

Specificity of Memory: Implications for Individual and Collective Remembering

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A great deal of research has attempted to clarify the nature and mechanisms underlying memory in individuals, and there is an increasing amount of work concerning collective remembering by societies and cultures. However, there have been few attempts to bridge the gap between these two levels of analysis, and the present volume represents a welcome step in that direction. There are, of course, many possible ways to try to bridge the divide between individual and collective memory. In the present chapter, we adopt an approach that reflects our backgrounds as researchers in the area of individual memory: we focus on a broad concept that has important implications for how we think about individual memory and that, we suggest, might also be relevant to the understanding of collective memory.

We refer to this concept as the *specificity of memory*: the extent to which, and sense in which, an individual's memory is based on retention of specific features of a past experience, or reflects the operation of specialized, highly specific memory processes. In some situations, memory is highly specific, and may include the precise details of a previous experience; in other situations, memory may be much more generic, including retention of only the general sense or gist of what happened. For example, when asked about last year's summer vacation, we may be able to recall in detail the exact meal we ate at a favorite restaurant, where we sat, who else was present, what the room looked like, and how we felt about the food we ate. But when asked about how we arrived at our vacation destination, we might remember only the general outlines of the airplane trip we took, recalling little more than a generic image of a large jet or an airport waiting area. Consider also another

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domain where specificity is important, albeit in a very different sense: skill learning. Sometimes practicing a skill produces a highly specific type of improvement, such as when practicing the piano results in an improved ability to play a specific piece, even though no general improvement transfers to other pieces. But some piano exercises will result in acquired skills that apply quite generally to many pieces. Just as recall can range from specific to general, so, too, can the benefits of practicing a skill.

In view of these considerations, it may not be surprising that questions concerning the specificity of memory loom large in a number of different areas of individual memory research (Schacter, Dobbins, & Schnyer, 2004; Schacter, Gallo, & Kensinger, in press). Although a comprehensive review of all aspects of memory specificity is beyond the scope of this chapter, we will attempt to convey a sense of some of the important findings and concepts that have arisen in regard to memory specificity in several domains of research. First, we will provide a brief overview of specificity issues in relation to one of the most intensively studied phenomena of human memory during the past two decades, known as *priming*: a facilitation or change in the ability of an individual to identify or produce a stimulus as a result of a recent exposure to that stimulus (Tulving & Schacter, 1990). Priming is an example of implicit memory, that is, a nonconscious form of memory that need not involve conscious or explicit recollection of a prior experience (Graf & Schacter, 1985; Schacter, 1987). We will focus on the specificity of priming – that is, when priming reflects retention of specific features of previously perceived items or specific responses made to those items (Schacter et al., 2004). Questions concerning the specificity of priming effects have been the focus of empirical and theoretical attention for nearly 30 years, and considering this research will allow us to refine exactly what we mean when refer to the specificity of memory. We will then consider how some recent findings concerning the specificity of priming relate to specificity in the encoding of new memories, thereby illustrating how thinking about memory specificity can potentially provide links between different domains of memory research.

Continuing to focus on encoding processes, we will next consider a topic that is relevant to both individual and collective memory research: the role of the self in encoding of memories. Issues concerning the self are at the interface between individual and collective memories, so the topic is especially germane to the present volume. Memory researchers have focused in particular on the benefits of encoding new information with respect to the self, and have attempted to elucidate whether those benefits reflect processes specifically related to the self, or reflect more general benefits associated with any type of meaningful encoding activity.

Finally, we will turn to the effects of emotion on memory. We will review studies that address the question of whether emotion enhances the specificity (and accuracy) of memory, or whether it enhances the ability to remember general features of past experiences. We consider research that focuses on the role of emotion in modulating memory errors, and ask whether such modulations depend on emotion-specific processes rather than on more generalized memory mechanisms.

In each of the sections in this chapter, we will consider cognitive studies that delineate the psychological/behavioral properties of the various memory phenomena, and will also discuss recent neuroimaging studies, using techniques such as functional magnetic resonance imaging (fMRI), that provide insights into the neural correlates of memory and other cognitive processes. We believe that neuroimaging evidence can help to shape our theoretical understanding of memory specificity in various domains, and we will attempt to illustrate this point in each section.

