

# Hierarchical Relational Binding in the Medial Temporal Lobe: The Strong Get Stronger

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**ABSTRACT:** Controversy exists over the functional role of the medial temporal lobe (MTL) in episodic memory. Some have suggested that the hippocampus plays a unique and qualitatively different role than other MTL regions, whereas others suggest that the entire MTL has one functional role, which is to support the consolidation of declarative memories. *Hierarchical relational binding theory (hRBT)* purports that the functional role of the entire MTL is the binding of features associated with an episodic experience. As the hippocampus sits at the top of this hierarchy, binding at this level is particularly efficient in reinstating event features at the time of retrieval. Thus, this theory offers a unified account of MTL that yields outcomes similar to theories that suggest a special role of the hippocampus. In this way, hRBT captures features of both single- and dual-process models of MTL and reconciles controversies about the nature of episodic recollection. © 2010 Wiley-Liss, Inc.

**KEY WORDS:** hippocampus; episodic memory; recollection; declarative memory; relational binding

## INTRODUCTION

Our ability to recollect past experiences stands as a paramount feature of human memory. These *episodic memories* are formed as ensembles of event features, which may include the location, time, people, perceptions, thoughts, and feelings associated with a past experience. Successful recollection of an episodic memory depends upon efficient encoding of such features at the time the event occurred. Considerable research has advanced our understanding of the neural basis of this encoding process, which involves online activation of salient sensory, conceptual, and emotional features. These event features, which are represented in disparate neocortical sites, are held online by the prefrontal cortex (PFC) as an active working memory representation (Shimamura, 2000, 2008; Miller and Cohen, 2001; D'Esposito, 2007).

The medial temporal lobe (MTL) has, of course, been viewed as critical for the long-term storage and consolidation of active working memory representations related to event features. Squire (Squire et al., 1984, 1989; Squire and Zola-Morgan, 1998) proposed that the MTL, by way of its many pathways to and from neocortical sites, forms rapid bindings of event features during encoding. After learning, these MTL bindings assist in reactivating specific event ensembles, thus strengthening them as a unit and facilitating retrieval. This “consolidation” theory has been useful as an

explanation of amnesia following MTL lesions, because patients with such lesions cannot retrieve well formed or context-bound memories. The theory also led to the distinction between declarative (episodic and semantic memory) and nondeclarative memory (skills, habits, and priming) [see Squire and Zola (1997) and Squire et al. (2004)]. An extension of this model was proposed by Eichenbaum and Cohen (1993), who specified the role of MTL in relational memory, a term that describes the limbic-cortical networks that are established. Shimamura (2002) developed relational binding theory (RBT), which describes the role of MTL binding in both storage and retrieval. According to RBT, limbic-cortical bindings that exist at the time of retrieval assist in the recollection of episodic ensembles.

## THE FUNCTIONAL ROLE OF THE MTL: LUMPERS AND SPLITTERS

The contribution of the MTL to relational binding rests on two important features. First, neurobiological findings of activity-dependent synaptic plasticity, such as those observed during long-term potentiation, suggest that the hippocampus has the capacity of binding the co-occurrence of multiple inputs [for review, see Lynch et al. (2007) and Morris (2006)]. This form of cellular plasticity is mediated by NMDA receptor channels, which are voltage-dependent and highly concentrated in the hippocampus (Petralia et al., 1994; Morris, 2006). Such forms of synaptic plasticity offer a mechanism for linking cotemporaneous inputs that converge onto a hippocampal neuron, thus providing a cellular mechanism for rapid relational binding [see Squire et al. (1989)].

A second critical feature of MTL binding is its apparent hierarchical organization. As shown in Figure 1, unimodal and polymodal association areas in the neocortex converge onto the MTL by way of projections to the perirhinal and parahippocampal cortices (Van Hoesen and Pandya, 1975; Suzuki and Amaral, 1994; Lavenex and Amaral, 2000). The perirhinal cortex receives its primary projections from high-level visual regions that make up the ventral visual path (Suzuki and Amaral, 1994). It also receives projections from other cortical regions, such as the superior temporal gyrus, insular cortex, and orbitofrontal cortex. The parahippocampal cortex receives

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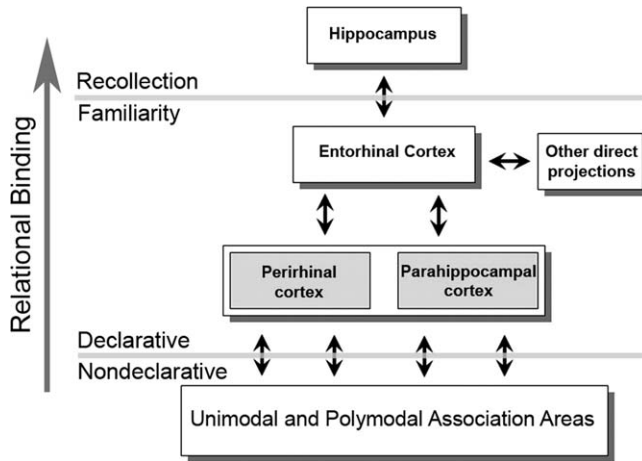
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**FIGURE 1.** Schematic of MTL hierarchy, showing initial unimodal and polymodal projections to the perirhinal and parahippocampal cortex—the first level of MTL binding. These two MTL regions project to the entorhinal cortex that sends projections to the hippocampus. A border has often been placed between MTL and other neocortical sites, suggesting a division between declarative and nondeclarative memory. Another border has often been placed between the hippocampus and other MTL regions, suggesting a division between recollection and familiarity. According to hRBT the entire MTL is devoted to relational binding [figure adapted from Lavenex and Amaral (2000)].

projections from a variety of other neocortical regions, including the posterior parietal cortex, retrosplenial cortex, dorsal superior temporal sulcus, and cingulate cortex. The entorhinal cortex receives most of its inputs from the perirhinal and parahippocampal cortices, and ultimately, MTL projections converge onto the hippocampus. From the hippocampus, reciprocal projections send information back through MTL regions and out to neocortical sites. Thus, relational binding within the MTL has the capacity to link in a hierarchical manner event features stored in disparate regions in the neocortex.

