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COMMENTARY

Bridging Divergent Neural Models of Recognition Memory: Introduction to the Special Issue and Commentary on Key Issues

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ABSTRACT: This special issue reviews progress that has been made in recent years in understanding neural processing relevant for recognition memory. Here we describe how the nine reviews that comprise this issue weigh in on some of the most pressing and hotly debated issues in the study of recognition memory, including: (1) the number of processes that support recognition, (2) the nature of these processes, and (3) how these processes map onto neural processing events and brain structures. We then discuss the challenges inherent in attempting to incorporate the fundamentally different types of information that result from various cognitive neuroscience methods (e.g., electrophysiological recordings of neurons, lesion-deficit studies, analyses of brain potentials and activations, modeling of behavioral responses, and phenomenological reports), and make suggestions for how to better integrate these disparate data types when making inferences about recognition memory. As the articles in this special issue make clear, great strides have been made in understanding how organisms are able to appreciate repetition. And yet, several controversies in this area have still not been resolved, but these articles clarify the core disagreements as well as the tests that must be conducted to seek resolution. This special issue as a whole should thus facilitate advancements in the future study of the neural mechanisms of recognition.

KEY WORDS: recognition memory; recollection; familiarity; explicit memory

INTRODUCTION

Recognition memory—the ability to determine that a stimulus or event has been experienced previously—is a major topic of research in the cognitive and neural sciences.[i] Despite this extensive research, or perhaps because of it, disagreements over fundamental issues abound. To some it may seem as though the field is merely producing increasingly deeper and more esoteric schisms rather than progress in generating a solid knowledge base about core phenomena. Here, we delve into the progress made in understanding recognition through contemporary approaches and ask what should be done in the future to promote further advance.

This special issue takes some valuable steps forward by bringing together divergent viewpoints on recognition so that they can be directly compared, with several goals, including: (1) to communicate points of agreement shared by most of this research community, and (2) to highlight the disagreements so that attention can be focused on the chief theoretical problems and possible solutions. In the process of producing these papers (beginning with group interactions in preparation for a symposium at the 2009 meeting of the Society for Neuroscience Voss and Paller, 2009a), a set of research groups came together in a collegial atmosphere with the hope of finding common ground and a foundation for constructive discussion that can avoid misunderstanding.

Nine authoritative reviews are included in the special issue, covering many central issues in the study of recognition. This is certainly not complete coverage, as other researchers have also contributed important findings and ideas. Accordingly, this set of reviews should be interpreted as an impetus for further work and not the final word on these issues. Indeed, it will be clear to the reader that the debates are not over. Although bridges are being built, reconciliation is largely not yet at hand. Nonetheless, clarifying the areas of agreement and disagreement will help focus future studies.

In the following sections we describe three key issues that constitute points of theoretical disagreement. An orientation to these issues with attention to terminological precision is helpful for interpreting the divergence of opinion expressed by contributors to the special issue. In addition, we offer our views on the difficulties inherent in pooling information across the various levels of analysis brought to bear on the challenge of understanding recognition. Whereas analyses range widely—from the activity of single neurons to the activity of networks to cognitive constructs to behavioral patterns to introspective reports of human participants—we argue that the most effective use of the multilevel approach requires careful consideration of the ways evidence from these multiple levels are potentially related.

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[i] As an illustration of the prominence of this research topic, a PubMed search for year 2009 alone yielded 5,533 published articles related to recognition memory. By comparison, a search on executive function yielded only 1,801 articles.

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ISSUE 1: HOW MANY PROCESSES OR SYSTEMS SUPPORT RECOGNITION MEMORY?