PRIMING: LESSONS FROM SPECIFICITY EFFECTS

As noted earlier, priming refers to a change in the ability to identify, produce, or classify an item as a result of a prior encounter with that item or a related item. On priming tests, subjects are not asked to remember any particular prior experience. Instead, they may be asked to identify a briefly presented object, produce a word in response to a three-letter word stem, or classify a letter string on a lexical decision according to whether it is a word (e.g., table) or a nonword (e.g., bltae). Priming occurs when subjects perform the task more accurately or faster for previously studied items than for new, nonstudied items. Work on priming began in the 1970s, largely separate from mainstream memory research, when researchers interested in the nature of word and language processing reported priming effects on lexical decisions that were thought to provide insight into the nature and structure of word representations (e.g., Scarborough, Cortese, & Scarborough, 1977). Memory researchers became interested in priming partly as a result of studies of amnesic patients, who exhibit little or no ability to remember their recent experiences (usually as a result of damage to the hippocampus and related structures in the temporal lobe; e.g., Squire, Stark, & Clark, 2004). Surprisingly, despite patients' severe impairments of explicit memory, studies conducted during the 1970s and 1980s demonstrated that they often show normal priming effects when given a task that does not require conscious recollection, such as word stem completion, where subjects are instructed to complete three-letter word stems with the first word that pops

to mind (e.g., Graf, Squire, & Mandler, 1984; Schacter, 1985; Warrington & Weiskrantz, 1974). At around the same time, research with healthy young adults revealed that a number of experimental manipulations, such as the length of the delay between study and test, or the type of encoding task performed, produced very different effects on priming tasks compared with explicit memory tasks such as recall or recognition (e.g., Jacoby & Dallas, 1981; Graf & Mandler, 1984; Tulving, Schacter, & Stark, 1982).

Almost from the beginning of research on priming, theoretical and experimental interest focused heavily on the specificity of the observed effects: the extent to which priming reflects retention of detailed information acquired during a specific prior episode, versus activation of a pre-existing abstract representation in long-term memory. Thus, for example, when subjects study a word (e.g., table) and later show priming by completing a stem (e.g., tab___) with a studied word rather than with an unstudied alternative (e.g., tablet), does such priming reflect memory for the specific features of the word presented on the list, or does it indicate that a more generic long-term representation of “table” was activated during the study task and affected later test performance? A number of important experimental papers revealed that priming effects show modality specificity on various tests (i.e., priming is reduced significantly by study-to-test changes in sensory modality), and also sometimes show specificity within a modality (e.g., changes in case or font of a word between study and test can reduce priming; see, for example, Roediger & Blaxton, 1987; Weldon & Roediger, 1987).

Since these early studies, numerous experiments have examined the nature and extent of specificity in priming. A number of different types of specificity effects have been distinguished. For example, Schacter et al. (2004) recently proposed a distinction among three types of specificity: stimulus, associative, and response. *Stimulus specificity* occurs when priming is reduced by changing physical properties of a stimulus between study and test, such as the typefont of a word or shape of an object; *associative specificity* occurs when priming is reduced because associations between target items are changed between study and test (e.g., subjects who form an association between a pair of words such as “officer-garden” or “table-cloud” show more priming when tested with “officer-garden” than “officer-cloud”); and *response specificity* occurs when priming is reduced because subjects make different responses to the same stimulus item at study and test. Stimulus and associative specificity effects have been thoroughly documented and explored in cognitive studies of priming, and more recently, by neuroimaging studies. Response specificity, by contrast, has only recently been the target of experimental investigation. We will first consider briefly

neuroimaging evidence pertaining to response specificity, and then consider neuroimaging studies of stimulus specificity.

Response Specificity

Implications for Mechanisms of Priming

Recent studies of response specificity in priming have been conducted with a view toward testing ideas that have been advanced to explain priming-related changes in brain activity observed in neuroimaging studies. In such studies, participants are scanned while they carry out a task used to assess priming, such as completing three-letter word stems with the first word that comes to mind or making judgments about pictures of familiar objects. During primed scans, participants are given target items (e.g., word stems or objects) that appeared previously during the experiment; during unprimed scans, the target items did not appear previously. Virtually all studies using such materials and procedures report *decreased* activity in several cortical regions during primed scans compared to unprimed scans, most consistently in areas within the frontal lobes and the extrastriate visual cortex (for reviews, see Henson, 2003; Schacter & Buckner, 1998; Wiggs & Martin, 1998).

Wiggs and Martin (1998; see also Grill-Spector & Malach, 2001; Schacter & Buckner, 1998) contended that priming-related decreases in human neuroimaging that neural representations of objects, words, or other stimuli are sharpened or “tuned” with repetition (for more recent discussion, see Grill-Spector, Henson, & Martin, 2006). By this view, when an object is presented repeatedly, the neurons that code features that are not essential for recognizing the object show decreased responding; in so doing, they weaken their connections with other neurons involved in coding the object. Thus, the network of neurons that codes the object becomes more selective, and this neural “tuning” or sharpening is linked with faster and more efficient responding (Wiggs & Martin, 1998).

