix, as measured with diffusion weighted imaging, is correlated with recollection but not familiarity (Rudebeck et al., 2009).

Figure 5. The effects of MTL damage on recollection and familiarity. Studies of recognition ROCs indicate that hippocampal damage leads to selective recollection deficits, and perirhinal cortex damage leads to selective familiarity deficits; patients with damage that includes both the hippocampus and the surrounding perirhinal cortex exhibit deficits in recollection and familiarity. Parameter estimates of recollection are measured as probabilities whereas familiarity is measured as d'. Note that similar results have been obtained using a variety of different measurement methods (see main text). Error bars reflect +/- 1 SEM, and bars without error bars present individual patient estimates.



Yonelinas et al. (1998; 2002)

Aggleton et al. (2005)

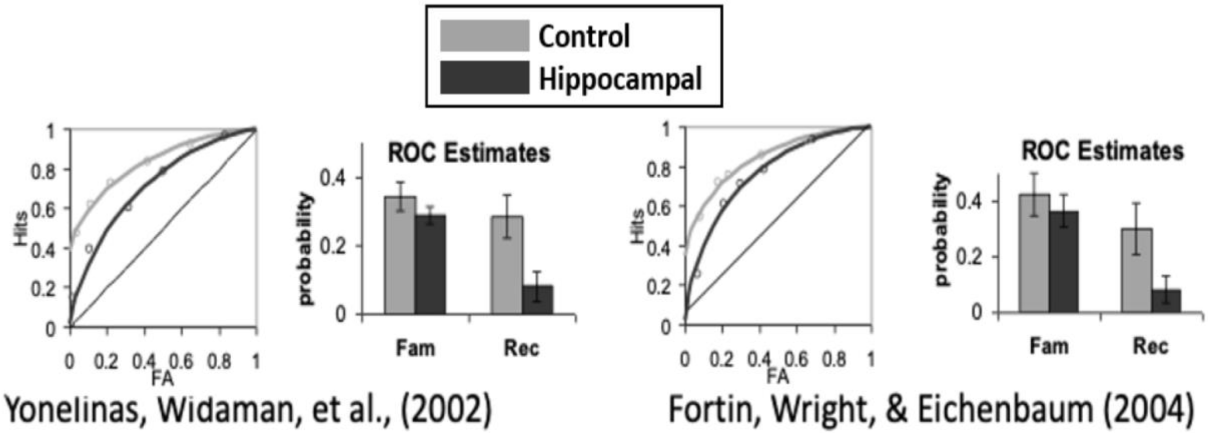
Bowles et al. (2007)

Similar dissociations have been observed in studies of aging, which indicate that age-related reductions in hippocampal volume are associated with declines in recollection, but not familiarity, whereas differences in cortical volume within the surrounding MTL cortex, including the perirhinal and entorhinal cortex, are related to familiarity, but not recollection (Wolk et al., 2011; Wolk, Signoff, & DeKosky, 2008; Yonelinas et al., 2007).

The above results from studies in humans have been further supported by results from studies of rats. For example, lesion and activation studies of rats indicate that the hippocampus is particularly important for recollection, as measured on spatial navigation tasks and object-location recognition tasks that require memory for object-location associations, whereas the surrounding medial temporal lobe cortex is sufficient to support familiarity, as measured in delayed nonmatch-to-sample and novelty preference tasks (Aggleton & Brown 2010; (Aggleton & Brown, 1999; Eichenbaum, Otto, & Cohen, 1994; Eichenbaum et al., 2007a; Good, Hale, & Staal, 2007).