A major theme in research on recognition concerns the way in which recollection and familiarity are supported by the brain and contribute to recognition. *Recollection* refers to the experience that most people would associate most strongly with the notion of "memory"—recollection occurs when one brings to mind a prior experience and aspects of its context (as if mentally reliving the event), which can empower the decision that something has been experienced previously. On the other hand, *familiarity* refers to the experience that occurs when a stimulus or event is determined to have been experienced previously, even if the retrieval of pertinent contextual or other detail is absent. For example, the sight of a man's face may prompt the conclusion that it is familiar even without any retrieval of relevant biographical knowledge or circumstances of viewing the face before.

There is good consensus that people can signal distinct memory experiences when they use these two types of behavioral response, and that in both cases recognition entails a decision to infer prior occurrence (i.e., explicit memory). In light of these widely accepted definitions, we hold that the terms "recollection" and "familiarity" have been used far too broadly in some cases, particularly when used in ways that cross category borders (or levels). The broader use of these terms has hindered clear communication and stoked controversy. As we discuss further below, it is problematic to use the very same term to refer to (a) a behavioral response that corresponds to a subjective experience in a recognition test, and (b) the neurophysiological processing or cognitive transactions that presumably give rise to these memory expressions. The concluding section of this paper proposes a remedy for this terminological confusion.[ii]

First, we now outline some of the approaches that have been applied to understand recognition memory. One useful approach is to construct quantitative models that attempt to decompose behavioral performance for a given set of experimental circumstances into one or more parameters. These parameters presumably correspond in some way to brain processes that support recognition (**Henson and Gagnepain, 2010**[iii] provide an excellent discussion of the factors that constitute a process). The models that are most successful in accounting for recognition across a variety of experimental circumstances include two parameters (which presumably correspond to recollection and familiarity) and are therefore referred to as "dual-process" models (Wixted, 2007; **Wixted et al., 2010; Yonelinas et al., 2010**). A major debate has concerned the nature of these two parameters and how exactly they support recognition. Battle lines have been drawn between two prominent sides of this debate, though an assumption of both models is that recognition responses can be based on the experiences of recollection and familiarity. The models differ primarily in: (1) whether recollection and familiarity are considered to sum to support recognition or to independently support recognition, and (2) whether recollection and familiarity both operate as continuous signal-detection processes or whether recollection acts as a categorical, threshold-like process.

The special issue articles by **Wixted et al. (2010)** and **Yonelinas et al. (2010)** clearly indicate that this debate has not been resolved. However, **Shimamura (2010)** makes a very important contribution by describing a new model that includes only one process (a "single-process" model) that fits behavioral data arguably as well as either of the other models, but essentially puts the concepts of recollection and familiarity entirely aside. Instead, **Shimamura (2010)** relies on a concept rooted in neurophysiological function, the concept of *binding*, which shows nonlinear properties.

In addition to providing a promising new model, the contribution by **Shimamura (2010)** raises the larger theoretical question regarding how modeling can inform our understanding of recognition. That is, given that an large number of models can be constructed to fit behavioral performance based on some set of parameters, how is it possible to sort out which model has the *right* parameters? How will we find out which parameters correspond to the way in which recognition is implemented by the brain? The answers involve relating parameters to neurophysiology, which can be done by specifying the nature of the parameters in neurophysiological or computational terms, or perhaps by probing neural substrates at the level of networks or systems.

ISSUE 2: WHAT ARE THE PROCESSES THAT CONTRIBUTE TO RECOGNITION MEMORY?

A very different class of modeling approach is to use neurophysiological or neurocomputational principles as a starting point. Several examples of recognition models of this sort are included here (**Cowell et al., 2010; Henson and Gagnepain, 2010; Norman, 2010**). For example, **Norman (2010)**

[ii]An additional point of confusion is that familiarity has sometimes been equated with semantic memory, which concerns the retrieval of knowledge about the world without retrieval of details regarding how this knowledge was acquired. Despite this similarity, familiarity in the context of research on recognition memory must be considered a form of episodic memory, not semantic memory, because it concerns an inference about a prior event (even though the specifics of that prior event are not available at the moment of the familiarity experience). A separate research agenda is needed to determine how retrieval processing that produces familiarity may relate to retrieval processing that supports semantic memory.