For decades, it has been acknowledged that the MTL plays a critical role in the formation of declarative or explicit memories. As shown in Figure 1, a border has often been drawn between the MTL and other neocortical regions, suggesting a qualitative split between MTL properties and those associated with other regions. Additional findings have suggested a second border between the hippocampus and other MTL regions. That is, some have argued that the hippocampus plays a unique role in the service of episodic memory that is qualitatively different from the role that other MTL regions play in memory formation (Mishkin et al., 1997; Nadel and Moscovitch, 1997; Aggleton and Brown, 1999). Specifically, it has been proposed that the hippocampus contributes particularly to the recollection of contextually rich episodic memories. Such views adopt a dual-process characterization of memory in which episodic retrieval is based on either a recollection process, referring to retrieval of fully formed episodic memories, or a familiarity process, referring to a less distinct or vague feeling of knowing. The phenomenology of these two aspects of episodic retrieval is undisputed. One can often recollect quite strongly the features of a past experience,

whereas at other times only a vague sense of familiarity is retrieved. Controversy exists as to whether this phenomenological distinction is best characterized as a split between the hippocampus and other MTL regions.

Neurobehavioral findings are mixed with respect to the specific role the hippocampus plays in episodic recollection. In studies of amnesic patients, some have observed selective impairment of recollection following hippocampal lesions (Vargha-Khadem et al., 1997; Holdstock et al., 2005), whereas others have not (Wais et al., 2006; Squire et al., 2007). In neuroimaging studies, there is evidence to suggest that recollection responses are particularly associated with hippocampal activity. For example, in the *Remember–Know* paradigm, hippocampal activity is pronounced when subjects classify items in terms of having recollected specific features of a prior experience (remember) compared to items that have only a vague sense of familiarity (know) [for review, see Eichenbaum et al. (2007)]. In other studies, however, the entire MTL appears to be devoted to recollective responses (Stark et al., 2007; Kirwan et al., 2010). Also, multiple MTL regions are responsive on tests of source recollection (Davachi et al., 2003). In these tests, memory is assessed for particular event features, such as the color or location of a previously learned stimulus.

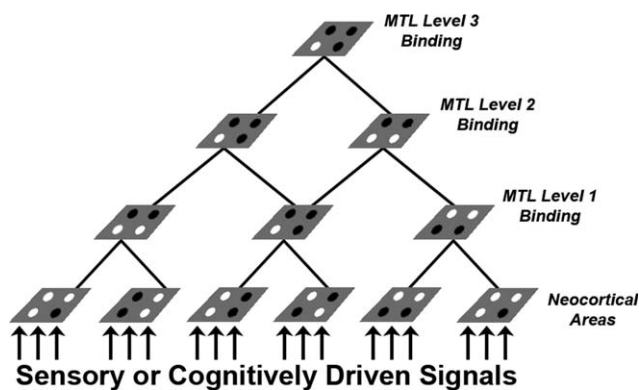
To a large degree, differences in one's orientation toward the functional role of MTL regions depend on whether one prefers to be a *lumper* or a *splitter*. That is, in the development of scientific theories, there is a tendency to categorize or group phenomenon as discrete and qualitatively unique entities. In systems neuroscience, stark borders have been constructed between broad concepts such as emotion versus cognition, perception versus memory, and top-down versus bottom-up processing. At first blush, it seems reasonable to classify such things as “perceptual” processes and distinguish them from “memory” processes. It also seems reasonable to split categories within these broad concepts. Thus, a division between hippocampus and other MTL regions may be justified, though just as reasonably one could split processes within the hippocampus and argue that the CA1 subfield plays a unique role within it. In the end, every neuron is to some extent unique and splitting can proceed down to molecular-level processes. The advantage of lumping structures together is that it helps to characterize properties of a neural circuit as a working unit, just as one might characterize in a car the functional role of the engine and separate it from the role of the transmission system. Indeed, it may be useful (for an auto mechanic) to consider these two automotive components as separable functioning units. Of course, each can be further split into subcomponents, and the border between the two is fuzzy.

The purpose of creating classifications—that is, whether to lump or split—is to develop ways to test the properties of neural circuits. Thus, the splitting of declarative memory from nondeclarative memory and of recollection from familiarity has served to generate empirical tests of these memory distinctions. After considerable research, findings generally support such distinctions, but the borders are always much less distinct than actually purported. With respect to the declarative versus non-

declarative distinction, attempts to demarcate clearly its border have been difficult. Indeed, there is controversy over the degree to which MTL processes serve perceptual processes as well as memory processes (Murray et al., 2007; Suzuki, 2009). What is needed beyond the splitting and lumping of functional units are theories that describe neural mechanisms that underlie these circuits. Descriptions of MTL function in terms of relational memory (Cohen and Eichenbaum, 1993) or relational binding (Shimamura, 2002; Shimamura and Wickens, 2009) are attempts at a functional approach. When a functional mechanism is outlined, stark classifications are less critical, as it is the functional properties of neural circuits that become important. Thus, if a putative high-level “perceptual” phenomenon requires relational binding, then the MTL should contribute to its expression, and arguments of whether the task taps “perception” or “memory” are unnecessary.