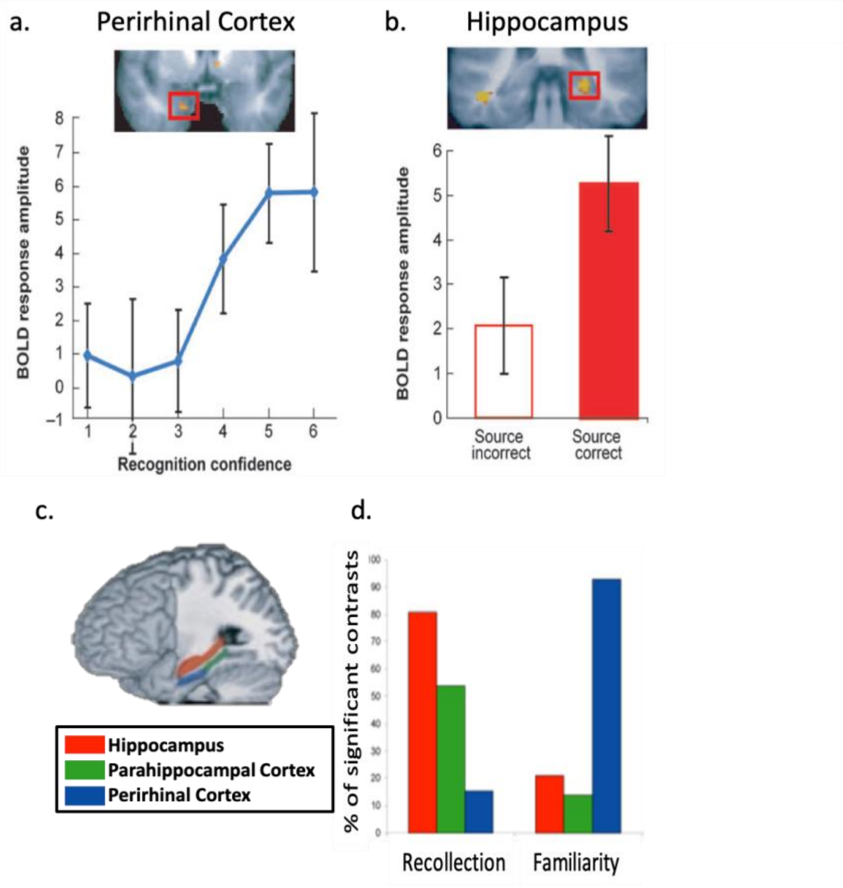
Although the tasks used in rodent studies are typically quite different from those used in humans, several studies have now used parallel methods in humans and rats. For example, ROCs have been examined in recognition studies of rats (Eichenbaum et al., 2010), and have indicated that selective hippocampal lesions impair recollection but spare familiarity-based recognition ((Fortin, 2004); for comparison of human and rodent ROC results see Figure 6; also see (Sauvage, Fortin, Owens, Yonelinas, & Eichenbaum, 2008)). Moreover, as in the human studies of aging, aged rats exhibit selective impairments in ROC estimates of recollection (Robitsek, Fortin, Koh, Gallagher, & Eichenbaum, 2008). Interestingly, an ROC study in rodents indicated that administering anesthesia during infancy causes a selective reduction in recollection later in life (Stratmann et al., 2014). While it is not possible to causally manipulate infantile anesthesia in humans, an ROC study of human teenagers has indicated that those who were given an anesthetic during childhood surgeries exhibited normal familiarity but reduced recollection estimates later in life (Stratmann et al., 2014).

Figure 6. The effects of hippocampal amnesia on recognition memory in humans and rats. ROC studies in both species indicate that hippocampal damage selectively disrupts recollection.



Numerous fMRI studies have also examined the role of different MTL regions in recollection and familiarity, and have provided converging evidence that recollection primarily involves the hippocampus, whereas familiarity involves the perirhinal cortex (for reviews, see (Diana, Yonelinas, & Ranganath, 2008b; Eichenbaum, Yonelinas, & Ranganath, 2007b; Skinner & Fernandes, 2007; Wais, 2008). For example, the top panel of Figure 7a shows that greater activation in the perirhinal cortex during encoding is related to increases in recognition confidence across intermediate levels of confidence (i.e., response confidence from 1 to 5 on a 6-point scale) rather than to high-confidence responses—which is consistent with a graded familiarity signal. In contrast, increases in hippocampal activity during encoding are selectively related to high-confidence recognition responses and are predictive of accurate source memory judgments, consistent with a recollection signal. Figure 7 c & d shows results from a review of fMRI remember/know, relational memory and ROC studies that included recollection and familiarity contrasts (from (Diana, Yonelinas, & Ranganath, 2007)). The review found that a vast majority of these studies reported hippocampal involvement in recollection, and only a few observed hippocampal involvement in familiarity. In contrast, a majority of studies showed that the perirhinal cortex was associated with familiarity, whereas only a few showed that it was involved in recollection. The differential roles of the hippocampus and perirhinal cortex in these studies have been observed during both initial encoding and at the time of retrieval, suggesting that these regions are involved in the initial formation of these memories and in their retrieval.