[iii]Boldface names refer to manuscripts in this special issue.

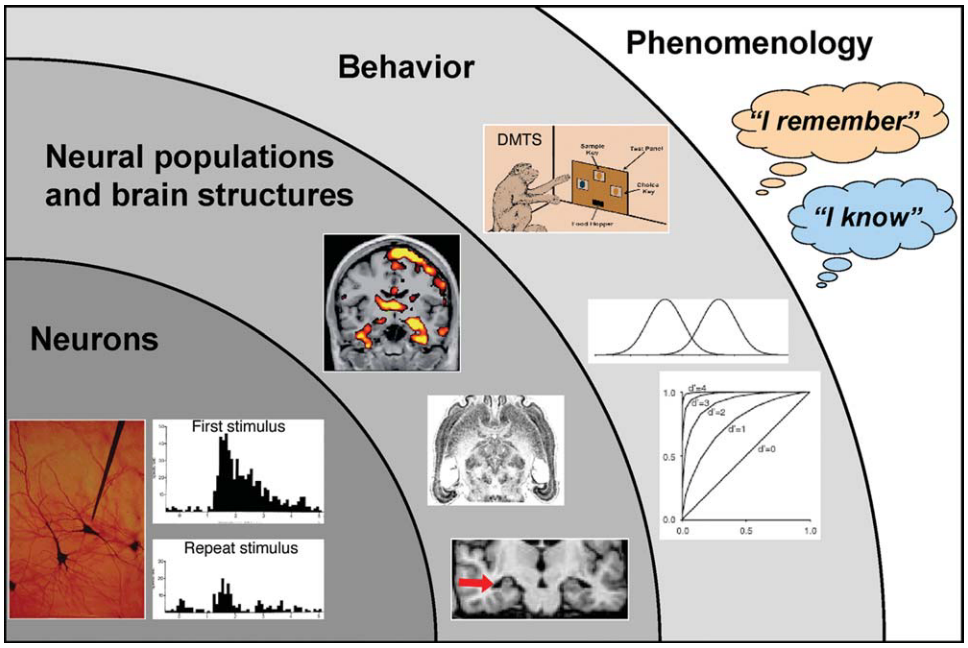

FIGURE 1. Different levels in the study of recognition memory. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

describes a prominent model of recognition built on the neuro-computational principles of pattern-separation and pattern-completion.

These models can be considered mechanistic, in contrast with the so-called measurement models (**Shimamura, 2010; Wixted et al., 2010; Yonelinas et al., 2010**) that essentially seek to determine the general quantitative principles of processes that contribute to recognition. It is possible to attempt to relate these quantitative principles to neurophysiological or neurocomputational principles (see especially **Yonelinas et al., 2010**), but the soundness of a measurement model is generally determined by how well the quantitative principles fit behavioral data rather than by whether the quantitative principles are neurophysiologically accurate. Thus, measurement models are specified on the behavioral level (see below and Fig. 1) and may or may not accurately describe the neural level.

Mechanistic models take on the question, "what *are* the processes that contribute to recognition?" Although a large number of alternative mechanistic models could conceivably be generated, the space is limited by the fact that these models are fundamentally based on neurophysiological or neurocomputational principles that are testable.[iv] These models are derived from these principles to attempt to account for the behavior that occurs in particular experimental circumstances. **Norman (2010)** and **Yonelinas et al. (2010)** make the important point that combining evidence from mechanistic models and measurement models is likely to prove a better strategy than relying solely on one class of model, because somewhat nonoverlapping information can be provided by each class of model.

[iv]Note that the nature of the parameters included in measurement models are also testable, such as in efforts to determine if the recollection parameter is threshold-like or continuous (**Wixted et al., 2010; Yonelinas et al., 2010**). These parameters in measurement models, despite being amenable to testing, map onto psychological constructs, and are not clearly connected to neurophysiological functions.

