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Superadditive Memory Strength for Item and Source Recognition: The Role of Hierarchical Relational Binding in the Medial Temporal Lobe

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Source memory depends on our ability to recollect contextual information—such as the time, place, feelings, and thoughts associated with a past event. It is acknowledged that the medial temporal lobe (MTL) plays a critical role in binding such episodic features. Yet, controversy exists over the nature of MTL binding—whether it contributes specifically to source recollection or whether it contributes equally to both item familiarity and source recollection. To resolve this issue, the authors propose that the MTL acts to bind contextual features through a process of hierarchical relational binding. That is, by way of multiple levels of associative bindings (i.e., bindings of bindings), the MTL links episodic features in a superadditive manner. To account for this binding feature, the authors develop a recognition model that includes positively skewed distributions of memory strength. Such skewed distributions can account for many empirical findings and regularities of both item familiarity and source recollection.

Keywords: source memory, hippocampus, episodic memory, recognition, recollection

Autobiographical memory refers to the manner in which life events are encoded, stored, and ultimately retrieved. Progress in behavioral methodology, cognitive neuroscience, and quantitative models has advanced the field by offering new techniques and findings (for a review see Squire, Wixted, & Clark, 2007; Svoboda, McKinnon, & Levine, 2006; Yonelinas & Parks, 2007). A particular feature of autobiographical memory is source memory—defined by Johnson, Hashtroudi, and Lindsay (1993) as "the spatial, temporal, and social context of the event; the media and modalities through which it was perceived" (p. 3). By this view, a distinction is made between item memory (i.e., central information) and source memory (i.e., contextual information). For example, when asked to recollect what you ate for dinner last night, one could retrieve the central information—what you ate—as well as source information, such as the time, location, people, thoughts, and feelings associated with the meal. Source memory enables the placement of past events within a contextual framework. As such, the recollection of source information is an essential, if not defining, characteristic of autobiographical memory.

The analysis of source memory has its roots in studies of memory disordered individuals, such as neurological patients with anterograde amnesia or frontal lobe dysfunction (Janowsky, Shimamura, & Squire, 1989; Schacter, Harbluk, & MacLachlin, 1984; Shimamura & Squire, 1987). Its scope broadened as the concept provided a useful, operational definition of autobiographical memory. That is, autobiographical memory could be confirmed if a participant remembered a specific contextual feature of a stimulus (e.g., where it was presented or when it occurred). The notion of source recollection also provided a theoretical basis for other memory phenomena, such as the distinction between remembering (i.e., memory with source recollection) and knowing (i.e., memory without source recollection) (Tulving, 1985).

Source Memory and Relational Binding

In the laboratory, source memory is investigated by presenting study items that vary in contextual features. For example, words may be presented in one of two colors, locations, or sizes. Source memory is assessed by having participants identify specific features of study items, such as determining whether a word was originally presented blue or yellow (in examples that follow, we generally refer to source-specific items as Source A and Source B items). In such tests, source memory can be construed as memory for associative or contextual features of a stimulus. Often both item (old vs. new) and source (Source A vs. Source B) recognition are assessed within the same study. Behavioral analyses have shown that source memory is particularly disrupted in conditions that limit attentional resources (Dodson & Shimamura, 2000; Mulligan, 2004) or in patients with attentional dysfunction, such as patients with frontal lobe impairment (Glisky, Polster, & Routhieaux, 1995; Janowsky et al., 1989). Furthermore, neuroimaging studies have shown that cortical regions associated with selective attention and executive control, such as the left ventrolateral prefrontal cortex, are particularly active during tests of source memory (Ranganath, Johnson, & D'Esposito, 2000; Rugg, Fletcher, Chua, & Dolan, 1999). These findings suggest that active online binding and organization of information—essential products of prefrontal function (see Miller & Cohen; 2001; Shimamura, 2000; 2002a)—are important for the encoding of source informa-

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tion. In other words, prefrontal activity coordinates online activity (i.e., working memory) and establishes a context within which episodic features are encapsulated as an active representation.

Neurocognitive theories of memory suggest that other neural processes are involved in the consolidation or storage of active representations. Squire (Squire, Cohen, & Nadel, 1984; Squire & Zola-Morgan, 1998) proposed that the medial temporal lobe (MTL), by way of its pathways to and from neocortical areas, enables rapid associative binding of active representations during learning. After learning, MTL bindings assist in reactivating cortical ensembles, thus strengthening or consolidating them as a unit. This consolidation theory offered an explanation of memory impairment observed in amnesia and led to the distinction between declarative (episodic and semantic memory) and nondeclarative memory (skills, habits, priming). It has had such a substantial impact on the field that it has been described as the standard model (Nadel & Moscovitch, 1997). This view has also been implemented in computational models (Alvarez & Squire, 1994; McClelland, McNaughton, & O'Reilly, 1995; see also Gluck & Myers, 1997; Norman & O'Reilly, 2003). Extensions of the standard model include those by Cohen and Eichenbaum (1993), who specified the role of MTL in relational memory, a term that describes the hippocampal–cortical networks established by the MTL. Also, Shimamura (2002b) developed a modified view, relational binding theory, which describes the role of MTL binding in both storage and retrieval.

The significance of MTL to relational binding is based 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 or indexing the co-occurrence of multiple inputs (for review, see Lynch, Rex, & Gall, 2007; Morris, 2006). This form of cellular plasticity is mediated by NMDA receptor channels, which are dependent on coactive inputs and are highly concentrated in the hippocampus (Morris, 2006; Petralia, Yokotani, & Wenthold, 1994). Activity-dependent synaptic plasticity offers a means of linking multiple inputs that converge onto a hippocampal neuron, thus providing a cellular mechanism for relational binding (see Squire, Shimamura, & Amaral, 1989).

A second critical feature of the MTL is its hierarchical organization. The MTL receives inputs from many disparate neocortical sites. As shown in Figure 1 (adapted from Lavenex & Amaral, 2000), neocortical inputs into the MTL converge initially onto the perirhinal and parahippocampal cortices. The perirhinal cortex receives its primary projections from high-level visual regions that make up the ventral stream (Suzuki & Amaral, 1994). It also receives projections from other unimodal and polymodal regions, including the superior temporal gyrus, the insular cortex, and the orbitofrontal cortex. The parahippocampal cortex receives projections from a variety of neocortial regions, including the posterior parietal cortex, retrosplenial cortex, dorsal superior temporal sulcus, and cingulate cortex. Thus, the perirhinal and parahippocampal cortices are privy to neural activity from many disparate neocortical regions (Lavenex & Amaral, 2000; Suzuki & Amaral, 1994; Van Hoesen & Pandya, 1975). The entorhinal cortex, the next MTL convergence zone, receives most of its inputs from the perirhinal and parahippocampal cortices. Ultimately, MTL projections converge onto the hippocampus, which sends reciprocal projections back to other MTL regions, which themselves send reciprocal projections back to target neocortical association areas. Thus, relational binding within the MTL has the capacity to link features of an episodic representation that reside in disparate neocortical sites.

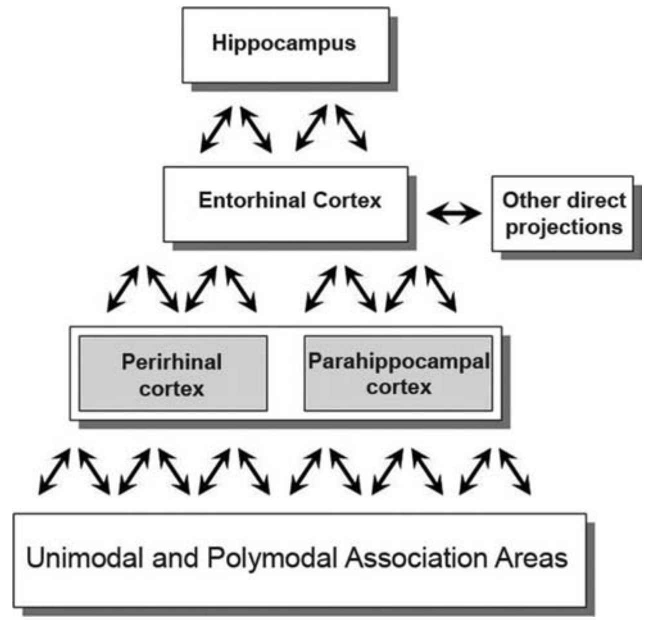

Figure 1. Adapted from "Hippocampal-Neocortical Interaction: A Hierarchy of Associativity," by P. Lavenex and D. G. Amaral, 2000, *Hippocampus, 10,* p. 427. Copyright 2000 by John Wiley & Sons. Adapted with permission. Neural architecture of the medial temporal lobe (MTL). Projections from unimodal and polymodal neocortical association areas project to the perirhinal and parahippocampal cortex—the first level of MTL binding. These two MTL regions project to the entorhinal cortex and ultimately to the hippocampus. Reciprocal pathways down through MTL regions enable relational bindings to influence neocortical representations.

There is general consensus that the MTL contributes to the binding of new memory representations. Controversy exists over the functional role of regions within the MTL. Squire and colleagues (Squire & Zola-Morgan, 1998; Squire et al., 2007) have argued that regions within the MTL are generally uniform in their service to consolidating (binding) neocortical units, though different MTL regions may be binding different featural units. Thus, larger MTL lesions will lead to greater memory impairment, but there is little differentiation among structures within the MTL as its entire circuitry is devoted to consolidation. Others have suggested that the hippocampus plays a unique and qualitatively different role in the service of autobiographical memory (Aggleton & Brown, 1999; Mishkin, Suzuki, Gadian, & Vargha–Khadem, 1997; Nadel & Moscovitch, 1997; Yonelinas et al., 2005). It is argued that the hippocampus contributes specifically to the recollection of contextually rich autobiographical memories. Recollection is closely related to source memory, as it is defined by the degree to which individuals have contextual memory of past experiences.

Neuropsychological and neuroimaging studies are mixed with respect to the specific role of the hippocampus in recollection. In studies of amnesic patients, some have observed particular impairment in episodic recollection. For example, Vargha-Khadem et al. (1997) assessed individuals who incurred hippocampal damage during childhood and found that they exhibited profound impairment in autobiographical memory with relatively good memory for semantic facts and linguistic skills (e.g., reading and writing). An adult case with a circumscribed hippocampal lesion also exhibited disproportionate deficits in recollection (Holdstock, Mayes, Gong, Roberts, & Kapur, 2005). There is evidence in neuroimaging studies of the remember–know paradigm to suggest that recollection responses are particularly associated with hippocampal activity (Aggleton et al., 2005; Yonelinas, Otten, Shaw, & Rugg, 2005; for review, see Eichenbaum, Yonelinas, & Ranganath, 2007). In this paradigm, participants classify recognized items in terms of either having a recollection about specific features of a prior experience (remembering) or simply having a familiarity with an item that was presented (knowing). Yet, many MTL regions monitor the effects of relational binding, such as that observed on tests of source memory (Davachi, Mitchell, & Wagner, 2003). Moreover, in some studies, the entire MTL appears to be devoted to the formation of declarative memory without any special role of the hippocampus in this process (Manns, Hopkins, Reed, Kitchener, & Squire, 2003; Stark, Bayley, & Squire, 2007; Wais, Wixted, Hopkins, & Squire, 2006).