Figure 7. fMRI studies of recollection and familiarity. In a study examining MTL activity during the encoding of words, a) increases in perirhinal cortex activity were related to increases in subsequent recognition confidence, whereas b) increases in hippocampal activity were related to increases in source memory accuracy (adapted from Ranganath et al., 2003). c & d) The proportion of studies examining recollection and familiarity-related activity that reported hippocampal, perirhinal and parahippocampal activity (adapted from Diana et al., 2007). Recollection is related to both hippocampal and parahippocampal activity, whereas familiarity is related to perirhinal activity.

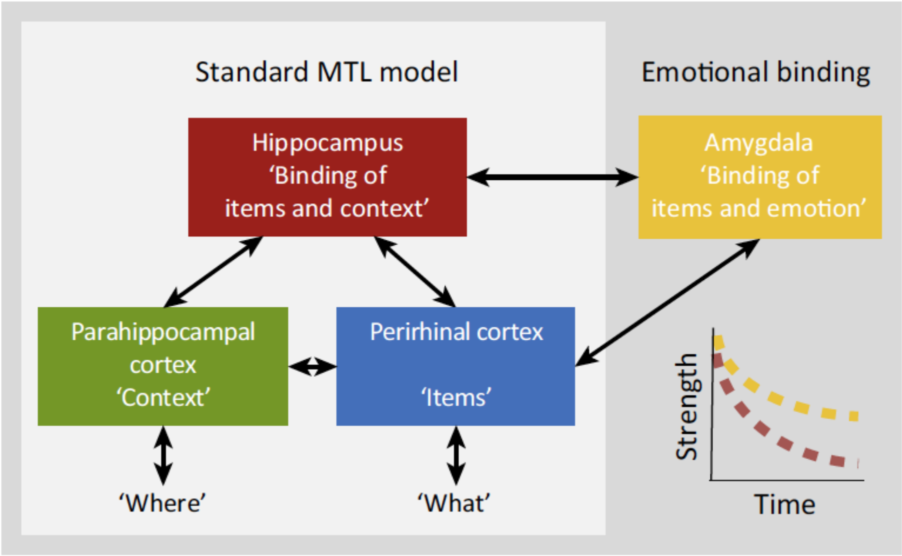


The fMRI studies provide two additional important insights about the role of the MTL. First, familiarity is related to <u>increases</u> in perirhinal cortex activity during encoding, but quite often it is related to <u>decreases</u> in activity during retrieval (for review see (Diana et al., 2007); but see (de Vanssay-Maigne et al., 2011; Kafkas et al., 2017). These results are generally consistent with the notion that greater processing of item information in the perirhinal cortex during encoding increases the subsequent familiarity of those items, whereas more efficient perirhinal processing of repeated items during retrieval signals episodic familiarity (Brown & Aggleton, 2001; R. N. A. Henson, Cansino, Herron, Robb, & Rugg, 2003). Second, the imaging results indicate that recollection is related not only to hippocampal activity but to parahippocampal activity as well (see green bars in Figure 7d). The lesion and imaging results are largely consistent with the CLS model, which links recollection to the hippocampus and familiarity to cortical regions in the MTL (also see neuroanatomical models proposed by Eichenbaum (Eichenbaum et al., 1994) and Aggleton and Brown (Aggleton & Brown, 1999)). However, one aspect of the results that these approaches leave unexplained is the finding that the parahippocampal cortex is also involved in recollection, rather than being related to familiarity. As described next, these findings led us to ask exactly what functional roles these different MTL regions played in supporting recollection and familiarity based responses.