ISSUE 3: HOW ARE RECOGNITION PROCESSES SUPPORTED BY DISTINCT BRAIN STRUCTURES?

There is good justification for placing emphasis in this special issue on neural processing that supports recognition. For instance, returning to the uncertainty regarding the nature and number of parameters needed to model recognition, the most straightforward path to resolving this uncertainty may lie in identifying how the brain supports recognition memory. Such evidence can lead to ways to constrain model parameters. From this mechanistic perspective, there can be no suitable answers regarding how recognition memory works that do not account for the relevant neural processing.

Contributions from brain structures in the medial temporal lobe (MTL)—chiefly the hippocampus, perirhinal cortex, entorhinal cortex (EC), and parahippocampal cortex—are unequivocally relevant. Furthermore, there are distinct populations of neurons in these structures that respond to stimulus repetition in fundamentally different ways. Stimulus repetition is the prime way to elicit neural activity apropos recognition. Indeed, all authors of articles included in this special issue agree on these points. The distinct neural populations and their characteristic responses are described in detail by **Brown et al. (2010)**.

However, there is considerable disagreement over exactly how processing in MTL structures supports recognition. Many of the special issue contributions focus on the proposal that different processing related to recognition memory is implemented by different MTL structures, with much emphasis on how processing differs between the hippocampus and elsewhere (**Brown et al., 2010; Montaldi and Mayes, 2010; Norman, 2010; Ranganath, 2010; Yonelinas et al., 2010**). Recollection and familiarity feature prominently in all of these models, with recollection (or the processes that support it) ascribed to the hippocampus and familiarity (or the processes that support it) to other structures. Nonetheless, there is substantial variability in terms of the details regarding how recollection and familiarity are characterized and in specific structure-to-function mappings, especially with regard to familiarity.

Other fundamental dimensions have been brought in to try to distinguish the roles played by different MTL regions in recognition. The type of information and the type of processing afforded by that information are often emphasized. The contributions by **Brown et al. (2010), Montaldi and Mayes (2010)**, and **Ranganath (2010)** include proposals that different MTL structures represent different types of information, such that these representational differences can be mapped onto the distinction between recollection and familiarity. For example, **Ranganath (2010)** proposes that processing in the hippocampus is essential for representing contextual information, which supports the contextual retrieval necessary for recollection, whereas perirhinal cortex is essential for representing item/object information, which is related to familiarity.

It is important to note that none of these models suggest simple, one-to-one mappings of recollection and familiarity onto distinct brain structures. Rather, they suggest that the processing within distinct MTL structures primarily contributes to recollective or to familiarity aspects of recognition. One-to-one mappings would not only constitute overly simple reductionism, but it is thoroughly appreciated that structures outside of the MTL also contribute to recognition (**Brown et al., 2010; Henson and Gagnepain, 2010; Shimamura, 2010; Wixted et al., 2010**).

Some investigators do not propose a strong functional subdivision of MTL structures. **Wixted et al. (2010)** argue that evidence for specific functional subdivisions based on the extant results on recollection and familiarity is exceedingly weak, owing to a failure to account for differences in memory strength between recollection and familiarity conditions. They take the position that MTL activity bears a correspondence with the strength of a memory (as indicated by the confidence a person expresses in a recognition response), and that strength can be a relevant variable for both recollection and familiarity. They also point out that recollection is particularly dependent on contributions from structures beyond the MTL, such as prefrontal cortex. There are thus parallels between the **Wixted et al. (2010)** position and **Shimamura's (2010)** Hierarchical Relational Binding model, in that Shimamura proposes that all MTL structures take part in the process of binding information into memory representations, and that the complexity of these bindings increases nonlinearly as processing progresses throughout the MTL anatomical hierarchy, with the hippocampus acting as the site of the highest-order binding.