### HIERARCHICAL RELATIONAL BINDING: LUMPING AND SPLITTING

As described earlier and depicted in Figure 1, MTL circuitry approximates a hierarchical network that begins with bindings in perirhinal and parahippocampal cortices and ends with converging projections to the hippocampus. Based on bindings at multiple levels of convergences, Shimamura and Wickens (2009) proposed *hierarchical relational binding* theory (hRBT) as a functional characterization of MTL processes. Figure 2 illustrates a schematic hierarchy of MTL binding. According to hRBT, neocortical sites that represent event features are activated during the encoding of an event by sensory or cognitively driven signals. These signals are maintained by the PFC as



**FIGURE 2.** Hypothetical MTL organization of hierarchical relational binding. Neocortical feature units of an episodic event are activated by sensory or cognitive driven cortical signals (white circles). These activations are bound at MTL Level 1. These bindings are then bound by MTL Level 2. If binding occurs at MTL Level 3, then a single unit at this level has the capacity of reinstating the entire set of neocortical units by way of hierarchical relational binding. Thus, as relational binding occurs at higher MTL levels, the reinstatement of event features during retrieval is superadditive.

working-memory representations. These active regions project to the initial level of MTL binding (i.e., perirhinal and parahippocampal cortices), which join features across localized neocortical zones. These initial bindings are bidirectional and by themselves facilitate in the consolidation of episodic ensembles. Level 1 MTL bindings are rather restricted or localized, as neocortical features bound in one MTL region, say in the perirhinal cortex, are separate from those bound in another, say in the parahippocampal cortex.

Activity that converges on to MTL Level 2 units induces further binding, which has the capacity of linking bindings formed at MTL Level 1. Level 3 bindings link bindings formed at Level 2 and so on. Figure 2 shows three levels of MTL binding, though even more convergence zones may actually occur within the MTL. Ultimate binding of bindings occurs by way of converging projections to the hippocampus. According to hRBT, some episodic features may only be bound by MTL Level 1 bindings, whereas others may bind at Level 2, and still others may include higher level bindings. As memory strength is related to the number of features that can be retrieved, multilevel relational binding has the capacity of creating disproportionately strong episodic memories. That is, the result of multilevel MTL binding is superadditive memory strength.

Figure 2 illustrates the manner in which hierarchical relational binding can induce superadditive memories. In this figure, sensory or cognitively driven signals activate an ensemble of event features located in disparate neocortical areas (white circle). These active units are bound by MTL Level 1 units, such that a Level 1 unit conjoins units in different neocortical regions. A prominent feature of hRBT is that an ensemble of event features can be successfully reinstated with rather sparse connections through MTL levels. In Figure 2, a single MTL Level 3 unit conjoins three units at Level 2, which, in turn, are linked to five units in Level 1, which then has the potential to activate 14 units in disparate neocortical areas. In this hypothetical structure, activation of a single hippocampal unit can reinstate a full set of event features stored in the neocortex. Importantly, as binding succeeds further into the MTL, the number of features that can be reinstated increases disproportionately. Consider an even simpler model in which MTL associations are binary, such that each MTL unit links two units at a lower level [see Shimamura and Wickens (2009)]. Thus, a Level 1 unit links two neocortical units, a Level 2 unit links two Level 1 units, and so on. In this simple model, one Level 2 unit can reinstate a total of four neocortical units (i.e., two Level 1 units, each linked to two neocortical features). With this hierarchy, a single Level 3 unit can reinstate eight neocortical units, disproportionately more than any single Level 2 or 1 unit. In hierarchical binding, the net effect is always superadditive, and, in this simple case, successful binding at each level after Level 1 exponentially increases the number of neocortical features that are bound by a single unit. The magnitude of superadditivity depends upon the fidelity and number of multilevel bindings. Importantly, as bindings occur at multiple MTL levels, memory strength increases disproportionately such that *the strong get stronger*.

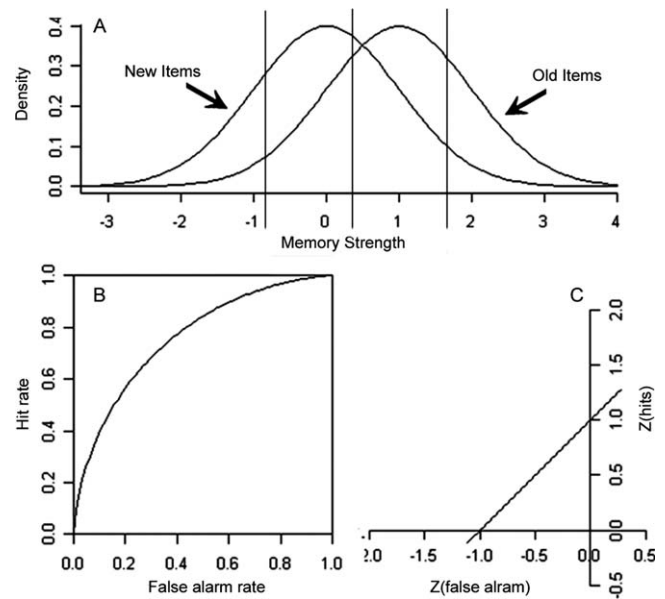
According to hRBT, the functional role of the MTL is to link in a hierarchical fashion neocortical activations that comprise episodic events. Thus, the entire MTL circuitry could be viewed as a *lumped* functional unit in the service of relational binding. Although the hippocampus is doing the same thing functionally as other MTL regions (i.e., relational binding), it does have a particularly important role in binding, as it is situated at the top of the binding hierarchy. As such, binding in the hippocampus enables an episodic ensemble to be most fully reinstated and, as a result, provides a much, much stronger recollective experience (i.e., Remember response) than that which would occur without binding at this level. In other words, one could claim an apparent *split* in MTL function, such that hippocampal activity is particularly important for episodic recollection. One can make this claim without ascribing its function as a qualitatively different one from that of other MTL regions. Thus, hRBT makes the same predictions as dual-process models. Specifically, increased hippocampal activity in fMRI studies, as observed in *Remember* versus *Know* responses, occurs, because successful hippocampal binding disproportionately increases the “re-collection” of event features during retrieval, which thus increases the probability of a *Remember* response. By this view, a single process (i.e., hierarchical relational binding) predicts essentially the same behavioral and neurocognitive results as those asserted to support dual-process views, yet one does not have to adhere to a stark border between hippocampal function and other MTL functions. In other words, the properties of hRBT allow one to be a *lumper and splitter* at the same time.