Although the neural tuning account emerges from studies concerned with perceptual priming of visual objects, it can be extended to other priming-like phenomena. For example, Raichle et al. (1994) reported that generating verbal associates to cue words yielded increased activation in several brain regions compared with simple reading of stimuli. Importantly, activation declined with repetition of the verb generation task, and this reduction correlated with reduced reaction times. Consistent with a neural tuning account, the activation reductions and associated reaction time decreases could indicate that semantic analysis of the materials is sharpened

or streamlined with repetition. An alternative possibility, however, is that semantic analysis of the repeated stimuli is largely bypassed in favor of rapid retrieval of previous instances that directly indicate the appropriate response. More generally, it is possible that activation reductions in some previous priming studies could reflect such response-specific effects rather than neural tuning.

Dobbins, Schnyer, Verfaellie, and Schacter (2004) attempted to directly contrast tuning and response accounts with an object decision priming task that had been used in previous neuroimaging research, in which subjects indicated whether an object is “bigger than a shoebox”; this task had yielded evidence of reductions in priming-related activation in regions of prefrontal and fusiform cortex (e.g., Koutstaal et al., 2001). However, in previous studies subjects made the same response to repeated objects; Dobbins et al. modified the task so that sometimes subjects made the same response to repeated objects, and sometimes they made different responses to repeated objects. In the first scanning phase, pictures of common objects were either shown once or repeated three times, and subjects indicated whether each stimulus was bigger than a shoebox using a “yes” or “no” response. In the next phase, the cue was changed so that subjects were now required to indicate whether each item was “smaller than a shoebox”; they made this judgment about new items, and a subset of those that had been shown earlier. In the final scanning phase, the cue was restored to “bigger than a shoebox” and subjects were tested on new items and the remaining items from the initial phase.

If priming-related reductions in neural activity that are typically produced by this task represent facilitated size processing, attributable to “tuning” relevant aspects of neural representations, then changing the cue and associated response should have little effect on priming (although it could disrupt overall task performance by affecting both new and primed items). According to the neural tuning account, the same representations of object size should be accessed whether the question focuses on “bigger” or “smaller” than a shoebox. By contrast, if subjects come to rapidly recover prior responses, and this response learning mechanism bypasses the need to recover size representations, then the cue/response change should disrupt priming-related reductions. When the cue is changed, subjects would have to abandon learned responses and instead reengage the target objects in a controlled manner in order to recover size information.

Both fMRI and behavioral data supported the latter account. During the first scanning phase, standard priming-related activation reductions were observed in regions previously linked with priming, including left

prefrontal and fusiform regions. When the cue was reversed, however, these reductions were eliminated in the left fusiform cortex and disrupted in prefrontal cortex; there was a parallel effect on behavioral response times. But when the cue was restored to the original format, priming-related reductions returned, and again there was a parallel effect on behavioral response times. These results suggest that the reductions depended on the ability of subjects to use prior responses during trials (note, however, that the effect was seen most clearly for items repeated three times before cue reversal; for further discussion of the important implications of this point, see more recent studies by Schnyer, Dobbins, Nicholls, Schacter, & Verfaellie, 2006; Schnyer et al., in press).

This evidence for response specificity in neural priming, as indexed by fMRI signal changes, and in behavioral priming, as indexed by changes in response latencies, is perhaps surprising because previous priming research had neither documented such effects nor even considered their possible existence (for discussion of prior studies related to response specificity, see Dobbins et al., 2004; Schacter et al., 2004). Clearly, there must be limitations on response specificity: a number of well-established priming effects occur when participants make different responses during study and test. For instance, priming effects on the stem completion task, in which subjects respond with the first word that comes to mind in response to a three-letter word beginning, are typically observed after semantic or perceptual encoding tasks that require a different response. Nonetheless, the existence of response specificity poses a challenge for various theoretical accounts of priming-related decreases in fMRI signal as well as for theories aimed at purely behavioral data (for further discussion of this point, see Schacter et al., in press).

Stimulus Specificity Links to Encoding Processes

Whereas neuroimaging evidence concerning response specificity was without much prior precedent in purely cognitive studies, neuroimaging evidence concerning stimulus specificity was preceded by a good deal of cognitive research. Much of this research involved studies in which words were used as target stimuli; the evidence showed that conditions exist in which there is an effect of changing sensory modality (auditory/visual) or within-modality perceptual features (case, typefont) on the magnitude of priming. Other studies used pictures of common objects as experimental stimuli, and showed that priming could be reduced by showing different exemplars of the same object at study and test (e.g., pictures of two

different tables, dogs, cars, and so forth) or by changing specific features of the same object, such as its orientation (for review, see Schacter et al., 2004; Tenpenny, 1995).