In summary, human lesion and neuroimaging studies are equivocal in determining the specific contributions of MTL regions to aspects of autobiographical memory. To what degree does the hippocampus play a specific role in recollective processes? Can the MTL be described fully as a neural process that enables relational binding? The failure of neurocognitive investigations in affirming a decisive conclusion about these issues is due in part to difficulty in the precision of identifying specific MTL damage in amnesia patients and specific MTL regional activation in neuroimaging studies. Another problem concerns the lack of specifically delineating the mechanistic underpinnings of MTL regions. In the following sections, we develop a quantitative model of recognition memory that attempts to incorporate and refine the role of the MTL in its service to human memory performance.

Operating Characteristics of Item and Source Memory

Issues of item familiarity, recollection, and source memory have benefited from quantitative modeling of recognition memory performance. Various approaches have been applied, the most common of which is signal detection theory (SDT). In SDT, it is assumed that memory strength for a study item is represented as a value along a single, continuous dimension (Green & Swets, 1966; Macmillan & Creelman, 2005; Wickens, 2002). In the simplest SDT models, Gaussian functions are used to characterize the distribution of items along this dimension (see Figure 2, Panel A). For old or new recognition memory performance, a decision criterion defines the level at which items with memory strength greater than the criterion are identified as old and those below that value are identified as new. Thus, the criterion delineates hits (p[old|old]) from misses (p[new|old]) for old items and correct rejections (p[new|new]) from false alarms (p[old|new]) for new items. The relative proportion of hits (H) and false alarms (FA) depends on the placement of the criterion. When measuring old or new recognition performance, confidence ratings (e.g., sure new, likely new, maybe new, maybe old, likely old, sure old) are usually obtained to assess performance at multiple decision criteria within the same experiment.

In equal variance Gaussian SDT models, old and new distributions are represented as Gaussian functions with their variances set at unity ($\sigma^2_{old} = \sigma^2_{new} = 1$). The mean of the new distribution is set at 0, and the mean of the old item distribution is defined as d'—the difference between the two means in units of the standard deviation. Under these circumstances, H and FA rates are determined by two parameters—d' and the decision criterion, c, as expressed by the following equations, in which Φ is the standard normal cumulative probability function ($\mu = 0$, $s^2 = 1$):

$$\mathrm{H} = \Phi(d' - c), \text{ and} \tag{1}$$

$$\mathrm{FA} = \Phi(-c). \tag{2}$$

An important tool for investigating the processes underlying recognition memory performance is the operating characteristic, commonly referred to as the receiver operating characteristic (ROC). In ROC analyses, cumulative H and FA proportions are plotted as a function of criterion level, from the strictest to the most liberal criterion. The equation of the ROC is given by eliminating c from Equations 1 and 2:

$$\mathrm{H} = \Phi(d' + Z[\mathrm{FA}]), \tag{3}$$

where Z is the inverse of the standard Gaussian cumulative distribution function Φ.

The shape of the ROC function is determined by the form of new and old distributions and their relative position to each other. When the distributions are Gaussian, ROCs are curvilinear (inverted-U shaped), and the extent of deviation from the diagonal is an index of memory strength (see Figure 2, Panel B). Another useful plot is the Z-transformed receiver operating characteristic (zROC), in which cumulative H and FA proportions are transformed as standard Gaussian scores (Figure 2, Panel C). In zROC space, linear functions are consistent with a model in which both old and new distributions are Gaussian in form. The zROC function crosses the abscissa at the difference of the distribution means, $\mu_{new} - \mu_{old}$, and its slope is the ratio of the two standard deviations, $\sigma_{new}/\sigma_{old}$. Thus, for equal variance Gaussian SDT models, the slope of the zROC is 1.

Threshold or finite-state models offer an alternative to continuous SDT models. Though largely rejected as viable models of sensory detection, threshold models have been used to model operating characteristics of memory. In a threshold model, the recognition responses are determined from a small set of memory states. In a simple threshold model of item recognition, the probability of responding "old" or "new" is characterized by a memory parameter (M) and a guessing parameter (g). That is, with probability M, old items surpass a memory strength threshold and are identified as old. Old items that do not surpass this threshold (with probability $1 - \mathrm{M}$) are guessed to be old with a probability of g. The sum of these two probabilities determines the observed H rate:

$$\mathrm{H} = M + (1 - M)g \tag{4}$$

New items do not have a representation in memory (they all fall below the memory threshold) but are guessed to be old with a probability g. Thus, the FA rate is determined by g alone:

$$\mathrm{FA} = g \tag{4}$$

Substituting FA for g in Equation 4 gives the ROC function:

$$\mathrm{H} = M + (1 - M)\,\mathrm{FA} \tag{5}$$

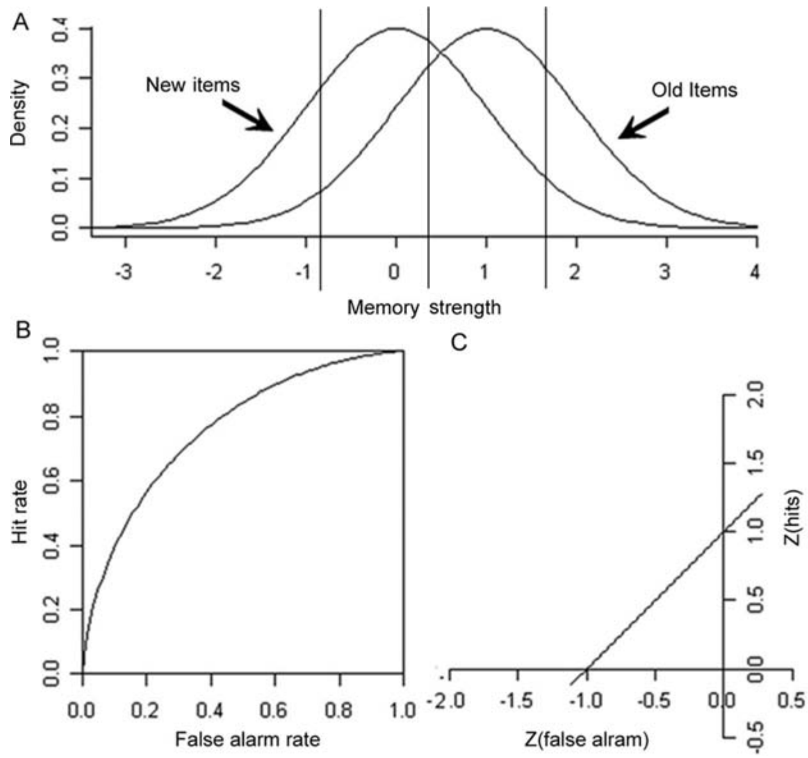

Figure 2. A: Panel depicts a standard signal detection theory model of item recognition memory in which old and new items are represented as Gaussian distributions with equal variance. The vertical lines refer to placements of criterion levels that define boundaries in which new (left of criterion) and old (right of criterion) responses are made. B: Panel depicts a receiver operating characteristic (ROC) function in which cumulative hit (H) and false alarm (FA) rates are plotted across the varying criterion levels. A curvilinear (inverted-U shape) ROC plot implies a continuous model of memory strength. C: Panel depicts a zROC plot in which H and FA rates are transformed as z scores. Linear zROC plots imply Gaussian distributions.

For a threshold model, the ROC function is linear, with a slope of $1 - M$ and a y-intercept of M (Figure 3, Panel A). The corresponding zROC curves are U-shaped (Figure 3, Panel B).

Batchelder and Riefer (1990) extended this threshold model to account for both item recognition and source identification. Analyses are based on data from a three-alternative forced-choice test. For each test item, participants determine whether it was originally studied as a Source A item or a Source B item or whether it is a new Item. According to Batchelder and Riefer (1990), source recognition performance is determined by two memory parameters—the probability of an item being detected (M) and the probability of source identification (S) conditional on item detection.[1] A test item can be in one of three states: detected as old and the source known, detected as old and the source not known, or not detected as old. Two parameters account for guessing behavior: If an item is not recognized, it is nevertheless guessed to be old with probability g, and if the source is unknown, it is guessed to be from Source A, with probability a. Figure 4 shows response probability paths that determine the manner in which memory and guessing parameters lead to source recognition responses for Source A items. Response probabilities are obtained by summing the probability paths that lead to specific responses. For Source A items, these probabilities are

$$\text{P(Source A|A)} = \text{MS} + M(1 - S)a + (1 - M)ga,$$

$$\text{P(Source B|A)} = M(1 - S)(1 - a) + (1 - M)\,g\,(1 - a), \text{ and}$$

$$\text{P(New|A)} = (1 - M)(1 - g).$$

Responses for Source B items are derived from a similar tree structure, and those for new items are derived from guessing probabilities associated with the unfamiliar state ($1 - M$ paths in Figure 4). The resulting threshold model has proved useful in characterizing aspects of source memory performance (see Batchelder & Riefer, 1990; Bayen, Murnane, & Erdfelder, 1996; Dodson & Shimamura, 2000; Meiser, 2005; Riefer, Hu, & Batchelder, 1994). As with other simple finite-state models, the Batchelder-Riefer model predicts linear ROC and U-shaped zROC curves (Figure 3).

The SDT and finite-state threshold models described above are starting points for theory development. In general, the equal variance Gaussian SDT and pure threshold models do not provide good fits of the operating characteristics of either item or source memory performance. With respect to item recognition, ROC analyses have consistently demonstrated curvilinear plots, suggesting that memory

[1] Batchelder and Riefer (1990) denoted these parameters as d and D. We change them here to avoid confusion with d'.