6. Binding of Items and Context.

To incorporate the existing neuroanatomical and behavioral findings, we proposed the Binding of Items and Context (BIC) model (Diana et al., 2008a; Eichenbaum et al., 2007a). The BIC model avoids a strict one-to-one mapping of memory processes with distinct brain regions, and incorporates recollection and familiarity within a broader neuroanatomical model of temporal lobe function (i.e., the 'Standard MTL model' in Figure 8; (Diana et al., 2008a; Eichenbaum et al., 2007a); for additional elaborations on that model see (Yonelinas, 2013; Yonelinas, Ranganath, Ekstrom, & Wiltgen, 2019b; Yonelinas & Ritchey, 2015a)). The model is

Figure 8. The binding of items and context (BIC) model of recollection, familiarity and the MTL. In the standard model, the hippocampus (red) is assumed to bind together the item and context information that it receives from the perirhinal (blue) and parahippocampal (green) cortices, respectively. This binding is assumed to support the formation of complex high-resolution event representations. In addition, for emotional events, the amygdala (yellow) is assumed to support the binding of item and emotional information and this information is expected to be particularly resistant to the effects of forgetting.



predicated on results of anatomical studies of the temporal lobe. These studies have indicated that most of the neocortical input to the perirhinal cortex comes from neocortical areas that process unimodal sensory information about qualities of objects (i.e., “what” information from the ventral visual stream). In contrast, most of the neocortical input to the parahippocampal cortex comes from areas that process polymodal spatial information (i.e., “where” information from the dorsal visual stream). Some connections exist between the perirhinal and parahippocampal cortices, but the “what” and “where” information converge mainly within the hippocampus. We suggest that the perirhinal cortex and parahippocampal cortex encode item and context information, respectively, and that the hippocampus binds that information together to create item–context associations.

In this way, item representations within the perirhinal cortex can support familiarity in standard tests of item recognition, because little specific contextual information is necessary to make a familiarity judgment. In contrast, the hippocampus is critical for recollection because it supports item-context bindings (i.e., remembering the specific contextual details of the study episode). Thus, the BIC model can account for the finding that the hippocampus is involved during encoding and retrieval of recollected items, whereas the perirhinal cortex is involved during encoding and retrieval of items recognized as familiar. In addition, for recognition tests requiring recollection of contextual information, recollection should also give rise to parahippocampal cortex activity representing the reactivation of the relevant contextual information. Therefore, the BIC model can account for the lesion and neuroimaging results reported in studies of recognition, and it fits broadly with known neuroanatomical properties of the MTL (for additional discussion of the BIC model see Bastin, Besson, Sion, Delhaye et al. 2019; Wang et al., 2013; Hunsaker, Chen, Tran & Kesner, 2013; Ranganath & Ritchey, 2012). There are, however, aspects of recognition memory that the original BIC model does not address (e.g., how does the model account for the effects of emotion on recognition? How do the bindings supported by the hippocampus differ from associations formed by other cortical regions?). Next, we briefly consider some steps that have been taken to address those issues, and highlight some of the questions that we believe will be important in guiding future studies.

Emotional Binding. One important limitation of the original BIC model was that it did not consider the importance of emotional arousal, or the role of the amygdala in episodic recognition memory. For example, it is well established that memory tends to be better for negative arousing events compared to neutral events, particularly over longer periods of time--and this emergent emotion advantage is critically dependent on the amygdala (Cahill, Babinsky, Markowitsch, & Mcgaugh, 1995; Markowitsch et al., 1994; Phelps, 1998; Ritchey, Dolcos, & Cabeza, 2008; Sharot & Yonelinas, 2008). One way of accounting for these results is to assume that the amygdala signals the hippocampus to preferentially consolidate recent emotional materials during the retention interval (McGaugh, 2000, 2004). However, another approach that we find to provide a better account of the existing data is that emotional memories hold an advantage because they benefit from an additional “emotional binding process” that is supported by the amygdala (see Figure 8; (Yonelinas & Ritchey, 2015a)). That is, for emotional events, the amygdala supports the binding of item and emotional information for those events—essentially linking the item information about the event with the emotional aspects of that event. In this way, a studied emotional item can lead to the recollection of the study context via the hippocampal binding, and the retrieval of the associated emotion via the amygdala. In contrast, memory for neutral items is supported by hippocampal bindings but not by amygdala bindings. As most studies of emotion and recognition have focused on negative and neutral materials, it is not yet clear whether the amygdala supports a similar binding function for positive emotion.

The emotional binding approach accounts for the finding that memory is generally better for negative emotional materials than neutral materials, because emotional memories benefit from two rather than just one of the MTL binding processes. In addition, it accounts for the finding that this advantage increases over time. That is, because emotional associations supported by the amygdala such as fear-conditioned responses to objects are forgotten relatively slowly (Fanselow, 1990; Gale et al., 2004), and memory for emotional items is assumed to be supported by two rather than just one form of MTL binding (i.e., an item will be forgotten only when both bindings fail), the emotional memories should be forgotten more slowly than neutral memories.