The essential features of MTL hierarchical relational binding are as follows [for details, see Shimamura and Wickens (2009)]:

1. The entire MTL functions as a unit geared toward binding coactive features of an episodic event.
2. Binding occurs in a hierarchical manner such that bindings at higher MTL levels are binding the bindings created at lower MTL levels.
3. At each MTL level beyond the first level, the effect of binding is superadditive, such that memory strength gains disproportionately with successful binding at each higher level (i.e., superadditive property).
4. The hippocampus is the final convergence zone in the MTL and thus successful binding at this level has the capacity of relating and reinstating rather fully ensembles of event features stored in disparate regions in the neocortex.
5. During retrieval, activation through MTL levels assists in the reinstatement of event features associated with specific episodic memories.

## QUANTITATIVE ANALYSES OF RECOGNITION MEMORY

Shimamura and Wickens (2009) presented a formal model of hRBT, which characterized the superadditive nature of MTL binding. The model was applied to quantitative analyses of *re-*



**FIGURE 3.** Top panel (panel a) depicts a standard SDT model of item recognition memory in which old and new items are represented as Gaussian distributions with equal variance. The vertical lines refer to the placements of criterion levels, which define boundaries between “new” and “old” responses. Panel b depicts a curvilinear (inverted-U shape) ROC function, which supports a continuous SDT model of memory strength. Panel c depicts a zROC plot in which hits and false alarm rates are transformed as z scores. Linear zROC plots imply Gaussian distributions.

ceiver operating characteristic (ROC) curves, which were obtained from tests of item and source recognition memory [see Banks (2000), Glanzer et al. (2004), and Slotnick et al. (2000)]. ROC curves describe recognition performance in terms of response rates across several levels of confidence. For example, on a test of item recognition, subjects judge whether a test item is old or new and then rate their confidence (e.g., *sure new*, *likely new*, *maybe new*, *maybe old*, *likely old*, and *sure old*). ROC curves are constructed by plotting cumulative response rates across confidence ratings, starting at the strictest rating (i.e., *sure old*) to the weakest rating (*sure new*).

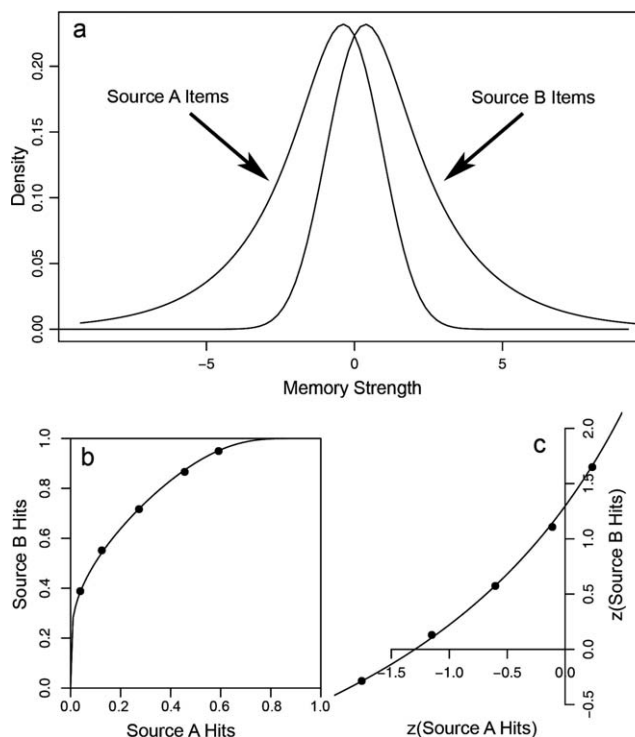
Signal detection theory is usually applied to describe ROC curves [see Green and Swets (1966), Wickens (2002)]. According to this framework, memory strength is viewed as a continuous variable, such that all old and new items are positioned along this single dimension. New items vary in memory strength according to their inherent familiarity, as defined by frequency or recency of occurrence. New items are normally distributed (i.e., Gaussian distribution) with a mean strength of 0 and a standard deviation of 1 (see Fig. 3a). Old items are also presumed to be normally distributed with a mean greater than 0. Given these assumptions, ROC curves, such as the one shown in Figure 3b, are constructed to characterize the strength and distribution of old items with respect to new items. Numerous studies have shown that item recognition performance conforms fairly well to the assumptions of signal detection theory (Ratcliff et al., 1992; Glanzer et al., 2004). Specifically, ROC curves are curvilinear in the shape of an inverted U (see

Fig. 3b). When response rates are transformed as  $z$ -scores, the resulting  $z$ ROC curves are roughly linear (see Fig. 3c), which suggests that Gaussian functions offer a valid characterization of old and new distributions. Also, the slope of  $z$ ROC curves for item recognition tends to be less than 1, which suggests that the variance of old items is larger than the variance of new items.

In the laboratory, source memory is investigated by presenting study items which vary in a specific feature. For example, words may be presented in one of two colors, such as yellow or blue. Source recognition is assessed by presenting a word without any color and asking subjects if the word was originally presented in yellow or blue (old source items are generally referred to as Source A and Source B items). Source memory is related to episodic recollection, because a correct source judgment indicates successful recognition of an episodic feature. Source ROC and  $z$ ROC curves can be constructed by having subjects rate their confidence for each source judgment (e.g., *sure yellow*, *likely yellow*, *maybe yellow*, *maybe blue*, *likely blue*, and *sure blue*). According to signal detection theory, source judgments are aligned along a single dimension that defines the degree to which Source A and Source B items can be discriminated [see Banks (2000) and Slotnick et al. (2000)]. As with item recognition, signal detection theory predicts curvilinear, inverted-U shaped ROC curves, and linear  $z$ ROC curves.