An alternative way to conceive of MTL function is expressed by the contribution by **Cowell et al. (2010)**. These investigators propose that MTL structures also perform nonmnemonic functions related to perception, in addition to functions central to recognition memory. That is, they develop the position that all structures participate in perception, with increasingly more complex features represented as processing progresses from ventral visual cortex throughout the MTL anatomical hierarchy to hippocampus.

Even though the nature of MTL function is described quite differently by different authors, this set of articles exemplifies the potential progress that can arise from approaches that attempt to include neural systems. The evidence on how neuronal responses differ across anatomical regions can provide a more complete picture of how networks of neurons in these regions provide the computational power that ultimately drives memory expressions.

LEVELS OF ANALYSIS

We next address an issue that may be at the heart of much of the uncertainty regarding neural models of recognition. In our view there is a serious shortcoming in the way the recollection/familiarity terminology has been used, a flaw that was not tackled directly in the other contributions to this special issue—yet it may represent an insidious barrier to progress in this area.

As discussed above, recollection and familiarity are first and foremost terms to describe expressions of memory, expressions evidenced by behavioral responses thought to be accompanied by specific types of subjective experiences. The literature on recollection and familiarity unfortunately encompasses another meaning for these two terms as signifying memory processes. A process is not the same—and should not be equated with—a memory expression. Recollection undoubtedly arises due to a set of neurocognitive processes. To refer to "the recollection processes" or to "the familiarity process" does harm to the conception that a set of precursor processes are initiated by a recognition cue and ultimately lead to recognition experiences of one type or another. If we wish to understand how recognition is achieved in the brain, we must take care not to equate the mechanism with the outcome. Of course, memory researchers understand this. Still, some of the controversy in this field has arisen because of this lack of precision with the terms recollection and familiarity, as researchers do not all hold the same meaning when using these terms. To move forward, these terms should be applied only to describe memory expressions.

A strength of research in this area is that the data presented in support of the various models consist of a variety of types of observations (Fig. 1). Investigators speak of recognition memory in single neurons (that show altered activity rates due to repetition), in populations of neurons (that show more or less activity in fMRI studies or are implicated in recognition impairments due to brain damage), in behavioral recognition responses (made by human and nonhuman animals), and in subjective experiences (that humans report in conjunction with recognition responses). Investigators also invoke recognition processes that are described with cognitive constructs, with varying connections to neural events. Certainly there are conceptual shortcomings in calling these various types of data "levels" (Dudai, 2002). Still, in spite of the limitations of a spatial metaphor, the term "level" can usefully denote a type of data derived from a certain method, or a theoretical construct based on certain sorts of data. Clearly, there are difficulties to overcome when combining data of one type with data of another type, whether these are referred to as levels or not.[v]

These difficulties are especially relevant with respect to recollection and familiarity. Recollection and familiarity are terms that in everyday usage describe states of phenomenological awareness occurring in conjunction with recognition—an individual experiences the feeling of familiarity, devoid of further recall, or of recollection that approximates reliving a prior event. **Yonelinas et al. (2010)** are correct when they link recollection and familiarity to the introspective method of William James. Indeed, the study of recollection and familiarity began in earnest with the "cognitive revolution" that justly defended the contents of introspective awareness as targets for scientific inquiry (Mandler, 2007; Yonelinas, 2002). At the same time, many of the functions of the brain normally go forward without any phenomenological awareness. Therefore, the knowledge that can be gained by introspection is fundamentally limited, and the study of neural mechanisms for recognition should not concern only processes linked with introspective report. Indeed, as discussed more below, neural processes that support recognition include some that can occur without any associated feelings of recollection or familiarity (see also Voss and Paller, 2009c).

How then are the phenomenological states of recollection and familiarity related to data from other levels of analysis? Answers to this question are presently in flux, though it is tempting to conceive of a simple mapping. For example, recollection might be the end result of the operation of one memory system and familiarity the end result of the operation of another—but there is some danger if such a scenario is tacitly assumed. With suitable caution, then, it is worthwhile to consider whether such an assumption serves our research goals. It may not, as such an assumption may obscure complex relationships among many relevant memory processes, some of which could contribute to both memory expressions.