The approach is also in line with several other findings in the emotional memory literature. For example, amygdala damage impairs memory for emotional materials, but has no appreciable effect on memory for neutral materials (Adolphs, Cahill, Schul, & Babinsky, 1997; Cahill et al., 1995; Markowitsch et al., 1994). This is consistent with the assumption that the amygdala supports emotional binding but is not involved in supporting nonemotional forms of binding. In addition, the emotional advantage in memory generally impacts recollection of the studied items rather than influencing familiarity-based discriminations (LaBar & Phelps, 1998; Ritchey et al., 2008; Sharot & Yonelinas, 2008). This is consistent with the assumption that item-related information from the perirhinal cortex supports item familiarity, whereas the amygdala is critical for recollecting item-emotion bindings. Moreover, because the amygdala binds emotion to item information it receives from the perirhinal cortex, rather than binding emotion to contextual information (i.e., it does not receive information directly from the parahippocampal cortex), the model can explain why emotion generally improves recollection of the emotional object itself (such as details of the object), rather than increasing recollection of contextual information, such as the particular study conditions (Sharot & Yonelinas 2007; Pierce & Kensinger, 2001; Waring & Kensinger, 2009). Finally, because the emerging emotion advantage is assumed to arise from amygdala-based binding rather than hippocampus-based binding, the model explains why hippocampal damage reduces recognition memory for both emotional and neutral materials, but does not impact the emotional memory advantage (Hamann, Cahill, McGaugh, & Squire, 1997; Hamann, Cahill, & Squire, 1997; Sharot, Verfaellie, & Yonelinas, 2007). In general, these results are inconsistent with consolidation accounts that assume that the amygdala modulates hippocampal memory representations. These accounts predict that emotion should benefit recollection of both item and context information, and should be disrupted by damage to either the amygdala or the hippocampus (Yonelinas & Ritchey, 2015b); for additional work extending this approach to studies of retrograde amnesia, as well as memory studies of sleep and stress see (Sazma, McCullough, Shields, & Yonelinas, 2019; Yonelinas, Ranganath, Ekstrom, & Wiltgen, 2019a).

Complex high-resolution binding. It is important to highlight that we do not assume that the hippocampus is the only brain region that supports the binding of different aspects of memory. For example, as we outlined above, the amygdala supports item-emotion binding. Moreover, as described earlier, the perirhinal cortex supports familiarity-based memory for arbitrary associations when items are unitized (Haist, Musen, & Squire, 1991; Haskins, Yonelinas, Quamme, & Ranganath, 2008; J. R. Quamme et al., 2007; Schacter, Chiu, & Ochsner, 1993). Additionally, other cortical regions are effective at forming associations in memory, as indicated by findings of novel learning in implicit and skill-learning tasks that do not depend on the medial temporal lobes (Haist et al., 1991; Schacter et al., 1993). However, recollection appears uniquely able to support a specific kind of binding: it supports memories for episodes that are rich in detail, such that they are both complex and high-resolution. Episodic memories are thought to be "complex" in the sense that an episode is characterized by a set of distinct associations between different event features, and they are "high-resolution" in the sense that they involve precise event information, such as the precise colors or relative locations of different objects within the event. Thus, given that the hippocampus has been found to underlie recollection, we propose that the hippocampus may be specifically involved in supporting complex, high-resolution bindings (Yonelinas, 2013).

Despite the clear link between recollection and the hippocampus, and the fact that recollection is uniquely characterized by complexity and precision, current theories of the hippocampus have failed to fully consider these properties of recollection. However, close inspection of current models of hippocampal function reveals that both of these aspects of recollection are often *implicitly* assumed. For example, in the CLS model described earlier, the hippocampus is assumed to support a pattern completion process: A partial cue leads to the activation of a sparse memory representation of the event, and that activation leads to the completion of the initial memory representation. The critical assumption for the present argument is that the hippocampus is not simply producing a recollective strength signal—rather, it is retrieving qualitative information about the earlier event that is not present in the retrieval cue. The process of pattern completion might therefore be expected to involve the retrieval of both precise information (e.g., the specific nature of the different aspects of the event) and highly complex information (e.g., the different sensory modalities involved), in line with our proposal that the hippocampus is involved in binding complex, high-resolution information.