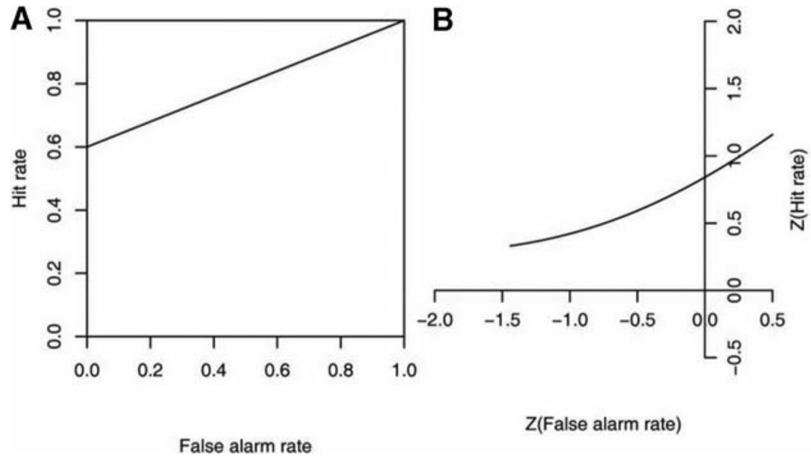

Figure 3. Receiver operating characteristic (ROC) and zROC functions for a multinomial model in which recognition performance is based on a high-threshold memory parameter (M) and a guessing parameter (g). Note the linear ROC and slightly U-shaped zROC predicted by such models.

strength is a continuous process and is not adequately described by a threshold model. Yet, the slope of zROC plots are typically less than one, suggesting that Gaussian equal variance SDT models do not provide an adequate fit of item recognition performance (Ratcliff, McKoon, & Tindall, 1994). One remedy for the problem is to adopt a Gaussian SDT model in which new and old items do not have the same variance. Specifically, the variance of the new item distribution is fixed at one (for identification of the model), whereas the variance of the old item distribution is a free parameter, σ^2_{old}. The H rate for an unequal variance Gaussian model then is:

$$H = \Phi\left(\frac{\mu - c}{\sigma^2_{old}}\right).$$

To describe source memory, Banks (2000) and Slotnick, Klein, Dodson, & Shimamura (2000) developed two-dimensional SDT models in which item detection and source discrimination are determined by two orthogonal decision axes. These models are based on bivariate Gaussian SDT models of sensory detection and discrimination (Tanner, 1956; see also Thomas, Gille, & Barker, 1982). One dimension is comparable with standard SDT models of item familiarity in which old (i.e., both Source A and Source B) and new item distributions are characterized by continuous Gaussian distributions with unequal variances. A second dimension is used to represent discriminations between Source A and Source B items (i.e., source memory strength). For ROC analyses, source recognition can be assessed in much the same manner as old or new item recognition. For example, participants could study words presented by a male or female voice and, at test, make source judgments (male or female) to visually presented test items. To construct source ROC plots, confidence ratings are obtained for all source judgments (sure male, likely male, maybe male, maybe female, likely female, sure female). When old or new recognition and Source A or Source B discriminations are obtained within the same experiment, ROC plots can be made for both dimensions for the same set of study items (see Hilford, Glanzer, Kim, & DeCarlo, 2002; Slotnick et al., 2000).

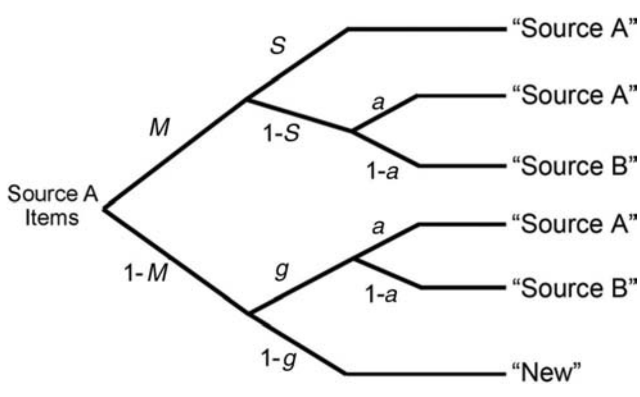

Figure 4. Probability tree structure of Source A items based on Batchelder and Reifer's (1990) multinomial model of source memory. In this discrete-state model, a correct source response ("Source A") is determined by combining several probability routes. For example, the top route depicts the joint probability of correctly identifying the item as old (M) and correctly identifying the item as a Source A item (S). As described in the text, other routes depend on guessing parameters—guessing that an item is old (g) and guessing that an item came from Source A (a).

As an alternative to SDT Gaussian models, Yonelinas (1994, 1999) developed a dual-process model. The model is based on the view that recognition performance is supported by two independent memory processes, recollection and familiarity (Jacoby, 1991; Mandler, 1980). Recollection necessitates memory for the spatial–temporal context of an event, whereas familiarity provides a general, less focused sense of knowing. In Yonelinas' (1994, 1999) dual-process model, recollection is viewed as a threshold process, essentially the same as that described by other finite-state models. Familiarity, however, is viewed as a continuous, graded process described by an equal-variance Gaussian SDT model. Recognition memory performance is based on a mixture of these two independent influences. That is, an item is judged as old if it surpasses a recollection threshold (with probability R), or in the absence of recollection, it is judged as old on the basis of familiarity (described by d'). The H rate is a function of these two processes:

$$\mathrm{H} = R + (1 - R)\Phi(d' - c). \tag{6}$$

New items never enter a recollective state, and thus FAs occur when a new item exceeds the familiarity criterion as described by Equation 2. Solving Equations 2 and 6 to eliminate the familiarity criterion c gives the equation of the ROC:

$$\mathrm{H} = R + (1 - R)\Phi[d' + Z(\mathrm{FA})]$$

Yonelinas' (1994, 1999) dual-process model has been successful in characterizing a broad range of memory findings (for review, see Yonelinas, 2002; Yonelinas & Parks, 2007). It is important to note that Yonelinas (1999) applied his dual-process model to account for source memory. He suggested that source identification depends primarily on recollection, and thus, "the ROCs should become relatively linear" (Yonelinas, 1999, page 1419). That is, when familiarity is comparable between Source A and Source B items, then source memory should depend exclusively or largely on recollection. In three studies of source memory, Yonelinas (1999) found linear ROC and U-shaped zROC functions, suggesting that source memory performance is well fit by a finite-state threshold model. A fourth experiment showed that in conditions in which source items differ in overall memory strength, source decisions can make use of familiarity. In that experiment, one list was presented on Day 1, a second list was presented on Day 5, and source identification (i.e., list discrimination) was tested immediately after the second-list presentation. The ROC function for this source test was curvilinear (inverted-U shaped) rather than linear (see also Quamme, Frederick, Kroll, Yonelinas, & Dobbins, 2002).

In an elegant set of studies, Glanzer and colleagues (Glanzer, Kim, Hilford, & Adams, 1999; Glanzer, Hilford, & Kim, 2004; Hilford et al., 2002) evaluated operating characteristics of both item recognition and source identification . Figure 5 depicts data from Glanzer et al. (2004, Experiment 5) in which empirically derived ROC and zROC functions were obtained from item recognition (top panel) and source identification (bottom panel). On the basis of such data and a review of extant findings, Glanzer et al. (2004) identified five empirical regularities associated with item recognition (IR):

IR1. The ROC is curved with an inverted-U shape.

IR2. The zROC function is linear.

IR3. The zROC slope is less than one.

IR4. The zROC slope declines as accuracy increases.

IR5. Increasing accuracy is associated with a simultaneous increase in the H rate and a decrease in the FA rate, a phenomenon known as the mirror effect.

IR1 is consistent with continuous SDT models but not consistent with threshold models. IR2 suggests that the underlying distributions are Gaussian. IR3 is consistent with an unequal variance Gaussian SDT model with $\sigma^2_{old} > \sigma^2_{new}$. These regularities are also consistent with Yonelinas' (1999) dual-process model. IR 4 suggests that the variability of the old item distribution increases with its mean strength, which is an implication not specifically predicted by any of the above-mentioned models. Regularity IR5 (the mirror effect) implies that manipulations that affect the distance between distributions also affect the placement of the criterion, which suggests that participants are basing their decisions on the relative heights of the distributions (the likelihood ratio) rather than the absolute placement on a hypothetical decision axis.

Glanzer et al. (2004; Hilford et al., 2002) also identified six regularities of source identification (SI):

SI1. The source ROC is curved with an inverted-U shape.

SI2. The source zROC is slightly U-shaped.

SI3. The linear component of the source zROC is 1.

SI4. The linear component of the source zROC is unaffected by accuracy.

SI5. The mirror effect holds.

SI6. Accuracy rates for item recognition and source identification are positively related.

Taken together, SI1 (inverted-U shaped ROC) and SI2 (U-shaped zROC) suggest that neither Gaussian SDT nor finite-state models can fully account for source memory performance. Specifically, a curved ROC function (SI1) is consistent with Gaussian SDT models but is not consistent with finite-state models. However, the U-shaped source zROC function (SI2) is consistent with finite-state models but not with Gaussian SDT models. Regularity SI3 implies that under the assumptions of SDT, whatever the form of the source distributions, the standard deviations are approximately the same. Regularity SI4 implies that the unity in slope is not affected by item memory strength. Regularities SI3 and SI4 likely depend on sources that are approximately equal in memory strength. As indicated by the similarity of the mirror effects for item recognition and source identification (Regularities IR5 and SI5), the same type of decision strategy appears to apply for both aspects of memory retrieval. SI6 suggests that manipulations that affect item recognition will have similar effects on source identification.

How can one account for both curved ROCs (SI1) and U-shaped zROCs (SI2)? According to the dual process model of Yonelinas (1999), source ROCs should be relatively linear, thus making zROCs U-shaped. Yet, curved ROCs are generally observed, even when source memory is equated (regularity SI1; Glanzer et al., 2004; Qin, Raye, Johnson, & Mitchell, 2001; Slotnick et al., 2000), which suggests that SI1 is the norm, not the exception. To maintain a dual-process account of source memory, it must be argued that a finite-state interpretation holds for source recollection, but as no measure is process pure, curvilinear ROCs may occur to the extent that familiarity influences source judgments, even when differences in familiarity strength are not manifest in measures of item recognition. This supposition makes it difficult to counter the dual-process model because whenever curvilinear source ROCs are observed, it can be argued that familiarity played a covert role, even if controls are implemented to demonstrate equivalent item strength across source items.