Empirical assessments of source ROC and  $z$ ROC curves are somewhat mixed. There is general consensus, however, that with typical source memory instructions and methods, source ROC curves are curved with an inverted-U shape, and  $z$ ROC curves are nonlinear with a slight *cupped* or U shape (Glanzer et al., 2004). The cupped shape of  $z$ ROC curves suggests that Source A and B distributions are not well characterized by Gaussian models, including recent models by Wais (2008) and Wixted (2007). To account for the cupped shape of source  $z$ ROC curves, Yonelinas (1994, 1999) proposed a dual process model in which source memory is determined largely by a threshold-based recollection process. As defined by Yonelinas and Park (2007, p. 809), "Recollection is indexed as the probability that subjects correctly recollect some aspect of the study." As recollection is a threshold response, source ROC curves are predicted to be relatively linear and  $z$ ROC curves cupped. Indeed, Yonelinas (1999) found under certain conditions, linear source ROC curves and cupped  $z$ ROC curves. Item recognition is based more evenly on recollection and familiarity. Familiarity is viewed as a continuous parameter and conforms to the properties of standard signal detection theory. Thus, the combined effect of recollection and familiarity is that item ROC curves are more curved and  $z$ ROC curves are linear. For ROC analyses of item recognition, both the unequal variance Gaussian model and the Yonelinas dual process model offer fairly good fits of observed data.

According to hRBT, there is no stark distinction between recollection and familiarity. It is asserted, however, that increases in relational binding are superadditive such that some episodic memories (those with hippocampal bindings) will be exceedingly strong and carry with them a recollective experi-



**FIGURE 4.** (a) Ex-Gaussian model of source recognition with skewed distributions of both Source A and Source B items. These two distributions are skewed in opposite directions. The model predicts inverted-U shaped ROC functions (b) and U-shaped  $z$ ROC functions (c).

ence. Based on this property, hRBT predicts that old item distributions will be continuous, yet positively skewed. For source recognition performance, a subset of items will be disproportionately remembered as a Source A item, and another subset will be disproportionately remembered as a Source B item. Thus, Source A and Source B distributions will both be skewed away from each other (see Fig. 4a). Shimamura and Wickens (2009) applied ex-Gaussian distributions to describe the skewing of old item distributions. The ex-Gaussian distribution is defined as the sum of two random variables, one with an exponential distribution (with rate parameter  $\lambda$ ) and one with a Gaussian distribution (with mean,  $\mu$ , and variance,  $\sigma^2$ , parameters). With respect to hRBT, the  $\lambda$  parameter defines the super-additive nature of binding, such that larger values represent more items that are fully bound by multiple MTL levels. The Gaussian mean parameter,  $\mu$ , defines a general increase in memory strength, characterized as the degree to which old items have rather shallow MTL bindings (Levels 1 or 2). The ex-Gaussian distribution is described by the following equation:

$$f_{\text{exG}}(x) = \int_0^{\infty} f_{\text{exp}}(t) f_{\text{Gauss}}(x-t) dt$$

$$= \int_0^{\infty} [\lambda e^{-\lambda t}] \left[ \frac{1}{\sqrt{2\pi}\sigma} \exp\left(-\frac{1}{2} \frac{[(x-t)-\mu]^2}{\sigma^2}\right) \right] dt.$$

TABLE 1.

Observed Data and Model Predictions for ROC and zROC Curves

	Item ROC	Item zROC	Source ROC	Source zROC
Observed data	Inverted-U	Linear (nearly)	Inverted-U	Cupped
Gaussian	Inverted-U	Linear	Inverted-U	Linear
Dual process	Inverted-U	Linear (nearly)	Relatively Linear	Cupped
hRBT	Inverted-U	Linear (nearly)	Inverted-U	Cupped

The single assumption of skewed, ex-Gaussian distributions for old items predicts empirically derived ROC and zROC curves for both item and source recognition (Shimamura and Wickens, 2009). Quantitative modeling of empirical data show that the ex-Gaussian model is as good or a better fit of item and source recognition performance compared to other extant models, including dual process and standard Gaussian models. Table 1 summarizes observed ROC findings and predictions from various models.

To account for the observed cupped zROC findings, standard Gaussian models must include additional assumptions. DeCarlo (2003) added the assumption that a proportion of old items will not include any source information, and these items are mixed with items that include source information. Lack of source information can be attributed to a failure to encode relevant source features during initial learning. As such, source memory for old items is based on a mixture of two Gaussian distributions, one that includes items with source information and another that includes items without source information. Similarly, Slotnick and Dodson (2005) suggested that at low levels of source memory, the preponderance of extraneous noise flattens ROC curves. In both cases, Gaussian models with an added probabilistic or thresholdlike parameter can produce source ROC curves that are more linear and zROC curves that are cupped.

For a dual-process model, it must be assumed that source memory recognition is never a “process pure” measure of recollection and that source ROC curves should only be “relatively linear” (Yonelinas, 1999). According to Yonelinas’ dual-process model, curvilinear source ROC curves will occur to the extent that familiarity influences source judgments. In other words, any influence of familiarity on a putative recollection test will make ROC curves appear curvilinear, and if this influence is relatively small, zROC curves will be cupped. The influence of familiarity on source recognition makes it difficult to disconfirm the dual-process model, because whenever curvilinear source ROCs are observed, it can be argued that familiarity played a role, even if controls are implemented to equilibrate familiarity across source items.

Although modifications to dual process and Gaussian models can account for source ROC analyses, they have conceptual limitations for theory building. Most problematic is that they approach deficiencies of pure, theoretically based models by combining the properties of both threshold and continuous models. That is, to make threshold models fit, continuous fea-

tures must be added and to make continuous models fit probabilistic (e.g., threshold) features must be added. The use of such hybrid models may better account for extant findings, but they lead to models that are difficult to falsify empirically. Any problems in fitting such models to observed data may be rectified by adding a dash of a continuous parameter or a pinch of a probabilistic one. Moreover, these modifications are not fully integrated into a functional theory in the sense of offering a psychological or neural basis of explanation. When does familiarity affect source recognition? How does one encode source information? What is the basis of noise during source identification? Alternatively, by the simple assumption of skewed distributions, which is grounded on MTL hierarchical relational binding, ROC and zROC curves for both item and source recognition data are well described. Thus, hRBT offers a parsimonious and functionally explicit model of item and source recognition memory.