Recently developed methods for measuring recollection have allowed this potential role of the hippocampus to be tested more directly. In classic laboratory tests of recollection, the tasks are designed to capture only one aspect of recollection (e.g., remembering whether the item was red or green, or on the left or right), or to indicate whether subjective recollection occurs or fails. However, a growing number of recognition studies have begun to examine the precision of the information that recollection provides rather than simply whether or not any type of recollection occurs; that is, these studies assess how *well* participants remember something rather than just *if* they remember it at all (Harlow & Donaldson, 2013; Harlow & Yonelinas, 2016), for similar approaches to studies of visual working memory see (Bays, Catalao, & Husain, 2009; Zhang & Luck, 2009)). These studies have demonstrated that recollection success and precision are experimentally separable, such that the ability to retrieve a specific detail does not necessarily entail that the memory for the event is highly precise. These results highlight the importance of disentangling these two different aspects of recollection when examining episodic memory. As one example, in studies of spatial navigation--in which subjects must remember the location of objects in a virtual room--patients with medial temporal lobe damage can accurately remember the general quadrant of the room that the objects were initially encountered; however, they are significantly impaired at remembering the precise location of those objects within the quadrant (Kolarik, Baer, Shahlaie, Yonelinas, & Ekstrom, 2018; Kolarik et al., 2016). This suggests that hippocampal damage does not disrupt one's ability to retrieve episodic memory for general locations, but it does result in degraded precision of the information retrieved. These results underscore the importance of separating success from precision in characterizing recollection, and they demonstrate that the hippocampus is not involved in all forms of binding.

Implicit memory and the MTL. One of the strengths of the BIC approach is that by focusing on the functional properties of these different MTL regions, rather than just the processes of recollection and familiarity per se, it is useful in integrating research from areas beyond episodic recognition. For example, there has been considerable debate about the extent to which the MTL plays a role in implicit forms of memory (e.g., tasks in which subjects are not explicitly using memory but prior experience influences behavior unconsciously). Some work has suggested that implicit memory is independent of explicit memory and the MTL (Gabrieli, 1998; Squire, 2009), whereas other work has suggested otherwise (Chun & Phelps, 1999; Hannula & Ranganath, 2009; Henke, 2010; Ranganath & Ritchey, 2012)—and the BIC model may be well-poised to help integrate these findings.

If the perirhinal cortex is involved in processing item information as proposed by the BIC model, it may be involved in supporting not only familiarity, but item-related implicit memory as well. For example, in conceptual implicit memory tests, subjects make semantic judgments (e.g., generate exemplars of different semantic categories, or make speeded semantic judgments about objects or words) more accurately and rapidly for items that have been previously studied. Patients with damage to the perirhinal cortex show deficits in conceptual implicit memory, whereas patients with selective hippocampal lesions do not (Wang, Lazzara, Ranganath, Knight, & Yonelinas, 2010; Wang, Montchal, Yonelinas, & Ragland, 2014); but see (Levy, Stark, & Squire, 2004). Moreover, activity in the perirhinal cortex during encoding predicts subsequent conceptual implicit memory performance (O'Kane, Insler, & Wagner, 2005; Voss, Hauner, & Paller, 2009; Wang et al., 2010). In addition, activity reductions in the perirhinal cortex during retrieval predict both conceptual implicit memory and familiarity-based recognition (Wang, Ranganath, & Yonelinas, 2014), and an examination of individual differences has indicated that familiarity—but not recollection—is correlated with conceptual implicit memory (Wang & Yonelinas, 2012).

These results are inconsistent with models that assume that implicit memory does not rely on the MTL, and instead suggest that the item representations in the perirhinal cortex are important for supporting not only episodic familiarity, but conceptual implicit memory as well. However, not all forms of implicit memory rely on the perirhinal cortex. For example, more perceptual forms of implicit memory such as word fragment completion do not appear to be strongly related to familiarity (Wagner & Gabrieli, 1998) or dependent on the perirhinal cortex, but rather they rely on regions earlier in the ventral processing stream (Wang et al., 2010); also see (R. N. Henson, Shallice, Gorno-Tempini, & Dolan, 2002; Schacter & Buckner, 1998). These results suggests that the item representations supported by the perirhinal cortex may be more conceptual in nature whereas earlier regions in the ventral stream may represent more sensory information. Other work has suggested that the hippocampus may also play a role in some forms of implicit learning such as spatial context learning (e.g., Chun & Phelps, 1999). Future work that examines the role of different MTL regions in other forms of implicit learning, and that further explores how that learning is related to recollection and familiarity, will be particularly informative.