Koutstaal et al. (2001) reported one of the first neuroimaging studies to examine specificity of object priming. Previous studies had shown that repeated processing of visual objects yields activation reductions in a number of cortical regions, including fusiform and lateral occipital cortices as well as several regions within inferior prefrontal cortex (see Henson, 2003; Schacter & Buckner, 1998; Wiggs & Martin, 1998). Koutstaal et al. compared priming for identical objects and different exemplars with the same name, using a task in which objects were presented repeatedly, and on each presentation, subjects judged whether the object was larger than a 13" square box. Overall, subjects responded more quickly to repeated objects compared with initial presentation, indicating the presence of behavioral priming. Such priming was accompanied by reduced activity in a number of brain regions. Most important, speed of responding and corresponding activation reductions were greater when the same object was repeated than when a different exemplar of the object was repeated, documenting stimulus specificity. The neural specificity effect was observed in various regions involved in visual processing, including bilateral occipital and fusiform cortices. Perhaps the most intriguing data came from a comparison of activation reductions in the right and left fusiform region for same and different exemplars: visually specific activation reductions for object priming were greater in the right than the left fusiform cortex, suggesting that the right fusiform region is involved in processing of and memory for highly specific perceptual features of repeated objects. This pattern was of interest because earlier behavioral studies of word priming effects, in which stimuli were projected to either the left hemisphere or the right hemisphere, had indicated that stimulus specificity effects (e.g., effects of changing typefont between study and test) are greater in the right than the left hemisphere (e.g., Marsolek, Schacter, & Nicholas, 1996).

The pattern of results reported by Koutstaal et al. (2001) – greater activation reduction for same than different object exemplars in the right than the left fusiform region – was replicated in a subsequent study by Simons et al. (2003), who also showed that activation reduction in the left fusiform region is sensitive to semantic (rather than perceptual) properties of studied objects. In a related study, Vuilleumier et al. (2002) used a behavioral task in which subjects decide whether pictorial images depict real or nonsense objects. Repeated stimuli were either identical, differed in size or viewpoint, or were different exemplars with the same name. Priming-related activation

reductions in right fusiform cortex were sensitive to changes in both exemplars and viewpoint. Overall, then, the neuroimaging data indicate strong stimulus specificity effects of a visual nature in the right fusiform region.

Are these effects restricted to priming paradigms, or do they indicate a wider role for the right fusiform region related to memory for the specific visual features of object stimuli? Garoff, Slotnick, and Schacter (2005) examined this issue in a neuroimaging study that focused on the encoding and subsequent recognition of visual objects. They drew a distinction between specific recognition, in which one remembers the exact visual details of a previously presented object, and nonspecific recognition, in which one remembers general information about an object but not the specific visual details. For example, if an individual studies a picture of a tiger, she might later remember the visual details of the object, and thereby exhibit specific recognition of the exact tiger that had been studied. Alternatively, she might remember in general having seen a picture of a tiger, without remembering any specific visual details, thereby exhibiting nonspecific recognition. Garoff et al. reasoned that if the right fusiform cortex plays a role in encoding of specific object features, then it should be more active at the time of encoding when an individual subsequently shows specific recognition for the object compared with than nonspecific recognition.

To examine the issue, Garoff et al. used what is known in neuroimaging research as a “subsequent memory” paradigm (e.g., Wagner et al., 1998). In a subsequent memory paradigm, subjects encode a list of items, and researchers measure brain activity associated with each of the individual items in the list; later, subjects are given a memory test for the previously studied items. These latter data are used to sort the items based on subjects’ responses into bins comprised of remembered and forgotten items. Then, brain activity at the time of encoding is compared for the two types of items. If brain activity at the time of encoding in a particular region is greater for a subsequently remembered than for a forgotten item, then researchers infer that the region plays a role in the encoding process. In the Garoff et al. study, subjects encoded a series of pictures of common objects while in the fMRI scanner. The next day, they were given a test that included some of the same items seen the previous day, similar items that resembled the previously studied pictures (e.g., if the subject saw a picture of a tiger on the list, a different tiger would be presented on the test), and new pictures that were unrelated to any of the pictures subjects had seen previously on the study list. Subjects were instructed to respond “same” when they thought that a picture was identical to the one they had studied the previous day, “similar” when they thought that the picture was a different example with

the same name as a previously studied picture (e.g., a different tiger than the one that had been seen on the list), and “new” when they thought that no picture with the same name had appeared previously on the study list. “Same” responses to same items indicate specific recognition, whereas “same” responses to similar items, and “similar” responses to same items both indicate some type of nonspecific recognition.