Recollection and familiarity are often studied within a source memory paradigm, in which a correct behavioral response can include recognition limited to the item per se (familiarity) or for the item plus its source or context (recollection). However, this mapping can be misleading. Retrieval can occur for context information other than the specific information that is probed by the memory test. For instance, the test might concern the background color on which the item was presented, and the subject may recall a mental image conjured by the item but not the background color (referred to as "noncriterial recollection"; **Wixted et al., 2010; Yonelinas et al., 2010).** Also, source retrieval might not necessarily be indicative of recollection, in that the background color might be correctly selected based on a feeling of familiarity for the associative relationship between the item and the color, especially if their interrelationship was stressed during learning (sometimes referred to as "unitization"; **Ranganath, 2010; Yonelinas et al., 2010**; but see **Wixted et al., 2010**). Thus, the types of correct responses in a source memory paradigm might not cleanly implicate recollection or familiarity. As a suitable route forward, investigators have built a stronger case by using multiple methods to provide converging evidence for behavioral distinctions between recollection and familiarity. Different types of paradigms and different types of modeling methods (e.g., signal detection theory, structural equation modeling, etc.) might all indicate that there are at least two "processes" operative during a recognition test. However, this approach is misleading in that findings from each method are ambiguous with regard to how these two processes relate to recollection and familiarity, and thus, ambiguity remains even when multiple estimation methods are considered collectively. The most valid approaches to study the experiences of recollection and familiarity may require asking the subjects about their subjective experience and making sure to take into account all other variables that might correlate with recollection and familiarity, such as confidence (**Wixted et al., 2010**).

This same consideration applies to neural data when the terms recollection and familiarity are used to refer to the neural processing events that presumably support the corresponding phenomenological reports. For instance, **Brown et al. (2010)** unimpeachably review the evidence that neurons in hippocampus versus perirhinal cortex respond to stimulus repetition in fundamentally different ways. However, it is misleading to label these different response profiles as clear-cut signals of recollection and familiarity without other evidence that currently is unavailable—direct relationships must be established between these neural response profiles and memory expressions of recollection and familiarity. Many studies have succeeded in fractionating the neural basis of recognition into two or more parts. Critically, it is the relationship between these parts and recollection/familiarity that is subject to doubt and that has led to excessive disagreement.

[v]The concept of "levels" fits with the standard materialistic assumption that higher levels depend on lower levels in an asymmetric fashion. A lesion to a neural system could cause a permanent disruption in the behavioral ability to indicate recognition, thus implying a causal relationship between neural processing and behavioral recognition. In contrast, disrupting the phenomenological report of recognition would not produce neural dysfunction. In this sense, causality runs from lower levels to higher levels rather than in reverse. However, we do not suggest an eliminative reduction whereby phenomena at higher levels are replaced entirely by descriptions on lower levels. Rather, we should strive for explanatory mechanisms that can eventually illuminate the complexities of relationships across levels.

We suggest that progress on this issue can best be made with approaches that bring in multiple levels when we do not prematurely accept assumptions about how neurocognitive processes relate to memory expressions. Focusing on neural processes pertaining to recognition is very important, even if it is not yet clear how these processes will map onto recollection or familiarity expressions. At the same time, an improved understanding of the phenomenology of recollection and familiarity can be gradually built. Indeed, it is quite likely that many of the processes relevant for recognition are not strongly yoked to phenomenological access. For instance, the hippocampal processing that is strongly linked to recollection can occur in conjunction with eye movements that show the appreciation of a relationship between an item and its studied context when there is no corresponding phenomenological report of recollection or familiarity (Hannula and Ranganath, 2009).