DeCarlo (2003) developed an alternative SDT model to account for the regularities of item and source recognition performance described by Glanzer and colleagues (Glanzer et al., 2004; Hilford et al., 2002). The model is based on the assumption that a proportion of old items do not include any source information due to a

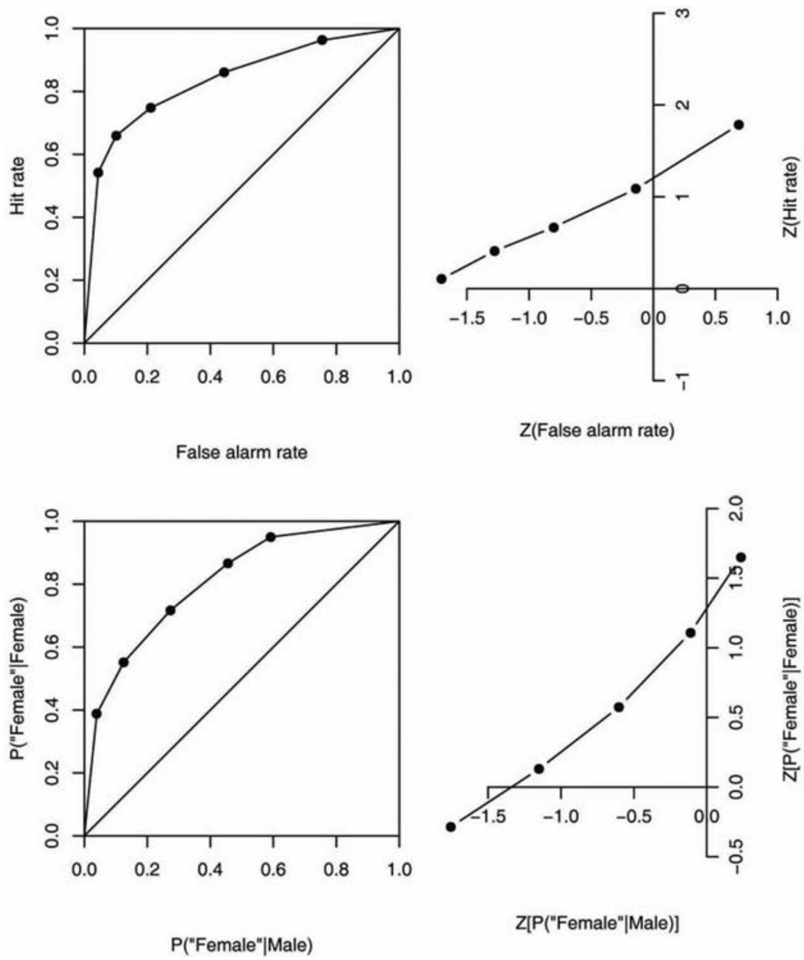

Figure 5. Receiver operating characteristic (ROC) and z-transformed receiver operating characteristic (zROC) functions for item recognition (top panels) and source recognition data from Hilford et al. (2002, Experiment 5), in which participants were presented words spoken by either a male or female voice. At test, participants made both old or new and male or female recognition judgments with confidence ratings. Note the curved ROC functions for both item and source recognition and the slightly U-shaped zROC function for source recognition. P = probability.

failure in attending to relevant source features during initial encoding. As such, memory for old items is based on a mixture of two Gaussian distributions, one that includes old items with source information and another that includes old items without source information. A parameter, λ, determines the proportion of items to which source information was attended. The H rate, then, is

$$H = \lambda\Phi(d' - c) + (1 - \lambda)\Phi(c). \tag{7}$$

Once again, the FA rate is given by Equation 2.[2]

In the DeCarlo (2003) model, mixing the two distributions disproportionately increases the proportion of low confidence items because the overlap of the two distributions occurs predominantly for items with little or no source information. Thus, source ROC functions become flatter and zROC functions become U-shaped. It is interesting to note the formal parallel between Yonelinas' (1999) dual process model and DeCarlo's Gaussian mixture model. As described by Equations 6 and 7, both models include a proportion of items distributed according to an equal variance Gaussian distribution. Yet, the Yonelinas model includes some items that are very strongly remembered (i.e., recollected), whereas the DeCarlo model includes some items that completely lack source information. Both adopt mixture models to perturb the equal variance Gaussian distribution, but in different directions. The Yonelinas model predicts disproportionately strong memories, whereas the DeCarlo model predicts disproportionately weak memories.

Similar to DeCarlo's (2003) interpretation, Slotnick and Dodson (2005) suggested that the appearance of linear source ROCs is caused by lack of source discrimination at low levels of item recognition. They reanalyzed source memory data (e.g., Yonelinas, 1999) and found that ROCs were consistent with an unequal-variance Gaussian SDT model when source analyses were re-

[2] DeCarlo (2003) described a more general mixture model in which the means of both distributions are free parameters.

stricted to items rated high in item recognition. That is, even for strongly recollected items, source memory strength appeared to operate as a continuous variable. They suggested that the appearance of linear ROCs in unconditionalized analyses is the result of increased noise at low levels of item recognition, just as DeCarlo (2003) suggested that there exists a set of (poorly remembered) old items that do not have any associated source information.

As indicated by modifications to equal variance Gaussian SDT and finite-state models, various additional factors—such as influence of familiarity, failure to attend to source information, or increased noise in source recognition—act to pull source ROC and zROC plots away from those predicted by the pure version of these models. Although these modifications account for regularities of source identification, they have certain conceptual limitations for theory building. First, they approach the deficiencies of basic Gaussian SDT and threshold models by combining the properties two models, thus taking advantage of each. The combination of two models into a hybrid model may better account for extant findings, but they often lead to models that are difficult to falsify empirically. Second, the modifications are not fully integrated, in the sense of offering a psychological basis of explanation (e.g., when does familiarity affect source recognition; how does one attend to source information; what is the basis of noise during source identification). In the next section, we describe an alternative in which the properties of both item and source memory derive from the same neurocognitive representation.

A Non-Gaussian Two-Dimensional SDT Model Based on MTL Binding

MTL-neocortical interactions facilitate the binding or consolidation of episodic memory representations. As shown 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. We propose that this neural architecture supports hierarchical relational binding. That is, distributed networks in neocortical regions that are activated during an episodic event are initially bound by projections to perirhinal and parahippocampus cortices. These initial bindings are then linked by converging projections to the next MTL level, the entorhinal cortex. Ultimate binding of bindings occurs by way of projections from the entorhinal cortex to the hippocampus. Given this hierarchical configuration, features of an episodic event can be successfully bound with rather sparse connections through levels of MTL binding. Successful MTL binding during study thus increases the probability of reinstating at retrieval the neocortical network associated with an episodic event. Indeed, neocortical representations or feature units that are linked by multiple levels within the MTL gain substantially in relational binding. The net gain is superadditive—that is, memory representations become disproportionately more fully bound as more MTL levels are involved.

To illustrate the superadditive nature of hierarchical relational binding, consider the hypothetical organization of MTL bindings shown in Figure 6. An episodic event activates a network of feature units in eight disparate neocortical areas (A_1, A_2, A_3 … A_8). These units have reciprocal connections to the first MTL level (i.e., perirhinal and parahippocampal cortices), and thus, binding at this level has by itself the potential of associating feature units in neocortical areas. Hierarchical binding occurs when Level 1 MTL bindings are bound at other MTL levels, such that higher MTL levels are binding the bindings of lower levels. In this simplified characterization, MTL Level 2 bindings can be construed as projections to the entorhinal cortex, and MTL Level 3 can be construed as projections to the hippocampus (perhaps specifically to the CA1 subfield). As MTL subregions become better defined functionally, the neural architecture of hierarchical relational binding within the MTL may be more complex than that illustrated in Figure 6.

By way of bidirectional pathways, each MTL level can independently contribute to the facilitation of associative binding. Overall memory strength is determined by the number of feature units that can be reinstated during retrieval, and this reinstatement is facilitated by activation flow through the MTL network. It is important to note that successful MTL bindings at multiple MTL levels disproportionately increase the probability of reinstating neocortical feature units. For example, if only MTL Level 1 bindings are established, a neocortical feature unit has the capacity of activating (i.e., binding) one other unit (e.g., A_1 can activate A_2, A_3 can activate A_4). If bindings also occur at MTL Level 2, then a neocortical unit can activate three other units (e.g., A_1 can activate A_2, A_3, A_4). When binding occurs at all three MTL levels, a single neocortical unit has the capacity of reinstating all eight units. Thus, as bindings occur from MTL Level 1 to Level 2 to Level 3, the total number of units that are reinstated increases in a superadditive manner.

In Appendix A, we provide a quantitative representation of a simple hierarchical network, such as the one in Figure 6, and show that it predicts superadditivity and a skewed distribution of memory strengths. If bindings are restricted to MTL Level 1, the increment in memory strength is simply additive and characterized by a simple Gaussian distribution. However, binding at subsequent MTL levels contributes to memory performance by increasing strength in proportion to the number of associated features that are bound. As illustrated in Figure 6, each Level 2 unit is associated with two Level 1 units. As such, successful binding at Level 2 has the effect of binding four neocortical feature units. Successful binding at Level 3 has the effect of binding eight neocortical

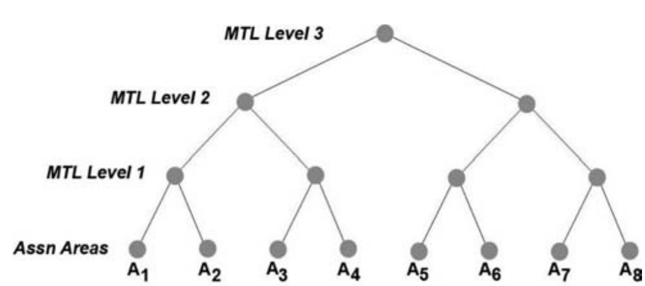

Figure 6. Hypothetical medial temporal lobe (MTL) organization of hierarchical relational binding. Neocortical feature units of an episodic event encoded in association (Assn) areas (A_1, A_2, A_3 … A_8) are first bound in a binary manner by MTL Level 1. These bindings are then bound by MTL Level 2 such that activation of a unit at this level has the capacity of reinstating four neocortical units. 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. Thus, as relational binding occurs at higher levels, the reinstatement of episodic features during retrieval is superadditive.

feature units. As a result, the mean increment to memory strength and its variance increase exponentially with the number of levels. At the same time, the probability that an item reaches a higher MTL level declines geometrically with the number of levels. As shown in Appendix A, when the effects of memory strength from all MTL levels are combined (i.e., mixed), the overall distribution is positively skewed. In complex hierarchical circuits, the same principles apply, although the amount of skewness will depend on the fidelity of MTL bindings, the extent of convergence across MTL levels, and the degree to which bindings interact.

A positive skewing of memory strength implies the application of non-Gaussian distributions. That is, hierarchical relational binding predicts nonlinear dynamics, such that memory strength is disproportionately increased for strong (i.e., well-bound) memories. We propose to model item and source memory with the ex-Gaussian distribution. The ex-Gaussian distribution has been applied in models of response time (Hohle, 1965; Luce, 1986; Ratcliff & Murdock, 1976; Spieler, Balota, & Faust, 2000) but has rarely, if ever, been applied to memory accuracy. An ex-Gaussian random variable is defined as the sum of two random variables, one with a exponential distribution (with rate parameter λ) and one with a Gaussian distribution (with parameters μ and σ^2). Its density function is the convolution of its two component distributions:

$$f_{exG}(x) = \int_0^\infty f_{\exp}(t) f_{Gauss}(x-t)dt = \int_0^\infty [\lambda e^{-\lambda t}] \times \left[\frac{1}{\sqrt{2\pi}\sigma} \exp\left(-\frac{1}{2} \frac{[(x-z)-\mu]^2}{\sigma^2} \right) \right] dt. \quad (8)$$

Further details and computational methods are in Appendix B.