Garoff et al. reasoned that if the right fusiform region is involved in encoding of visual details of object, then it should be more active at the time of encoding for trials associated with subsequent specific recognition than with subsequent nonspecific recognition. This is precisely what was found: the right fusiform region was significantly more active at encoding for same pictures that receive a “same” response the next day, compared with same pictures that received a “similar” response or similar pictures that received a “same” response. Moreover, the right fusiform region was the only region in the entire brain to exhibit this pattern of greater activation at encoding for subsequent specific versus nonspecific recognition.

These results not only provide insight into the neural mechanism of encoding processes that support specific recognition, they also suggest a previously unsuspected link between the processes that subserve stimulus specificity in priming and encoding/recognition. This study thus provides one example of how thinking about specificity of memory may provide a conceptual bridge across areas that might be otherwise treated separately.

We next turn to a research domain in which neuroimaging has also played a useful role in allowing researchers to address a rather different type of issue concerning memory specificity: the specificity of encoding processes involved in making judgments that relate new information to the self.

SPECIFICITY, THE SELF, AND ENCODING PROCESSES

In the previous section, we considered neuroimaging evidence from subsequent memory paradigms concerning the encoding origins of specific and nonspecific recognition. Although this line of research has developed relatively recently, memory researchers have long been interested in how encoding processes influence memory. For example, the influential depth of processing framework (Craik & Lockhart, 1972) maintains that memories are closely linked to, and are the natural by-products of, encoding operations that are performed during the analysis of incoming information. According to this framework, deep or semantic encoding operations that elaborate the meaning of incoming information tend to produce higher levels of subsequent memory than do shallow encoding operations that

focus on more superficial, nonsemantic information. However, soon after the appearance of the depth of processing framework, it was reported that encoding operations that relate information to the self support even higher levels of subsequent retention than do semantic encoding operation that do not involve reference to the self.

For example, in an early study (Rogers, Kuiper, & Kirker, 1977), participants answered orienting probes about a series of words. Some probes directed participants' attention to the words' reference to oneself (e.g., "does this word describe you?"), others directed participants to the word's semantic meaning ("is this word a synonym of 'happy'?"), and others probes focused participants on the structural features of the words ("is this word in uppercase font?"). Recall was highest in the condition that referenced the self compared to the remaining conditions. Whereas the depth of processing framework would lead to the prediction that any task that focuses on meaning should similarly enhance memory, the words that were self-referenced were recognized more frequently than those encoded through other meaning-based judgments, such as the synonym condition. Further studies established that the enhancement was specific to referencing the self, rather than any person or type of social information (e.g., Kuiper & Rogers, 1979).

Identification of the so-called self-reference effect, that is, enhanced memory for information encoded in relation to oneself, was interpreted to suggest that the self constitutes a unique and special structure in memory. The rich schema evoked by the self (Cantor & Mischel, 1977; Markus, 1977) was postulated to afford detailed cues and organizational structure to support memory, features that are unmatched by other types of semantic information (e.g., Rogers et al., 1977). This led to claims that the self was "special" and constituted a unique structure capable of enhancing memory.

Subsequent research, however, challenged the notion of self as special. The self-reference effect could be minimized, or even eliminated, when compared to tasks orienting to a personally known, intimate other (Bower & Gilligan, 1979; Ferguson, Rule, & Carlson, 1983) or social desirability (Ferguson et al., 1983). These results suggest that any rich, highly familiar cognitive structure could be used to enhance memory, although an advantage for self-referencing over these comparison conditions does emerge in within-subjects designs (McCaul & Maki, 1984) and was documented in a meta-analysis (Symons & Johnson, 1997). Evaluative dimensions, such as good/bad, could be the primary organizing principle to enhance memory, and underlie the self-reference effect because the concept of "self" spontaneously orients one to these evaluative aspects. Thus, the self-reference effect might simply

represent another example of a depth of encoding manipulation (Craik & Lockhart, 1972; Craik & Tulving, 1975).