Parallel considerations pertain to the neural phenomenon of repetition suppression in perirhinal cortex, which has been emphasized as the basis for familiarity (**Brown et al., 2010; Cowell et al., 2010; Norman, 2010**). Repetition suppression in earlier stages of the ventral visual stream has been associated with perceptual priming, which occurs when experience with a stimulus enhances its perceptual analysis, leading to faster or more accurate behavioral responding to the stimulus with repetition (Wiggs and Martin, 1998). Critically, perceptual priming occurs without any necessary phenomenological experience—that is, the stimulus need not feel any more familiar or any different from new stimuli in other respects in the realm of explicit memory. To the extent that priming phenomena can be linked to repetition suppression in perirhinal cortex (**Ranganath, 2010; Yonelinas et al., 2010**), the phenomenological experience of familiarity might be the wrong description for the processing supported by perirhinal cortex. An appropriate tactic is thus to emphasize mechanisms of perceptual processing within perirhinal cortex and earlier ventral stream regions (**Cowell et al., 2010; Henson and Gagnepain, 2010**), which has the advantage of not assuming in advance how these mechanisms might or might not relate to memory retrieval.

Yet another example stems from our own work concerning event-related brain potential correlates of recollection and familiarity. It has widely been assumed that familiarity can be generically indexed by a particular brain potential known as "FN400" because, for example, effects on FN400 often correlate with phenomenological reports of familiarity (Rugg and Curran, 2007). However, this relationship is identified when familiarity occurs for words or nameable pictures, but is generally not found when familiarity occurs for nonverbal stimuli such as complex geometrical patterns, faces, or nonsense words (e.g., Danker et al., 2008; Voss et al., 2010; Voss and Paller, 2009b; Yovel and Paller, 2004). Why would the neural underpinnings of familiarity change depending on the nature of the stimuli for which familiarity is expressed? One answer is that this neural correlate of familiarity can arise because either (a) it is a direct measure of the neural events that produce the experience of familiarity in a generic sense, or (b) it is a direct measure of a neurophysiological process that serves as a precursor to familiarity in certain circumstances, or (c) it is a direct measure of a process that tends to co-occur with familiarity.

Indeed, we have argued that FN400 potentials assumed to reflect familiarity actually reflect implicit conceptual access (i.e., conceptual priming, Paller et al., 2007). FN400 effects may occur when to-be-recognized stimuli are meaningful but not when they are relatively devoid of meaning, because critical conceptual processing varies across these conditions (Voss et al., 2010; Voss and Paller, 2009b). Moreover, this conceptual processing may correlate with the experience of familiarity when circumstances are right. The extent to which this conceptual processing is a precursor to familiarity remains to be fully determined.

The complexities of interpreting this sort of evidence demonstrate that the explanatory power of neural correlates of memory depend on the specificity with which these measures can be linked to memory processes. Recent findings suggest that implicit conceptual access indexed by FN400 may occur in circumstances unrelated to familiarity and therefore FN400 may not reflect a one-to-one mapping with familiarity (Voss and Federmeier, in press). Studying conceptual processing that may support or at least co-occur with familiarity-based recognition in a particular set of circumstances will enable comparisons with other types of experiences that also entail these conceptual processes.

An important point to take from this focus on neural processes that support recognition is that it is preferable to study recognition memory mechanisms while refraining from prematurely accepting hypotheses about whether these mechanisms map simply onto memory expressions of recollection and familiarity. Outstanding issues of high current relevance concern how various process operate, how these processes are organized within and across independent neural systems, and how these processes and systems interact (see **Henson and Gagnepain, 2010**). It will ultimately be important to specify how data obtained at one level of analysis relates to data at different levels. A focus on studying neural processes is pertinent to considering the more distant goal of understanding how memory experiences (and psychological constructs generally) are enabled by brain processing. Recognition memory, while important, is only one of a large set of memory phenomena, and characterizing the relevant neural processes will be invaluable for discovering how recognition is related to other expressions of memory as well as to nonmnemonic functions.

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