It should be noted that our application of skewed distributions was derived directly from the neural architecture of MTL and the property of superadditivity in a hierarchical network. With hierarchical relational binding, stronger memories become disproportionately stronger, thus leading to old item distributions that are positively skewed. We selected the ex-Gaussian distribution to characterize the skewing that results from superadditivity, although any sufficiently flexible skewed distribution would work about as well. As a characterization of skewing, the ex-Gaussian distribution has several advantages: (a) It is a three-parameter distribution, giving independent control of its mean, variance, and skew; (b) it is a generalization of the Gaussian distribution, allowing models based on skewed and unskewed distributions to be compared; and (b) it is computationally tractable enough to apply rigorous methods of fitting and testing.

In its two-dimensional form, our SDT model integrates item recognition and source identification, but we first describe these two processes separately. For item recognition, only old item distributions are skewed as new item distributions are not associated with MTL binding. Thus, new items are represented by a symmetric Gaussian distribution (to identify the model, we fix $\mu_{\text{new}} = 0$ and $\sigma_{\text{new}} = 1$). Memory strength for old items is influenced by two factors: overall mean strength (μ_{old}) and the extent of MTL hierarchical binding (λ). Thus, old item distributions have a skewed ex-Gaussian distribution (Figure 7, Panel A). The skew of the old item distribution has two important consequences. First, it increases the variance of the old item distribution relative to new item distributions, which is consistent with IR3. Second, with increasing skew (i.e., greater hierarchical relational binding), the old item variance increases along with its mean. Thus, the model predicts that increasing memory strength inherently increases the variance of old item distributions, consistent with IR4. It is important to note that these regularities, viewed previously as mere empirical observations and not predicted by extant models, arise directly from the structure of our model without any further assumptions.

With respect to source identification, hierarchical binding increases the association of contextual features to items, thereby linking Source A features to Source A items and Source B features to Source B items. In this way, relational binding acts to further discriminate the two sources. Thus, in our two-dimensional SDT model, both Source A and Source B items are represented by ex-Gaussian distributions, but with opposite skew (Figure 8, Panel A). When the strength of source memory is comparable for the two sources, the same parameters apply to each set of source items. Thus, the basic ex-Gaussian source model depends on two parameters, λ and μ, with the variance parameter fixed to identify the model ($\sigma = 1$; essentially the same restriction that fixes the new-item variance in the Gaussian models). Importantly, the skewed distributions produce curvilinear ROCs (SI1) and U-shaped zROCs (SI2), without any further assumptions. Moreover, for sources with equal strength, their variances are similar (SI3) and there is no change of the zROC slope with increasing accuracy (SI4). Thus, empirical regularities associated with source identification fit completely with our model.

To illustrate our theory, we fitted the ex-Gaussian model to item and source recognition data taken from Glanzer et al. (2004, Experiment 5). We selected this data set because it shows all the regularities of item recognition and source identification listed above. For item recognition, new items were characterized by a standard Gaussian distribution ($\mu_{\text{new}} = 0$ and $\sigma_{\text{new}} = 1$), and maximum-likelihood estimates of the ex-Gaussian parameters of the old item distribution are $\lambda = .474$, $\mu_{\text{old}} = .262$, and $\sigma_{\text{old}} = 1.047$. Because the actual moments of the ex-Gaussian distribution depend on all of its parameters (see Appendix B), it is simpler to express the old-item distribution as having a mean of 2.37, a standard deviation of 2.35, and a skew coefficient of 1.43. Figure 7 shows the best-fit ex-Gaussian ROC (Panel B) and zROC (Panel C) functions to the item recognition data of Glanzer et al. (2004, Experiment 5).

Table 1 compares model fits of four models of item recognition: Gaussian (unequal variance), Yonelinas' (1999) dual process, DeCarlo's (2003) Gaussian mixture, and our ex-Gaussian model. The four models can be categorized as either adjusting the shape of the old item distribution (unequal-variance Gaussian and ex-Gaussian models) or as mixing two sets of old items with qualitatively different memory strengths Yonelinas' dual process and DeCarlo's Gaussian mixture models). Four measures of fit are given in Table 1: the likelihood ratio statistic (G^2), its associated upper-tail descriptive level (p value), the Akaike information criterion (AIC), and the Bayes-

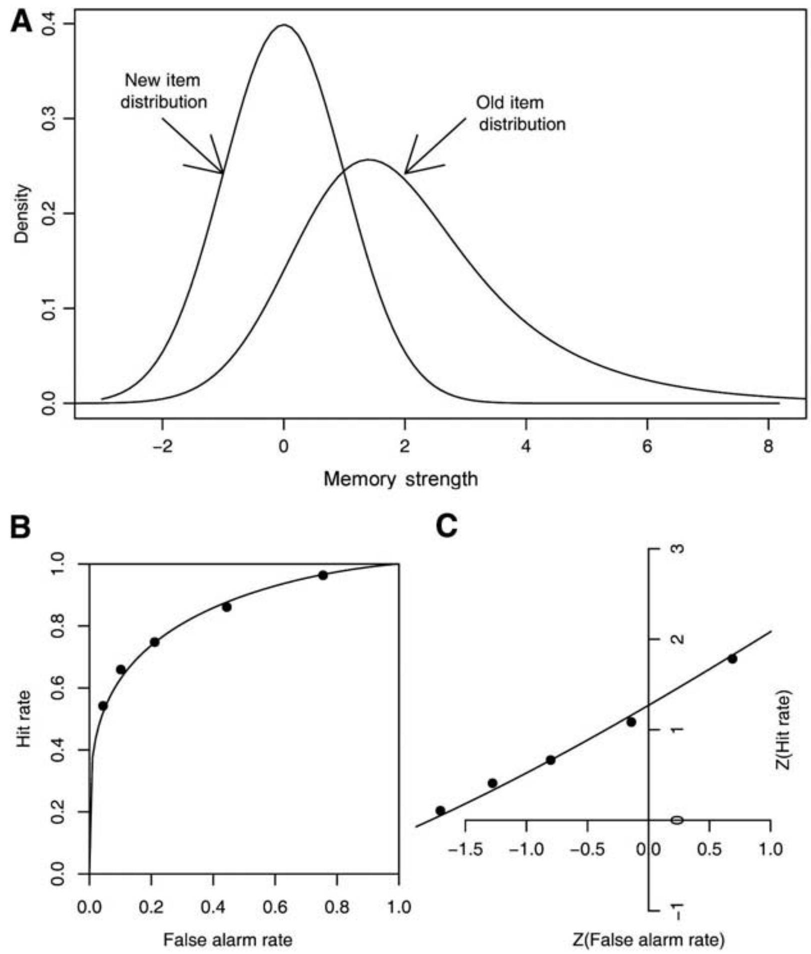

Figure 7. A: Ex-Gaussian model of item recognition, with a Gaussian distribution of new items and skewed distributions of old items. B: This model predicts curved receiver operating characteristic (ROC) and (C) nearly linear zROC functions.

ian information criterion (BIC) .[3] As shown in Table 1, the ex-Gaussian model fits the item recognition data extremely well. The two models associated with adjustments of distribution shape seem to offer better fits than do the two based on distribution mixtures. We emphasize, however, that we apply these fits to demonstrate the viability of our model, not as a means for precise quantitative comparison. The models are not hierarchically related, and the pooling of participants in Glanzer et al.'s (2004) data render the observations dependent, inflating the G^2 statistics (in particular, the upper-tail p values should not be taken as test statistics).

We also fitted source identification data from Glanzer et al. (2004, Experiment 5), assigning ex-Gaussian distributions for both Source A and Source B items. Figure 8 shows the best-fit ex-Gaussian ROC (Panel B) and zROC (Panel B) functions. The ex-Gaussian model with the parameter estimates (λ = .476, μ = −.665) fits the source identification data extremely well. These estimates correspond to a mean difference of 2.87 between source distributions (twice the distribution mean because the individual distributions are placed symmetrically on either side of zero) and a standard deviation of 2.54. The skews of the two source distributions are 1.47, with sign dependent on the source.

We compared the fit of the ex-Gaussian model with three other source memory models: Gaussian (equal-variance), Yonelinas' (1999) dual process, and DeCarlo's (2003) Gaussian mixture. We restricted each model by assuming symmetrical distributions for Source A and B items. The assumption of symmetry is appropriate for this data set, as can be tested by observing how little the fits of the equal-variance and unequal variance Gaussian models differ, $\Delta G^2(1) = 0.336$, $p = .56$. Thus, the equal-variance (i.e., symmetrical) Gaussian model serves as a benchmark, as the other three

[3] We include the descriptive level, the AIC, and the BIC to help compare models with different number of degrees of freedom. However, there are problems that render the application of any one of these measures an incomplete arbiter of the best model. Among these are which measure to use and how to resolve the inevitable contradictions among them. For example, the BIC adjustment for the number of free parameters associated with a model, log(2016) = 7.6 per parameter, makes the unequal-variance Gaussian model preferred to our ex-Gaussian model, even though they are hierarchical and the difference between them has a significant descriptive value of p = .035. We interpret these measures as showing that the ex-Gaussian model offers as good a fit as any other extant model.