These considerations raised doubts about whether the self plays a specific role in enhancing memory; thinking about the self might instead engage processes that could enhance memory for any type of information. For example, in the adjective judgment task used by Rogers et al. (1977), self-referencing offers a relational organizational structure into the implicit categories of “me” and “not me” (Klein & Kihlstrom, 1986). In this case, recall of one self-relevant word can cue recall of another item based on their common organization around the concept of “self” (Einstein & Hunt, 1980). When the semantic conditions also share categorical relationships, recall and organization (defined as the order of output in recall) is similar for self-referenced and semantically related words. Klein and Loftus (1988) illustrated the effects of item-specific elaborative processes, extending Klein and Kihlstrom’s work to suggest that organization is not the only way in which self-referencing benefits memory. Elaboration can drive the effects under some circumstances, a claim that was further supported by a meta-analysis (Symons & Johnson, 1997). These findings led Greenwald and Banaji (1989) to conclude that self-referencing relies on “ordinary” memory systems and to suggest that the self is analogous to other mnemonic structures in that arbitrary novel information can be meaningfully associated and easily accessed when rich cues are generated. In the case of self-referencing, the cues are memorable because they are self-generated, based on highly elaborated and organized existing knowledge.

The debate over self as a “special” structure in memory effectively reached a standstill when studies could not identify a unique process that caused the self to be memorable. With the advent of functional neuroimaging, which provided researchers with a new tool to examine possible dissociations between self-encoding and other forms of encoding, the debate was re-introduced. In a study using positron emission tomography (PET) to compare self and semantic encoding, participants were scanned as they judged whether adjectives described themselves, described Brain Mulroney (a former Canadian prime minister), described socially desirable traits, or counted the number of syllables in a nonsemantic control condition (Craik et al., 1999). The authors found a boost in memory for the self condition relative to the other conditions, but the neural activation pattern was quite similar for all three semantic conditions compared to the syllable judgments. Although a unique signature associated with the self did not emerge in the primary analyses, partial least squares analysis identified a predominantly right-hemisphere prefrontal activation associated with self judgments.

Because in the literature to date encoding processes had been observed primarily in the left hemisphere, the localization of self judgments to the right hemisphere was surprising because the hemisphere had been largely associated with retrieval processes (Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). The authors interpreted the location of the self judgments to suggest that episodic retrieval draws heavily on self-referencing.

A later study extended these findings using a larger sample size and fMRI, which is not subject to some of the constraints on task design and spatial localization that are associated with PET. The authors identified neural regions that respond to self-judgments as distinct from neural regions that respond to judgments about semantics or another person (Kelley et al., 2002). In their study, participants viewed a series of adjectives, and alternated between judging whether the word described them (self-reference condition), described George Bush (other-reference condition), or was presented in upper- or lowercase font (case condition). Some regions (i.e., left inferior prefrontal cortex and anterior cingulate) tracked the meaningfulness of the judgments, with self and other judgments increasing activity relative to case judgments. Critically, there were also regions (i.e., medial prefrontal cortex and posterior cingulate) where self differed from the other and case conditions. If depth of encoding alone mediated the advantage for self-referencing, a single region, such as left inferior prefrontal cortex, would be expected to increase its activity across the different encoding manipulations, with maximal activation during the self judgments. Instead, Kelley et al.'s findings suggest that distinct neural regions are associated with self-referential encoding, compared to other social and nonsocial encoding manipulations, and these unique neural regions likely indicate a discrete set of cognitive operations engaged by the self.

Although this study suggests an intriguing distinction between processing of self and other, Kelley et al. (2002) did not directly link the medial prefrontal activity to memory performance; thus, the medial prefrontal activity could reflect a response to thinking about oneself but could be unrelated to successful memory encoding. In a follow-up study, Macrae and colleagues adopted a subsequent memory approach in order to investigate the role of medial prefrontal cortex in encoding processes (Macrae, Moran, Heatherton, Banfield, & Kelley, 2004). When words initially were judged for self-description, those items that were later remembered activated medial prefrontal cortex, as well as parahippocampal gyrus, more than those items later forgotten. These data suggest that the medial prefrontal regions associated with the self *do* play a functional and specific role in encoding processes. Macrae et al. posit that medial prefrontal cortex could represent a module

analogous to the role of the amygdala in emotional memory, contributing as a “critical component of the human memory system” (p. 651). What is not known is whether it is most appropriate to consider medial prefrontal cortex a memory structure per se, recruited solely in the service of self-relevant information, or whether the region may prioritize self-relevant information as it interacts with the episodic memory system. Regardless of the precise mechanism, it seems clear that the contribution of medial prefrontal cortex is essential to self-referential memory, much as the research from our laboratory, reviewed in other sections of this chapter, suggests roles for the right fusiform in forming and retrieving precise perceptual memories, or the amygdala for emotional memories.