Do hippocampal bindings play a role in working memory and perception? A growing body of work has indicated that the MTL is not limited to supporting long term episodic memory, but that it can also play a role in working memory and perception under certain conditions. We believe that the BIC model provides useful guidance in determining when the MTL will and will not play a critical role in such tasks. Although traditional MTL models assumed that working memory and perception are supported by regions outside the MTL (Gabrieli, 1998; Squire, 2009), a number of studies have shown that hippocampal damage can disrupt performance on working memory and perception tasks, and that the hippocampus is often active during these tasks (Graham, Barense, & Lee, 2010; Lee et al., 2005; Yonelinas, 2013). A number of these studies have suggested that the hippocampus may be particularly important in working memory and perception tasks that require relational binding, such as remembering the color or location of objects, or making perceptual judgments about complex stimuli such as multiple-feature objects and scenes. These results are consistent with the idea that the hippocampus is critical in binding together the different aspects of an event, whether it is in the past or ongoing—a notion shared by the BIC approach and relational memory models (Cohen et al., 1999). However, it must be acknowledged that there are many counterexamples in the literature, in which binding seems to be required for a working memory or perception task but the hippocampus is not involved (Baddeley, Allen, & Vargha-Khadem, 2010; Jeneson, Mauldin, & Squire, 2010; Shrager, Levy, Hopkins, & Squire, 2008). As one example, Baddeley et al. (Baddeley et al., 2010) found that a patient with selective hippocampal damage was not impaired on a battery of working memory tasks that required remembering relational information such as object-color and object-location pairings.

These results suggest that it is not just the involvement of binding or relational information that determines whether the hippocampus will be involved in a working memory or perceptual task. Rather, we suggest that the hippocampus will be particularly important in tasks that require the binding of multiple high-resolution aspects of the ongoing event. For example, when subjects must maintain the precise color or location information for multiple items in working memory, or when subjects must detect configural differences or changes between multiple stimulus features.

This account accurately describes the results from many existing studies, and has been further verified in a number of subsequent studies designed to test this account directly (Yonelinas, 2013). For example, in a "same/different" perceptual discrimination task in which the potential changes involve a subtle configural alteration (e.g., slight global distortions) of a scene, hippocampal patients are found to be significantly impaired, and in the same task, hippocampal activity in control subjects correlates with confidence in the perceptual judgments (Aly, Ranganath, & Yonelinas, 2013, 2014). Similar to findings using perceptual judgments, studies of working memory have shown that hippocampal patients are not impaired at detecting changes in the color or location of studied items when the discrimination requires only low-resolution information (e.g., knowing an object changed from red to blue). However, they are impaired at equally difficult discriminations (which are equated in difficulty by reducing the set size) that require a more precise color or location judgment (e.g., an object changed from royal blue to lighter blue) (Koen, Borders, Petzold, & Yonelinas, 2017). In addition, MTL patients are even impaired in working memory for single items when the task requires memory for multiple high-resolution changes (i.e., the object could change in color, location or orientation; Goodrich & Yonelinas, 2019). The results indicate that despite being designed to account for recollection and familiarity, the BIC model is also useful in accounting for results from studies of working memory and perception, and in generating useful novel predictions in those domains. It will be important to determine whether this approach will be useful in helping to explain results from other recent studies that have implicated the medial temporal lobes in other cognitive tasks such as problem solving, language, and planning (Duff & Brown-Schmidt, 2012; Miller, Botvinick, & Brody, 2017; Sheldon & Levine, 2016).

Additional challenges. There are a number of additional questions about the role of the MTL in recognition memory that will be important to address more fully. For example, we don't yet know what role the entorhinal cortex plays in recognition. The entorhinal cortex comprises transitional cortex between the hippocampus and the surrounding perirhinal cortex and parahippocampal cortex. Although most human lesion and neuroimaging studies have not yet aimed to separate the roles of these different structures, a few recent studies have suggested that the entorhinal cortex may play a role in familiarity similar to that of the perirhinal cortex (Brandt et al., 2016; Kafkas et al., 2017). Given that the entorhinal cortex is one of the regions that is disrupted very early in Alzheimer's disease, determining its role in recognition could be critical for early diagnosis.