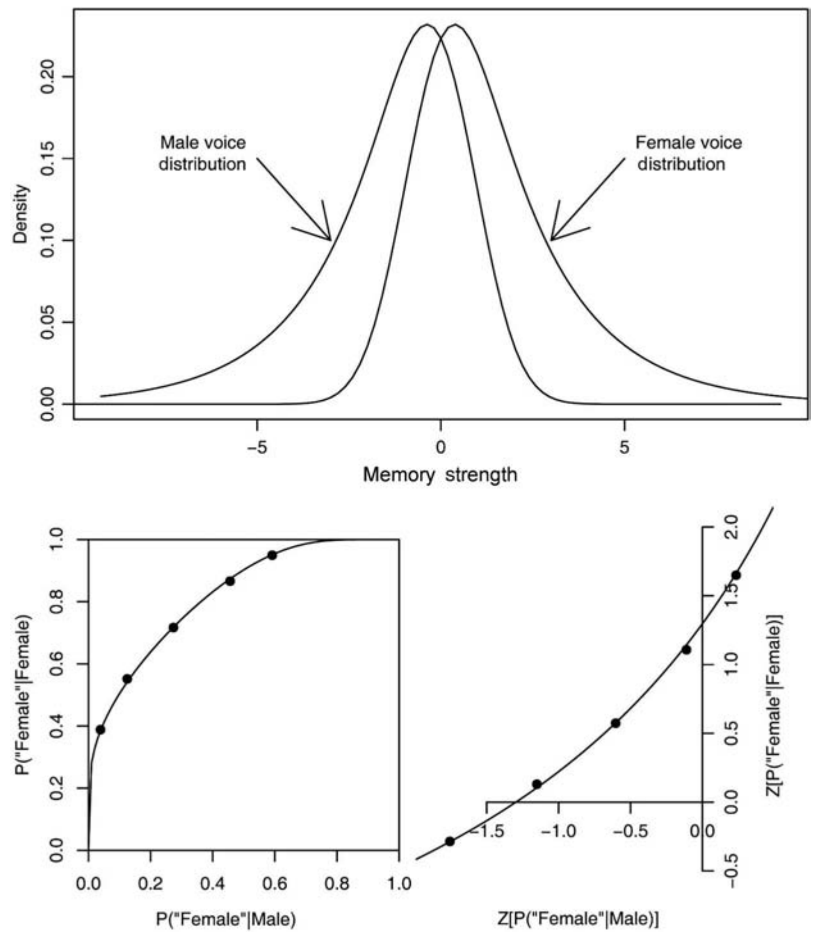

Figure 8. Ex-Gaussian model of source recognition with skewed distributions of both old item distributions—those presented with a male voice (Source A) and those presented with a female voice (Source B). These two distributions will be skewed in opposite directions. The model predicts inverted-U shaped receiver operating characteristic (ROC; bottom left panel) and U -shaped zROC (bottom right panel functions).

models are variants of it. Figure 9 illustrates how each model varies from the equal variance Gaussian model. The Yonelinas (1999) dual-process model mixes a finite-state recollection parameter with symmetrical Gaussian distributions for Source A and B items (Figure 9, Panel A), DeCarlo's (2003) model mixes a third Gaussian distribution (N) with symmetrical Gaussian distributions for Source A and B items (Figure 9, Panel B), and the ex-Gaussian model treats the Source A and Source B distributions as skewed away from the origin (Figure 9, Panel C). As shown in Table 1, source memory performance is well fitted by Yonelinas' dual

Table 1
Model Fits and Parameter Estimates of Item and Source Recognition Performance

Item recognition	G^2	*df*	*p*	AIC	BIC	*M*	*SD*	Mixing	Skew
Gaussian (unequal variance)	13.859	3	0.00310	27.859	71.973	1.88	1.48	—	—
Yonelinas dual-process	21.610	3	0.00008	25.010	79.124	0.91	1.00	0.42	—
DeCarlo Gaussian mixture	20.680	3	0.00012	34.680	78.794	2.10	1.00	0.79	—
Ex-Gaussian	9.280	2	0.00966	25.280	75.696	2.37	2.35	—	1.43
Source identification									
Gaussian (equal variance)	24.656	4	0.00006	36.656	70.309	1.30	1.00	—	—
Yonelinas dual-process	1.121	3	0.772	15.121	54.384	0.62	1.00	0.27	—
DeCarlo Gaussian mixture	0.864	3	0.834	14.864	54.126	2.15	1.00	0.46	—
Ex-Gaussian	0.865	3	0.834	14.865	54.127	1.43	2.54	—	1.13

Note. Data from Glanzer et al. (2004). *M*, *SD*, mixing, and skew refer to model parameters Experiment 5. G^2 = likelihood ratio statistic; AIC = Akaike's information criterion; BIC = Bayesian information criterion.

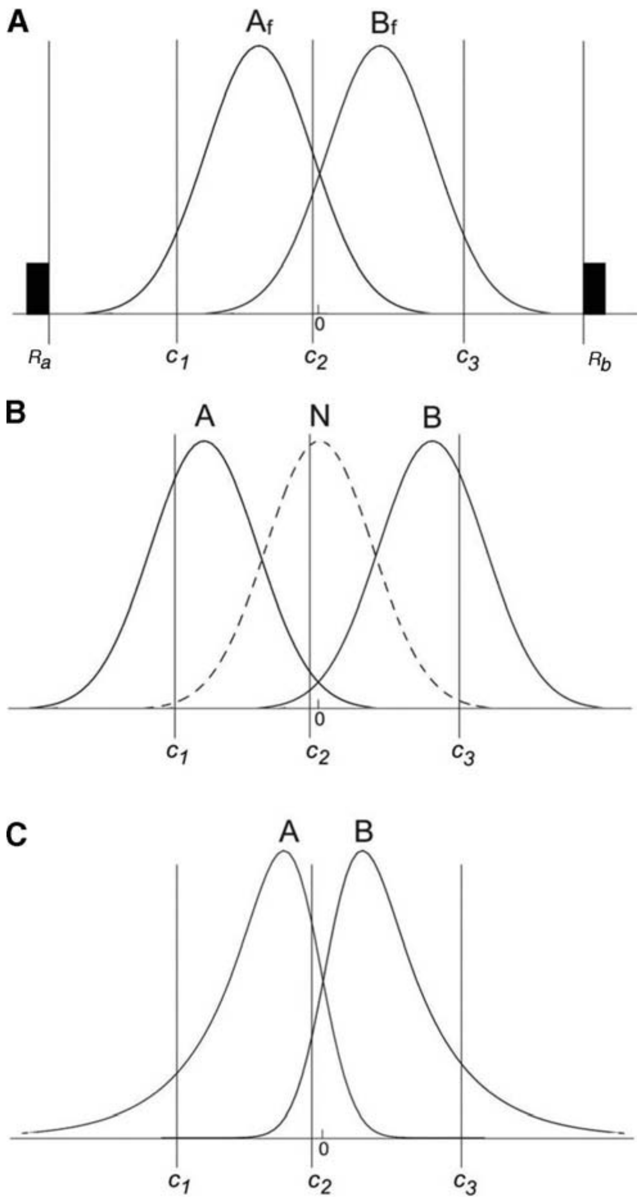

Figure 9. Characterizations of source memory. A: Panel shows Yonelinas' (1999) dual-process model in which recollection is represented by two high threshold criteria (R_a and R_b) and familiarity is represented as two Gaussian distributions for Source A (A_f) and Source B (B_f) items. B: Panel shows DeCarlo's (2003) mixture model in which performance is based on items with source information (A and B) and a distribution of items without source information (N). C: Panel shows the ex-Gaussian model in which Source A and B distributions skewed in opposite directions. c_1, c_2, and c_3 refer to criterion levels.

processes, DeCarlo's Gaussian mixture, and ex-Gaussian models. These three models clearly perform better than the equal-variance Gaussian model, but beyond that, all are satisfactory.

To verify that the fits in Table 1 are not a particular property of this data set, we fitted the four models to the other sets of data given by Ratcliff et al. (1994) and Glanzer et al. (2004). The general properties of Table 1 were confirmed. For item recognition, the ex-Gaussian model did well, although for some data sets it was not any better than the unequal-variance Gaussian model (which is a special case of the ex-Gaussian when the exponential component decays very rapidly). In most cases, our model fit better than did the mixture models. For source identification, the ex-Gaussian model fit about as well as the mixture models and generally better than the Gaussian models. Undoubtedly, data sets could be found for which these generalizations do not hold, but they show that our ex-Gaussian model can treat both item recognition and source identification well.

Figure 10 depicts the two-dimensional version of our model, showing the decision space and the distributions of new items and the two types of old items (i.e., Source A and Source B). The vertical dimension is the decision axis for item recognition; points in two-dimensional space are projected onto it for old or new judgments. The horizontal dimension is the decision axis for source identification; projections onto it determine whether an item is judged to be from Source A or Source B. The new item distribution is a symmetrical Gaussian distribution centered at (0,0). When an item is studied, its location is shifted away from the origin in a superadditive manner toward the direction of its source. As a result, both Source A and B items have distributions that are skewed both away from the new item distribution and away from items of the other source. These distributions thus differ fundamentally from the bivariate Gaussian distributions proposed by others (Banks, 2000; Slotnick et al., 2000; Wixted, 2007). As we have shown, the single assumption of imparting a skewing factor to memory strength for old items predicts many of the regularities described by Glanzer et al. (2004).

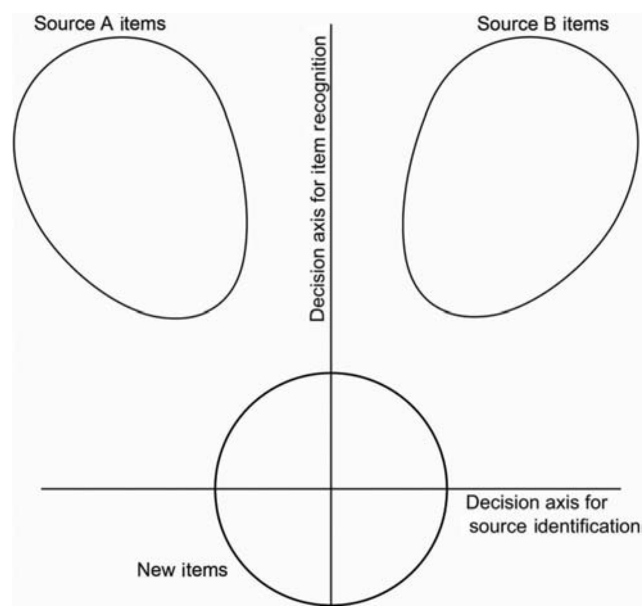

Figure 10. A two-dimensional depiction of the skewed signal detection theory model. The vertical dimension is the decision axis for new/old responses and the horizontal dimension is the decision axis for Source A or Source B discrimination. The distribution of new items is represented by a two-dimensional Gaussian distribution (shown as a circle) with its midpoint at the origin. The two old distributions (Source A and Source B items) are represented by oblong shapes that are positively skewed away from the origin.

Implications of the Skewed Two-Dimensional SDT Model

We have used the skewed two-dimensional SDT model to describe the process of hierarchical relational binding in the MTL. We predict that the degree of skew varies specifically with increases in contextual binding or, more generally, with the degree of interitem associations. We assume that both item memory (i.e., feature strength) and interitem associations depend on MTL binding, though the degree of interitem associations depends largely on binding at multiple MTL levels. As such, our model makes direct reference to a distinction between item- or feature-specific information and the associative binding of such information.

Our skewed two-dimensional SDT model has properties similar to other models that emphasize the role of the MTL in associative or relational binding (Bussey, Saksida, & Murray, 2005; Davachi, 2006; Eichenbaum et al., 2007; Lavenex & Amaral, 2000; Mishkin et al., 1997; Suzuki, 2007). Bussey et al. (2005) proposed a hierarchical network within the ventral visual stream such that successive levels act to build on more and more complex conjunctions of visual features with the highest level occurring at the perirhinal cortex. Our hierarchical binding model of MTL could be viewed as an extension of the Bussey et al. (2005) model that incorporates the conjunction of other unimodal and polymodal features. That is, the hierarchy of the Bussey et al. (2005) model ends at the perirhinal cortex, which is the MTL entry point in our hierarchical binding model. We suggest that the kind of featural conjunctions presumed to occur within the ventral visual stream are also occurring in other neocortical regions, which themselves converge onto the perirhinal or parahippocampal cortices. The unique contribution of the MTL may be its position as the ultimate convergence zone of diverse bindings of bindings. Such hierarchical bindings are efficient for memory retrieval because rather sparse re-activation at the hippocampal apex can potentially reinstate a broad network of episodic and semantic features that are distributed widely in the neocortex.