Many other studies show that the distinction between self and other is robust, and often reflected in the activity of medial prefrontal cortex. During recognition of previously studied positive and negative words, a region of medial prefrontal cortex was more active for self-referenced negative words compared to other-referenced negative words (Fossati et al., 2004). A second peak in medial prefrontal cortex responded to the valence of previously studied self-referenced words (positive > negative). Medial prefrontal cortex is activated during self-reference judgments of both positive and negative traits (Fossati et al., 2003), and activity in the region is heightened for self-descriptive traits (Moran, Macrae, Heatherton, Wyland, & Kelley, 2006), although further research is needed to test the contributions of valence and self-descriptiveness to encoding processes. Despite extensive cognitive changes, the self/other distinction holds with age, with younger and older adults similarly recruiting medial prefrontal regions and better recognizing self-referenced relative to other-referenced words (Gutchess, Kensinger, & Schacter, 2006).

Converging evidence from a number of other methods also supports the distinction between self and other recognition that has been established using neuroimaging. Many of these studies involve recognition of morphed faces, in which the faces of the subject and a familiar or famous other are blended into a single face. In these tasks, participants must recognize each morphed face as closer to their own face or the other person’s face, across varying degrees of morphs (e.g., 80% self, 20% other). Wada testing, in which the left or right hemisphere is anesthetized in patients, reveals that the right hemisphere governs self-recognition (Keenan, Nelson, O’Connor, & Pascual-Leone, 2001), consistent with the initial PET study by Craik et al. (1999). Transcranial magnetic stimulation (a method that uses magnetic currents to interfere with neurotransmission in localized brain regions), also identifies a distinction across hemispheres, with temporary lesions of right inferior parietal regions disrupting self recognition (Uddin, Molnar-

Szakacs, Zaidel, & Iacoboni, 2006) and evidence for greater motor-evoked potentials in the right hemisphere associated with self recognition (Keenan et al., 2001). Evidence from split-brain patients, for whom the hemispheres have been separated by cutting the corpus callosum to restrict seizure activity, supports a self-other distinction. However, the studies are inconsistent regarding the role of the left and right hemispheres, with some supporting the idea of a right hemisphere advantage for self (Keenan, Wheeler, Platek, Lardi, & Lassonde, 2003) and others revealing a left hemisphere advantage for self recognition (Turk et al., 2002). The different findings across studies regarding the role of left and right hemispheres may reflect differences across tasks, or even individual differences across the split-brain patients. Critically, unique neural regions associated with the self emerge consistently across multiple methods.

Thus far, self has been primarily targeted as a structure with which to bolster memory performance at a general level. In contrast to the types of memory discussed in the other sections of this chapter, there has been little attention to the amount of detail associated with those memories, and whether that detail is a veridical representation of prior experience. If the benefit of self-referencing is derived primarily from the schematic nature of the self, then the retrieved information may rely on gist rather than detailed representations. Furthermore, reliance on the schematic self should also lead to systematic patterns of errors and distortions of memory. Some evidence for this comes from an investigation of the “false alarm effect,” which refers to high levels of false alarms for novel information that is related to the prototype, in this case, of the self (Rogers, Rogers, & Kuiper, 1979). In this study, participants rated adjectives on a scale to denote whether the adjective was like them, or unlike them. Two and a half months later, the same participants incidentally studied a subset of these adjectives and received an old/new recognition test on the entire set of adjectives. Based on initial ratings of self-description, each participant’s data were divided into quartiles, with sets ranging from the most self-descriptive to the least self-descriptive. Whereas hit rates were unaffected by the degree of self-reference, false alarms to new items were lowest for the items that were the least self-relevant, and tended to increase across quartiles as items became more self-relevant. This finding suggests that the self contributes to memory not only by enriching retrieval cues and organization but also can lead to memory errors, perhaps through a sense of familiarity as a result of chronic activation of self-relevant information.

The challenge still lies ahead for future work to clarify the impact of the self on memory through systematic consideration of the way in which it

distorts memory. For example, does information closely related to the self concept lead to false alarms due to a feeling of familiarity (i.e., “Friendliness’ is a chronically activated trait for me because it is important to my self concept”), or does it actually convey recollective qualities based on one’s autobiographical experience (i.e., “When I see the word ‘friendly’, I vividly recall many past episodes of my friendly behaviors”)? It is also possible that the false alarms are more related to social desirability, rather than the self per se (Ferguson et al., 1983). The tendency to endorse positive items as self-relevant may lead to heightened levels of false alarms for positive traits, and suggests a close relationship between the memory systems associated with self and emotion (although distinct neural regions underlie these effects; Moran et al., 2006).