### DUAL PROCESS VERSUS SINGLE PROCESS VIEWS

Hierarchical relational binding shares many characteristics with Yonelinas’ dual-process model (Yonelinas, 1994, 1999). Both models suggest the presence of a subset of disproportionately strong memories. In the Yonelinas model, some old items surpass a “recollection” threshold and are thus very strongly remembered. In hRBT, the nonlinear dynamics of multilevel bindings create old item distributions that are positively skewed, such that strong memories get even stronger. Such bindings facilitate context-based associations (i.e., source memory) as well as interitem associations. One way to link the two views is to consider the threshold  $R$  parameter as an approximation of the  $\lambda$  parameter, which defines the skewing influence associated with hierarchical relational binding. These two parameters have very similar consequences on memory performance. As such, our model is consistent with many of the behavioral findings used to support Yonelinas’ dual-process model [see Eichenbaum et al. (2007) and Yonelinas and Parks (2007)].

There are, however, important conceptual differences between hRBT and Yonelinas’ dual-process model. The dual-process model defines recollection and familiarity as two independent and fundamentally separable processes, each with its

own dissociable neural circuitry. Specifically, it splits MTL regions, such that the hippocampus serves recollection, whereas familiarity is served by other MTL regions. According to hRBT, the entire MTL serves hierarchical relational binding and works as a functional unit. By this view, a *recollective* experience is defined as the phenomenology of retrieving or “re-collecting” an ensemble of features tied to a specific past event. Multilevel MTL bindings, particularly at the highest level, the hippocampus, contribute most to such experiences.

A familiarity experience occurs whenever a fully reinstated event ensemble is not recollected. It is achieved by bindings primarily at low levels of MTL binding (and perhaps by minimal hippocampal bindings), which help to reinstate smaller packets or subsets of event features, but not enough to enable a fully formed recollective experience. Familiarity responses may also be achieved purely by neocortical bindings. The phenomenon of priming may be viewed as a “familiarity” response driven only by neocortical activations and thus a response that does not involve any MTL bindings. Also, unitized associations such as those that involve within-object features (e.g., linking a color or shape to a bottle) may be driven only by localized neocortical bindings or by low-level MTL bindings. Bindings of such subsets of an episodic event may lead to familiarity response with high confidence, though without a strong “recollective” experience. For example, one may very strongly remember having seen a green bottle during a study phase but not recollect the entire spatial context in which it was presented.

A second difference between hRBT and Yonelinas’ dual-process model is the nature of the operating characteristics associated with recollection. According to Yonelinas’ dual-process model, recollection is defined as a threshold process, as it is probabilistic—a test item can only succeed or fail to elicit a recollective experience, there is no in between. If recollection does not exceed a threshold value, then the retrieval is based solely on familiarity. Although recollection is viewed as a threshold process, it is acknowledged that the process may be graded, though noninformative or not functioning at subthreshold levels of memory strength (Yonelinas et al., 1996; Parks and Yonelinas, 2007). The critical point of Yonelinas’ dual-process model is that an item’s memory strength needs to pass a threshold before it is recollected. According to hRBT, relational binding is a graded process, though with nonlinear dynamics. Behavioral findings suggest that source recollection occurs in a graded manner, even for items with low to moderate levels of confidence [see Dodson et al. (1998) and Wixted (2007)]. Moreover, in nearly all extant ROC analyses of source memory (Slotnick et al., 2000; Qin et al., 2001; Hilford et al., 2002; Glanzer et al., 2004), curvilinear ROC functions have been observed. Dual-process theorists argue that measures are never “process pure” and thus may be influenced by familiarity. Yet, the pervasive finding of curvilinear ROC curves for source recognition is informative and suggests that the operating characteristic of source memory is best viewed as a graded process with skewed distributions.

According to Yonelinas’ dual-process model, the hippocampus acts as a thresholded mechanism that enables recollective

experiences. By this view, the hippocampus functions as an all-or-nothing mechanism that triggers recollective experiences. It seems rather unlikely that any circumscribed brain region would serve such a broad phenomenological experience as triggering episodic recollection. Moreover, the neural architecture of MTL circuitry suggests that the hippocampus is part of a larger network as it projects to and receives inputs from other MTL regions. Nevertheless, the hippocampus may be a *necessary* component for recollection, such that without hippocampal activity, the experience of recollection cannot occur. Although plausible, it has been known since early analyses of H. M. that patients with MTL damage can recollect episodic memories in a declarative manner, if the memories pertain to remote experiences that occurred well before the onset of amnesia (Marslen-Wilson and Teuber, 1975; MacKinnon and Squire, 1989). Finally, neuroimaging findings suggest that hippocampal activity is graded and modulates with different levels of source recollection, which is more consistent with a continuous rather than threshold model of source recollection (Staresina and Davachi, 2008).

The functional properties of hRBT help resolve the debate between dual-process and single-process views. As described earlier, the hippocampus does have a particularly important role in recollection, as it is situated at the top of the relational binding hierarchy and is thus able to reinstate more fully an episodic memory. However, the hippocampus and other MTL regions contribute to both item familiarity and recollection as they all are involved in binding event features. According to hRBT, there are no stark boundaries between brain structures, such as between MTL and the rest of the neocortex or between the hippocampus and the rest of the MTL. A single functional property, albeit with nonlinear dynamics, can produce “dual-process” like experiences without the need to force stark classifications between brain regions. With respect to lumpers and splitters, there is no need to split the functional role of the hippocampus as qualitatively different from other MTL regions. Differences in the phenomenological experiences of recollection and familiarity can be explained by the nonlinear dynamics of hierarchical relational binding.