Our model shares many characteristics with Yonelinas' (1999) dual-process model. Both models suggest the existence of some disproportionately strong memories. In the Yonelinas (1999) model, a subset of old items—those surpassing a recollection threshold—are very strongly remembered. In the skewed two-dimensional SDT model, old item distributions are positively skewed, such that strongly remembered items are those that are influenced substantially by hierarchical relational binding. One way to link the two models is to consider the threshold R parameter as an approximation to the skewing influence associated with hierarchical relational binding. Both Yonelinas' (1999) R parameter and the exponential parameter λ play similar roles in their respective models because they determine the prevalence of strongly remembered items. Moreover, the neurocognitive substrate of both models suggests that the hippocampus plays a particularly important role in source recollection. As such, our model is consistent with many of the behavioral findings used as support of Yonelinas' (1999) dual process model (see Eichenbaum et al., 2007; Yonelinas & Parks, 2007).

There are, however, important conceptual differences between our model and Yonelinas' (1999) dual-process model. Whereas Yonelinas' (1999) model defines familiarity and recollection as two independent and separable processes, we suggest that one process—hierarchical binding—accounts for extant neurobehavioral findings. It is important to note that we make a distinction between the feature units in neocortex and the hierarchical binding of these units in MTL. According to our model, the ability to bind features depends on memory for the features themselves. Thus, item and source memory should generally be correlated (regularity SI6). There is, however, an asymmetry in this relationship, because MTL bindings depend on memory for features but memory for features do not necessarily depend on MTL bindings. Indeed, neocortical features could be activated without any MTL bindings, such as activations that occur by feature priming or by reinstating well established cortical-cortical networks, such as those that exist for fully consolidated representations (see Squire et al., 1989; Squire & Zola-Morgan, 1998). Yonelinas' (1999) dual-process model predicts correlations between tests of item and source recognition in a different manner. It is presumed that item recognition is mediated by both familiarity and recollection, whereas source memory is mediated largely by recollection. Thus, correlations between the two tests depend on the extent to which recollection mediates performance on both tests.

With its emphasis on features and their bindings, relational binding theory can account for behavioral findings that suggest a distinction between item and interitem associations. For example, Hockley and Cristi (1996) found that encoding strategies that facilitate interitem associations do not necessarily facilitate item recognition. In other findings, the mere strengthening of item-specific information (e.g., increasing stimulus duration or repetition) does not always increase the variance of old item distributions (Ratcliff, Sheu, & Gronlund, 1992; Ratcliff et al., 1994; see also Yonelinas, 1994). We can account for such findings because some tests will emphasize interitem associations (i.e., MTL hierarchical relational binding), whereas others will emphasize item memory (i.e., strengthening only neocortical feature units or binding only at the initial MTL level). Skewing and its associated increase in variance will be minimal under conditions of low relational binding. Dual-process models can account for such findings by equating recollection with the formation of interitem associations (see Mandler, 1980). If recollection is defined as such, then one could construe relational binding as the underlying mechanism that supports recollection. In any event, the advantage of relational binding over dual-process views is that the mechanism for establishing interitem associations (i.e., relational binding) is an inherent feature of the model and is defined explicitly.

A second difference between our model and Yonelinas' (1999) dual-process model is the nature of the operating characteristics associated with recollection. According to Parks and Yonelinas (2007, page 190), "recollection provides qualitative information linking the test item to a prior event" Recollection is described as a threshold process, because it either succeeds in linking a test item with a prior event or it fails. If it fails—that is, if recollection does not exceed a threshold value—then it is noninformative, and recognition is based solely on familiarity. Although the operating characteristics of recollection is that of a threshold process, it is acknowledged that the process of recollection can be graded, though noninformative or not functioning at subthreshold levels of memory strength (Parks & Yonelinas, 2007; Yonelinas, Dobbins, Szymanski, Dhaliwal, & King, 1996). The critical point of Yonelinas' dual-process model is that an item's memory strength needs to pass a threshold before it is recollected. Below the threshold (e.g., for items with low or moderate levels of confidence), recollection does not play a role in recognition performance.

We regard relational binding to be a graded process 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, Holland, & Shimamura, 1998; Wixted, 2007). Moreover, in nearly all extant ROC analyses of source memory (Glanzer et al., 2004; Hilford et al., 2002; Qin et al., 2001; Slotnick et al., 2000), curvilinear ROC functions have been observed, even when familiarity of the two source items are comparable. According to dual-process theory, source memory should depend largely on a thresholded recollection process, and source ROCs should generally be linear. To account for curvilinear ROCs, dual-process theorists must acknowledge that such measures are never process pure and may be influenced by familiarity. We argue that the pervasive finding of curvilinear ROCs for source recognition is diagnostic and suggests that the operating characteristics of source memory strength is best characterized as a graded process that is best modeled by skewed distributions.

A third important difference between Yonelinas and Parks' (2007) dual-process model and the skewed two-dimensional SDT model is the neurocognitive substrate presumed to underlie source memory. Yonelinas and Parks' (2007) model attributes recollection specifically to hippocampal function and thus suggests that the output of the hippocampus operates as a thresholded process. Yet, it seems unlikely that any neural structure with tens of thousands of neurons would elicit a thresholded neural response. Indeed, recent neuroimaging findings support the view that recollection responses are associated with graded hippocampal activation (Staresina & Davachi, 2008). Dual-process theory could account for such graded activations by suggesting that the hippocampus registers recollection in a graded manner, but such activations are somehow noninformative until it reaches a threshold level, after which recollection is continuous. In our model, the hippocampus is situated at the apex of the hierarchy of MTL bindings, where it is best able to link and reinstate episodic features in neocortical networks. Thus, to the extent that MTL bindings succeed to the level of the hippocampus, the probability of reinstating such strongly bound episodic features will be disproportionately increased. It is important to note that the binding mechanism in the hippocampus is not qualitatively different from that which occurs at other MTL levels.

The skewed two-dimensional SDT model proposed here addresses several issues associated with item and source memory. First, recognition memory has been characterized by single process (global memory matching) models (Hintzman, 1988; Humphreys, Pike, Bain, & Tehan, 1989; McClelland & Chappell, 1998; Murdock, 1982; Shiffrin & Steyvers, 1997) and by dual-process (recollection and familiarity) models (Jacoby, 1991; Mandler, 1980; Yonelinas, 1994; for review, see Diana, Reder, Arndt, & Park, 2006; Yonelinas & Park, 2007). The skewed two-dimensional SDT model defines two components that act on memory strength—a graded item strength process that increases item-specific information and hierarchical binding, which binds inter-item associations. However, the model does not imply the existence of two qualitatively independent memory mechanisms. There is no need to suggest two uniquely functioning processes such as recollection and familiarity. Indeed, associative binding may an essential feature of all cortical regions. Yet, due to the position of the MTL—and particularly the apical position of the hippocampus—a broad spectrum of episodic features, characterized by a distributed network of disparate neocortical units, can be quickly and efficiently bound as an episodic memory.

Recently, Wixted (2007) proposed a dual-process model of item recognition that operates within the framework of SDT. He proposed that item recognition is based on the summed influences of two continuous distributions— one for recollection and another for familiarity. Thus, rather than conceptualizing recollection as a thresholded variable, its influence on memory strength is continuous and is therefore functionally operable at all levels of recognition performance. Wixted (2007) developed this model in terms of Gaussian distributions for both recollection and familiarity, though he acknowledged that other distributions could be applied. When recollection and familiarity are defined by Gaussian distributions, the summed influences of these two processes is described by another Gaussian distribution.

To the extent that source identification is mediated specifically by the single dimension of recollection, then the continuous dual-process model proposed by Wixted (2007) has properties similar to two-dimensional Gaussian models proposed by others (Slotnick et al., 2000; Banks, 2000). Such Gaussian models cannot account for U-shaped zROC functions for source identification. Thus, the continuous dual-process model proposed by Wixted (2007) offers no better fit to source-identification data than do other Gaussian SDT models. Yet, there are similarities between Wixted's (2007) two-dimensional SDT dual-process model and our model. First, our model has the same quantitative properties as Wixted's model, except we apply skewed (ex-Gaussian) distributions for old items. Second, in both models, item strength (i.e., Wixted's familiarity component) and hierarchical binding (i.e., Wixted's recollection component) are combined to yield a memory strength value for a particular item. Third, Wixted's conceptualization of recollection as a graded, continuous process is closer to our conceptualization of hierarchical relational binding than is Yonelinas' (1999) thresholded notion of recollection.

It is interesting that in some global matching models of recognition memory, it was necessary to include non-Gaussian mechanisms of trace enhancement. In Hintzman's (1986, 1988) Minerva 2 model, the effective strength of the match of a recognition probe to memory S is subject to a cubic transformation $A = S^3$ before being used. Thus, a trace with twice the memory representation has eight times the impact. A different approach is taken in Shiffrin and Steyvers' (1997) REM model, in which the natural distribution of features is assumed to be skewed, such that the most diagnostic values are relative rare, a characteristic that is picked up by their Bayesian decision rule. In each of these cases, the effect yields a positively skewed distribution of old items.

Relational binding theory helps resolve a debate about the role of the hippocampus in recognition performance. As described above, some have suggested a special role of the hippocampus in recollection (see Aggleton & Brown, 1999; Eichenbaum et al., 2007), whereas others suggest that the entire MTL serves both recollection and familiarity (Manns et al., 2003; Stark, Bayley, & Squire, 2007; Wais et al., 2006). In our view, the hippocampus does have a particularly important role in binding, as it is situated at the top of the relational binding hierarchy and is thus able to reinstate an episodic memory more fully. However, the hippocampus and other MTL regions will contribute to both item familiarity and source recollection, as they all are involved in binding episodic features. As indicated above, there is no need to postulate the functional role of the hippocampus as qualitatively different from other MTL regions. Thus, we predict that MTL damage will produce impairment in behavioral tasks associated with relational binding (recollection, interitem associations) and item strength (e.g., familiarity, item memory), though as discussed above binding at multiple MTL levels serves relational binding in a superadditive manner. To the extent that a retrieved memory is based on item strength in the absence of relational binding, such as Mandler's (1980) butcher-on-the-bus experience, we predict that such familiarity responses could specifically rely on activation of neocortical feature units alone or in combination with binding at the initial MTL level. However, as all MTL levels are involved in reinstating item information, even selective hippocampal damage could potentially impair item recognition.