It will also be important to determine the extent to which the parahippocampal cortex is limited to supporting spatial context, or whether it might also support other nonspatial forms of context. Although there is evidence that it is particularly sensitive to processing spatial information such as that found in complex scenes, it can, in some cases, track the familiarity of objects as well (Kafkas et al., 2017). Interestingly, the extent to which information is treated as context, and therefore supported by the parahippocampal cortex, may depend on the encoding circumstances. For example, one study examined memory for pairs of visual fractal images in which one fractal was encoded as an object in the center of the screen, and another was encoded as a background context. In a subsequent memory test, perirhinal cortex activity was observed when subjects retrieved fractals that had been encoded as items, whereas parahippocampal activity was observed for fractals encoded as contexts (Wang, Yonelinas, & Ranganath, 2013). This suggests that the parahippocampal and perirhinal cortices are not limited to supporting two different types of visual information per se, but whether that information is processed as an item or a context. Finally, the medial temporal lobe regions that we have focused on clearly do not operate in isolation, and there is a growing literature (Ranganath & Ritchey, 2012) examining how broader neural networks—including the prefrontal cortex, for example—contribute to recollection and familiarity (also see recent reviews by (Bastin et al., 2019; Ritchey, Libby, & Ranganath, 2015; Thakral, Wang, & Rugg, 2017; Vilberg & Rugg, 2014)).

7. Conclusions.

The study of recognition memory has proven useful in furthering our understanding of episodic memory at both a behavioral and neural level. Although single-point measures of recognition are found to be inadequate to describe recognition performance, methods such as the assessment of receiver operating characteristics have proven useful in characterizing performance and in separating measures of response bias from the memory processes underlying performance. Results from behavioral studies, lesion studies, and brain imaging studies have indicated that there is more than a single memory process underlying performance, and have indicated that recollection and familiarity-based recognition responses are functionally and neurally distinct. In general, recollection is found to be a slow, thresholded process leading to the retrieval of qualitative information about previous events, such as the spatial or temporal context of the study event. Familiarity, on the other hand, is a relatively fast and automatic process, providing a memory strength signal that is useful in differentiating new items from recently presented items (or unitized pairs of items). Recollection is critically dependent on the hippocampus, which supports complex high-resolution bindings that link the objects and contextual information of an event, whereas familiarity is dependent on the item-processing stream that culminates in the perirhinal cortex. The parahippocampal cortex is critical in representing contextual information that often defines the study episode and is bound by the hippocampus into recollected memory representations. Lastly, the amygdala supports the binding of item and emotional information that is critical in supporting memory for negative emotional events. These MTL regions are not specialized for recollection and familiarity per se, nor is there a direct one-to-one mapping between these processes and brain structures. Rather, the involvement of these regions is determined by the encoding and retrieval demands of the specific recognition task at hand. Furthermore, these regions are not limited to supporting episodic memory, but rather they play critical roles in other related processes such as implicit memory, working memory, and complex perception.

There have been various models that have been proposed to account for the dissociations between recollection and familiarity, ranging from very simple measurement models to more complex neuroanatomical and neurocomputational approaches. Our view is that each approach offers important insights and advances our understanding of recognition ins complementary ways. Moreover, we believe that a consistent story is beginning to emerge across all these levels. While early models of recognition memory focused on characterizing the behavioral nature of the processes involved in supporting recognition judgments, more recent models have incorporated neuroanatomical findings and have adopted neurocomputational approaches in order to capture the empirical regularities in behavioral, patient and neuroimaging studies. The emerging view is relatively simple, and it has proven useful in generating new predictions that are being actively investigated, but it will inevitably need to be modified further as our understanding of episodic memory and its underlying neural processes advances. We are, however, optimistic that the multiple level approach will help move the science of memory forward, whether the specific predictions are ultimately supported or falsified. Regardless of the outcome of these future studies, the current recognition memory models have been useful in clarifying how the processes underlying recognition memory are differentially impacted by a variety of behavioral manipulations and disease states.

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