### NEURAL IMPLICATIONS OF MTL HIERARCHICAL RELATIONAL BINDING

The proposed characterization of MTL is related to other views that describe the role of the MTL in terms of relational or associative binding (Mishkin et al., 1997; Lavenex and Amaral, 2000; Norman and O’Reilly, 2003; Bussey et al., 2005; Davachi, 2006; Diana et al., 2007; Eichenbaum et al., 2007; Suzuki, 2007). For example, Bussey et al. (2005) proposed a hierarchical circuit within the ventral visual stream such that successive levels of visual processing act to create more complex conjunctions of visual features. The highest level of this hierarchy occurs by way of conjunctions formed in the perirhinal cortex. MTL relational binding could be viewed as

an extension of the Bussey et al. (2005) model taking conjunctions further into the MTL to incorporate bindings of event features that are represented outside the ventral visual stream. Indeed, Bussey and Saksida (2007) suggested the possibility of extending ventral stream conjunctions into the hippocampus, though they did so in the service of implicating the hippocampus in the role of integrating perceptual features. In fact, feature conjunctions and convergence zones may be general properties of many cortical circuits, thus blurring the border between MTL and other cortical regions. By this view, the unique contribution of the MTL is its position as the ultimate convergence zone for the binding of disparate neocortical activations. Hierarchical bindings are efficient for memory retrieval because rather sparse re-activations at the hippocampal apex can potentially reinstate an ensemble of event features distributed widely in the neocortex.

Norman and O'Reilly (2003) developed an elegant computational model of MTL processes, which is based on the *complementary learning systems (CLS)* framework (O'Reilly and McClelland, 1994, 2002; McClelland et al., 1995). According to CLS, two contrasting retrieval strategies define human memory. On one hand, episodic retrieval depends on retrieving specific ensembles of cortical features that define past episodic events. The hippocampus is particularly important in this computation as it enables *pattern separation*, a process that sharpens the ability to discriminate episodic memories from one another. On the other hand, retrieval of factual knowledge or *semantic retrieval* depends upon the ability to activate as many associates from a retrieval cue as possible. Thus, when asked, "What is the role of the hippocampus in memory?" one may activate numerous associations to the cue rather than any particular one linked to a past experience. Spreading activation of distributed neocortical networks is thought to determine the success of semantic retrieval. By this view, episodic retrieval depends on retrieving specifics, whereas semantic retrieval depends upon retrieving generalities. These two complementary processes form the basis of episodic versus semantic retrieval. The hippocampus is viewed as particularly important for pattern separation as well as the reinstatement of specific episodic ensembles during retrieval (i.e., *pattern completion*). Distributed cortical activation is viewed as important for semantic retrieval.

The CLS framework is compatible with hRBT as pattern separation describes the role of the MTL in the initial binding of event features and pattern completion describes its role during retrieval. Norman and O'Reilly (2003) applied their model to account for the distinction between recall and familiarity. Recall, which is akin to recollection, involves pattern separation and completion mechanisms associated with the hippocampus. Although the model describes a stark distinction between the hippocampus and other MTL regions and its operating characteristics consistent with a dual-process view of episodic recollection, the effect of activations through the network was continuous. Thus, unlike the Yonelinas dual process model, the authors argued that "... results from our hippocampal model are not consistent with the idea that recall is a high-threshold process" (Norman and O'Reilly, 2003, p. 636). Elfman et al. (2008)

used the CLS framework to model the operating characteristics of source ROCs and supported the dual-process nature of episodic recollection. As the functional properties of hRBT are similar to dual-process models but do not demand a threshold process, it too may be mapped onto CLS, a framework which describes in greater detail the mechanistic underpinnings of MTL processes.

To the extent that MTL is involved in binding event features during encoding and reinstating them during retrieval, its functional role is particularly related to episodic retrieval. However, it has been known since early neurocognitive analyses of amnesic patients that semantic retrieval of newly learned material is severely impaired. For example, Cermak and O'Connor (1983) studied an amnesic patient who was a physicist and expert in laser technology. When presented with a newspaper article on a recent development in laser research, the patient could easily interpret and explain the new findings, yet minutes after reading the article, the patient could not remember its contents. Moreover, repeated instructions to rehearse the information proved futile in establishing new links to his extant knowledge. This finding and others (Shimamura and Squire, 1987) suggest that amnesic patients are impaired in adding new facts to existing semantic knowledge.

Clearly, MTL binding must serve the ability to acquire new semantic facts. In particular, MTL binding facilitates the linking of new semantic facts to existing knowledge structures, a phenomenon often described as *schema building*. Even rodent studies suggest that memory for schema-based semantic associations depends on the hippocampus (Tse et al., 2007). There are, however, prominent differences between semantic and episodic memory. Semantic memory is supported largely by pre-existing knowledge. For example, the addition of a new fact about the hippocampus can be integrated within a web of pre-existing knowledge, such that successful retrieval of the new fact could be obtained by reinstating any of a number of linked associations to that piece of knowledge. Thus, extensive prior knowledge allows multiple links to new semantic information thus increasing the success of semantic retrieval. Episodic memories are by definition encapsulated as a specifically bound set of event features linked to particular experiences in one's life. Evidence from amnesic patients suggests that episodic retrieval is generally more impaired than semantic retrieval of recently learned information. Such findings are consistent with hRBT, as the role of the MTL is to facilitate the reinstatement of bound event features, a necessary component of episodic retrieval. Yet, in the case of semantic learning, that is when one thinks about a new fact within the context of pre-existing knowledge (e.g., studying for an exam), semantic features are bound as part of an event ensemble at the time of learning. According to hRBT, such semantic features are also bound in the same manner as other event features, such as emotional and perceptual features. What makes semantic retrieval different from episodic retrieval is (1) the enormous contribution of pre-existing knowledge (i.e., extensive neocortical support) for semantic retrieval and (2) the necessity of reinstating a particular set of event features for episodic retrieval. These two dis-



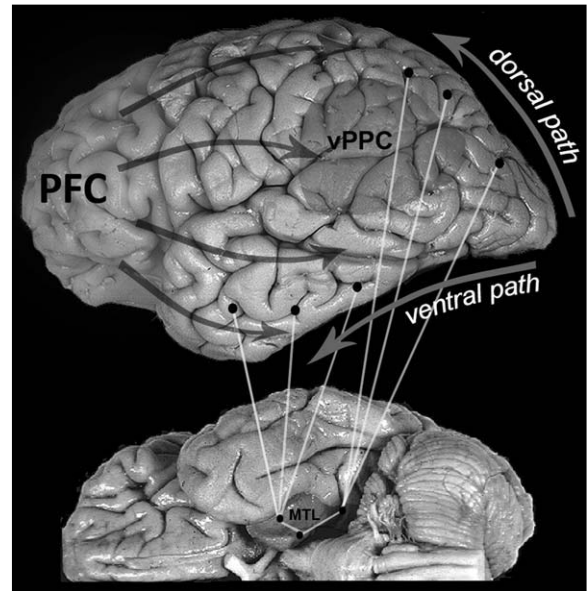
inctions map onto the two complementary aspects of memory defined by the CLS [see O'Reilly and Norman (2002)].