Memory representations that are based only on neocortical representations or those that involve only the first level of MTL binding will not exhibit superadditive memory strength. By this view, damage to MTL regions past its initial binding level should disproportionately affect source recollection, and activations in these regions as observed in neuroimaging studies should show increases during task manipulations that depend on recently formed interitem associative memory. Tests that rely primarily on featural or item-specific memory may be based solely on neocortical activations or on initial MTL bindings (i.e., activation in perirhinal and parahippocampal cortices). As our model honors neuroanatomical projections into the MTL, it is assumed that MTL binding of features associated with the ventral stream (i.e., features associated with object information) will occur initially in the perirhinal cortex, whereas features associated with the dorsal stream (i.e., spatial information associated with an episodic memory) will occur initially in the parahippocampal gyrus. In general, these neurobehavioral predictions fit the extant data and emphasize the role of the MTL in relational binding (see Eichenbaum et al., 2007; Staresina & Davachi, 2008). It is likely that more refined behavioral assessments and neuroimaging techniques, such as high resolution fMRI (see Zeineh, Engel, Thompson, & Bookheimer, 2007), will offer reliable means of highlighting the specific contributions of regions within the MTL. It is predicted that activations associated with source recollection will increase in MTL regions related to higher levels of binding, with the hippocampus showing the strongest activations.

A third issue concerns attentional factors associated with source encoding and recollection. In neuropsychological analyses of source memory (Janowsky et al., 1989; Schacter et al. 1984; Shimamura & Squire, 1987) and, more recently, in neuroimaging analyses (Ranganath et al., 2000; Rugg et al., 1999; Wheeler & Buckner, 2003), the prefrontal cortex has been shown to contribute significantly to performance. It is generally considered that the prefrontal cortex is involved in cognitive control processes associated with selective attention, working memory, and directed retrieval (see Buckner, 2003; Shimamura, 2002a, 2008; Wagner, 2002). Such influences are presumed to occur in addition to those mediated by the MTL and suggest that source memory depends critically on working memory processes (e.g., selective attention to source features). In our model, hierarchical relational binding refers to MTL mechanisms associated with memory formation and does not address prefrontal contributions.

To the extent that the prefrontal cortex helps in maintaining and coordinating online activity, failure to attend to or encode episodic features would certainly disrupt later retrieval of source information. DeCarlo's (2003) mixture model and Slotnick and Dodson's (2005) notion of extraneous noise during source judgments may describe contributions of prefrontal function to source memory performance. Specifically, Slotnick and Dodson's (2005) reanalysis of source recognition data by restricting responses on the basis of item recognition performance suggests that near-linear ROC functions are likely to occur as a result of having little or no source memory for items poor in item strength. In essence, this view suggests that floor effects perturb the shape of ROC functions when source memory performance is not conditionalized. Although useful, one concern with conditionalized analyses is that they can discard important information by evaluating levels of performance separately. Specifically, any restriction of the range of memory strengths could reduce the naturally occurring skewed nature of old item distributions. Although the combination of floor effects and Gaussian distributions may be sufficient to account for the extant findings of source ROCs, we suggest that our relational binding model offers an equally attractive alternative. We predict that task manipulations that increase memory by increasing associative binding (i.e., interitem associations) will result in increases in skewing for both old item and source distributions (see Figure 10).

Finally, the skewed SDT model can be extended to account for other aspects of memory. For example, the associative recognition paradigm addresses the nature of memory for specific paired associations. In the typical associative recognition paradigm, participants are presented word pairs (*uncle–pencil, flower–office, radio–window*) and later asked to determine if a test pair matches an intact study pair (*flower–office*) or consists of two mismatched items (*uncle–window*). As all words in the test phase have been previously presented, performance is based primarily on the strength of the associative link between word pairs rather than item familiarity. The parallels between the associative recognition paradigm and the source memory paradigm are clear—both involve the linking of two features of an episodic event and both depend heavily on relational (interitem) associations. Quantitative analyses of associative recognition include SDT, finite-state, and dual-process models (Kelley & Wixted, 2001; Macho, 2004; Rotello, Macmillan, & Reeder, 2004; Yonelinas, 1997). In terms of the skewed two-dimensional SDT model, associative recognition may be modeled by assuming that the skew parameter defines the degree to which matched pairs are associated and discriminated from unmatched pairs.

In summary, the two-dimensional SDT model proposed here accounts for the empirical regularities observed in item and source memory performance as well as or better than other extant models. It is based on the view that the MTL establishes hierarchical relational binding, which acts to consolidate contextual frameworks built from episodic features stored in neocortical circuits. As such, it extends the consolidation model proposed by Squire and colleagues (Squire et al., 1984; Squire et al., 1990; Squire & Zola-Morgan, 1998). The superadditive nature of hierarchical relational binding and the implied skew in the distribution of item strength resolves such controversies as the distinction between single and dual-process models, the distinction between item and source memory, and the distinction between the role of the hippocampus and other MTL structures.

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Appendix A

Quantitative Description of Superadditivity in a Hierarchical Network

Assume that a study item is represented by a set of neocortical feature units that has the potential of being bound within a hierarchical network such as the one illustrated in Figure 6. Successful binding increases the probability that an item (i.e., set of feature units) can be reinstated at the time of retrieval. At the first level, a single unit can bind to one other unit with associative strength represented by a random increment with mean μ and variance σ^2. If binding occurs at the next level, the number of units that are reinstated increases by a factor β ($\beta = 2$ in Figure 6). At the third level, the number of units that can be reinstated is β^2, and so forth. In general, the increment of strength W_j for an item processed by the jth level is the sum of the number of bound units,

$$W_j \sim N(\beta^{j-1}\mu,\ \beta^{j-1}\sigma^2).$$

An item that is processed through Level i has a total strength that is the sum of the memory strength increments acquired up to and including Level i:

$$X_i = \sum_{j=1}^{i} W_j \sim N\left(\frac{\beta^i - 1}{\beta - 1}\mu,\ \frac{\beta^i - 1}{\beta - 1}\sigma^2\right).$$

If the probability α that an item processed at one level is also processed at the next level, then the probability that an item receives i levels of processing has a geometric distribution,

$$p_i = (1 - \alpha)\alpha^{i-1}.$$

In this illustration we do not fix an upper bound on the number of levels, though the contribution of the later levels is negligible unless α is large or $\beta \approx 1/\alpha$. The strength acquired by an arbitrary studied item is a mixture of the increments X_i with proportion p_i.

$$Y = \sum_i p_i X_i = (1 - \alpha)\sum_i \alpha^{i-1} X_i.$$

The moments of Y are calculated from this sum and the moments of the X_i; for example,

$$E(Y) = \sum_i p_i E(X_i) = \frac{(1 - \alpha)\mu}{\beta - 1}\left[\beta \sum (\alpha\beta)^{i-1} - \sum \alpha^{i-1}\right]$$

$$= \frac{\mu}{1 - \alpha\beta}.$$

Calculation of the higher moments, both about zero and about the mean, is straightforward, though tedious. In the particular case of $\beta = 1$, the third central moment (the skew) is

$$\nu_3 = \frac{\alpha}{(1 - \alpha)^2}\left[3\mu\sigma^2 + \frac{(1 + \alpha)\mu}{1 - \alpha}\right].$$

All the terms in this expression are positive, and so the distribution of acquired strengths has positive skew. Because the model is continuous in its parameters, the skew is likewise positive for β μ 1 in a neighborhood of 1.

Appendix B

Properties of the Ex-Gaussian Distribution

An ex-Gaussian random variable is the sum of independent exponential and Gaussian random variables:

$$X = E + G$$

The exponential component has the density function

$$f_E(x;\lambda) = \lambda e^{-\lambda x},\ \lambda > 0,$$

where λ is the rate parameter of a Poisson process that yields this distribution. The exponential component can equally well be parameterized by its mean, $\tau = 1/\lambda$. The Gaussian component is parameterized by its mean μ and variance σ^2 (or its standard deviation σ):

$$\phi(x;\mu,\sigma^2) = \frac{1}{\sqrt{2\pi}\sigma}\exp\left[-\frac{1}{2}\frac{(x-\mu)^2}{\sigma^2}\right].$$

The moments of the ex-Gaussian distribution depend on all three of its parameters; the first four are

$$E(X) = E(E) + E(G) = \frac{1}{\lambda} + \mu = \tau + \mu,$$

$$\mathrm{var}(X) = \mathrm{var}(E) + \mathrm{var}(G) = \frac{1}{\lambda^2} + \sigma^2 = \tau^2 + \sigma^2,$$

$$\gamma_X = \sqrt{\frac{\mu_{3,X}}{\sigma^3}} = \frac{2}{\sqrt{(1+\sigma^2\lambda^2)^3}}, \text{ and}$$

$$\kappa_X = \frac{\mu_{4,X}}{\sigma^4} - 3 = \frac{6}{(1+\sigma^2\lambda^2)^2}.$$

Because λ^2 and σ^2 are positive, the skew and the kurtosis are positive, and the distribution is somewhat leptokurtic.

Evaluation of the convolution that determines the distribution of an ex-Gaussian random variable shows that the density function can be expressed by exponential and Gaussian functions:

$$f_{eG}(x) = \int_{-\infty}^{x} f_E(x - z;\lambda)\varphi(z;\mu,\sigma^2)dz = \lambda C e^{-\lambda x}\Phi(x;m,\sigma^2),$$

where $m = \mu + \lambda\sigma^2$, $C = \exp\left[\lambda\mu + \frac{1}{2}\lambda^2\sigma^2\right]$, and $\Phi(x;\mu,\sigma^2)$ are the cumulative Gaussian distribution function. Integration of this density by parts gives the cumulative distribution function:

$$F_{eG}(x) = \int_{-\infty}^{x} f_{eG}(s)ds = \Phi(x;\mu,\sigma^2) - Ce^{-\lambda x}\Phi(x;m,\sigma^2).$$

Both expressions are easily calculated in any statistical or programming language that includes a function for the cumulative Gaussian integral. In particular, writing a maximum-likelihood routine to estimate the parameters is straightforward. Such a routine was used to obtain the estimates reported in the text, a copy of which may be obtained from Thomas D. Wickens.

The ex-Gaussian distribution reduces to the Gaussian distribution with parameters μ and σ^2 when λ μ ’38 or τ μ 0. By treating negative values of τ as indicating negative skew, this hierarchy allows a standard likelihood-ratio test to be used to compare an ex-Gaussian distribution with a Gaussian distribution. Two hierarchical comparisons involving the skew are particularly relevant to the analysis here: a Gaussian–ex-Gaussian model (Figure 7), compared with an unequal-variance Gaussian model, and a symmetric ex-Gaussian model (Figure 8), compared with an equal-variance Gaussian model. Both tests are on one degree of freedom.

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