### EPIODIC RETRIEVAL AS A WHOLE BRAIN PHENOMENON

As stated earlier, episodic retrieval depends first upon efficient storage of salient event features at the time of encoding. These event features are activated by the sensory, conceptual, and emotional processes operating during the initial experience. Sensory inputs, such as those activated along the visual dorsal and ventral paths, represent spatial relations and object-based features of an episodic memory. These inputs are monitored and controlled by the PFC, which assists in the maintenance and updating of active representations (Miller and Cohen, 2001; D'Esposito, 2008; Shimamura, 2008). Considerable research has shown that increased PFC activity during encoding predicts the success of subsequent retrieval (Paller and Wagner, 2002). Thus, at the time of encoding numerous sensory, conceptual, emotional, and executive processes are engaged to create and store episodic memories. As described by hRBT, the MTL links active event features as bound episodic memories and facilitates in the long-term storage (i.e., consolidation) of them after the initial encoding event. By this view, the encoding of episodic memories must be considered as a whole brain phenomenon. Figure 5 identifies some of the cortical regions involved in the encoding and storage of episodic memories.

During retrieval, successful episodic recollection depends upon the reinstatement of event features associated with a particular past experience. In general, retrieval is initiated by rather sparse cueing (e.g., What did you do last weekend?). Without significant sensory cues, retrieval must begin by top-down executive control processes that act to search for and reactivate relevant event features. Considerable research has shown that the PFC is involved in the executive control of retrieval search processes (Cabeza and St. Jacques, 2007). These processes help activate relevant features, suppress irrelevant features, and bring online encapsulated ensembles of an episodic memory. According to hRBT, MTL paths are activated during retrieval and facilitate in the reinstatement of bound event features. Indeed, computational algorithms associated with hippocampal circuits, such as pattern separation and pattern completion (O'Reilly and Norman, 2002), offer important mechanisms for the role that the MTL plays in episodic retrieval. As mentioned earlier, these mechanisms are compatible with the functional properties of hRBT.

The ventral posterior parietal cortex (vPPC) is particularly active during the successful retrieval of episodic memory [for review, see Cabeza et al. (2008), Hutchinson et al. (2009), Shannon and Buckner (2004), and Vilberg and Rugg (2008)]. This region (see Fig. 5), which includes the supramarginal gyrus, angular gyrus, and temporal-parietal junction (BA 39 and 40), is more active in recognition memory tests when correct yes responses (i.e., hits) are compared to correct no responses (i.e., correct rejections). Moreover, the vPPC is more



**FIGURE 5.** Critical components of episodic recollection. Events are initially encoded by bottom-up sensory signals (e.g., from dorsal and ventral paths) and top-down prefrontal cortex (PFC) signals, which keep event features online (black dots). These features are bound by the medial temporal lobe (MTL) as hierarchically bound episodic ensembles. During episodic retrieval, PFC signals and bottom-up cues initiate search strategies that facilitate the reinstatement of event features. The ventral posterior parietal cortex (vPPC) is particularly active during successful retrieval, suggesting that this area facilitates in the reinstatement of episodic ensembles (brain image adapted and reprinted from *Digital Anatomist Interactive Atlas*, University of Washington, Seattle, WA, copyright 1997).

active for old items judged as highly recollected (i.e., remember items) compared to those judged as only familiar (i.e., know items). Also, the vPPC monitors the degree to which specific event features can be remembered on tests of source recollection (see Cabeza et al., 2008). Finally, during retrieval vPPC activity is functionally related to PFC and hippocampal activity and is correlated with memory performance (Klostermann and Shimamura, 2008).

Various theories have attempted to account for the role of the vPPC in episodic retrieval. The Attention to Memory (AtoM) theory (Cabeza et al., 2008) asserts that the vPPC facilitates in the selection of bottom-up sensory features that, along with MTL processes, help to reinstate perceptual features associated with episodic memories. The episodic buffer theory (Vilberg and Rugg, 2008) argues that the vPPC acts as a temporary store of multimodal features that make up an episodic memory. These theories capture some but not all aspects of retrieval-related vPPC activity. One critical finding is that vPPC activity is tied to brain regions that encode event features. For example, Klostermann et al. (2009) found only right vPPC activity during retrieval of non-Western music that is processed primarily by the right hemisphere. In other studies, left-lateralized vPPC activity is observed, which suggests that verbal or semantic processes are typically implemented during retrieval.

Given such findings, retrieval-related activity in the vPPC may represent high-level or multimodal bindings that tie event features in the neocortex.

Considering the many brain regions involved in the encoding, storage, and retrieval of episodic memories, it is clear that the phenomenology of recollecting our past is a whole-brain experience. As such, one must consider lumping the entire brain in the service of such a complex process. Moreover, it is clear that no single component within this neural circuitry can be viewed as solely responsible for a recollective experience. At this moment in neurobehavioral research, there is enough data to begin to develop functional characteristics of neural circuits involved in learning and remembering rather than arguing about whether there is a stark border between the MTL and other cortical regions or between the hippocampus and other MTL regions. Moreover, given the framework outlined here, it is essential to consider how MTL circuits participate in conjunction with other brain regions, such as the PFC, vPPC, and sensory and emotional circuits, in the service of both episodic encoding and retrieval.

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