The studies discussed throughout this section demonstrate that the self engages specialized structures for the encoding and retrieval of self-relevant information. However, there is not consensus in the literature that self represents a “special” modality in memory (e.g., Gillihan & Farah, 2005). More work remains to be done in order to characterize the nature of the self representation and its relationship with other processes. The types of paradigms used in neuroimaging studies of self and memory are limited. It could be the case that the designs employed thus far inflate the appearance of the self as “special”, much as was the case for the initial behavioral literature. For example, regions of medial prefrontal cortex have been shown to respond broadly to social information (e.g., Mitchell, Heatherton, & Macrae, 2002). In order to provide convincing evidence that the self is specifically associated with a distinct type of memory, broader exploration of these inter-related processes, as well as the specificity and qualities of self-referenced memories, is needed within the domain of memory. In addition, the roles of medial prefrontal cortex and other regions must be detailed during the formation and retrieval of self-relevant true memories, and false memories, under a variety of conditions.

SPECIFICITY AND ACCURACY OF EMOTIONAL MEMORIES

In *The Principles of Psychology*, William James stated, “It is a notorious fact that what interests us most vividly at the time is, other things equal, what we remember best. An impression may be so exciting emotionally as almost to leave a scar upon the cerebral tissues.” Many people share James’s intuition that when an event contains emotional importance, we remember that event in a highly specific manner, with extensive detail and clarity. The term

“flashbulb memory,” coined by Brown and Kulik (1977), captures the picturelike vividness that individuals often believe to accompany their memories of highly surprising and emotionally evocative events. For example, when individuals are asked what they remember about the personal circumstances in which they learned of an emotional event (e.g., the death of Princess Diana or the terrorist attacks of September 11, 2001), they often will claim to remember very specific details, such as where they were and what they were doing (e.g., Budson et al., 2004; Christianson, 1989; Kensinger, Krendl, & Corkin, 2006; Paradis et al., 2004). Studies of emotional remembering, then, raise important issues concerning memory specificity. We will address these issues by considering first research that has examined the accuracy of emotional memories and whether they are subject to distortion, and then turning to studies that have attempted to compare directly the specificity of emotional and non-emotional memories.

Numerous studies have demonstrated that these memories of emotional events are prone to significant distortions over time. Individuals often report details after a 6- or 12-month delay that conflict with those that they reported soon after the event. Moreover, although individuals can be highly confident about their memories, there often is little or no correlation between their confidence and the consistency of their memories (Neisser & Harsch, 1992; Schmidt, 2004; Schmolck et al., 2000; Talarico & Rubin, 2003). These data emphasize that emotional events do not leave indelible traces; rather, emotional memories, like nonemotional ones, are susceptible to distortion. However, studies of flashbulb memories have not allowed strong conclusions to be drawn regarding whether emotional memories are more accurate (and therefore specific) than nonemotional memories. It is nearly impossible to find nonemotional public events that are wholly comparable to the emotional ones (e.g., in media coverage, time spent discussing the event, etc.). It also is difficult (if not impossible) to assess the objective accuracy of participants’ memories, requiring measures of consistency to be used as a proxy for memory accuracy.

In a recent study (Kensinger & Schacter, in press), we tried to circumvent the first difficulty by examining how participants’ memories for an event were affected by the emotional importance of that event to them. In particular, we assessed participants’ memories for the final game of the 2004 American League Championship Series between the Boston Red Sox and the New York Yankees. The Red Sox had come back from a 3–0 series deficit to overcome the New York Yankees, reversing decades of defeat by the Yankees. We asked young adults to tell us what they remembered about the game (e.g., important plays), and about the personal context in which

they watched the game (e.g., who they were with, where they were), both within a few days of the event and after an approximately six-month delay. By examining the memories of participants who found the outcome of the game to be positive (i.e., Red Sox fans), negative (i.e., Yankees fans) or non-emotional (i.e., fans of neither team), we were able to examine the effect of emotion on memory consistency. The critical finding from this study was that participants who found the game to be negative were more consistent in their responses at the two time points than were other participants. The individuals who found the game to be positive, in contrast, showed more inconsistencies in their reports, and they also were overconfident in the accuracy of their responses (i.e., they demonstrated high confidence in their answers even when those responses were incorrect or inconsistent with their initial reports; see also Levine & Bluck, 2004 for a demonstration of overconfidence in individuals who were happy about the verdict in the O. J. Simpson trial). These data provide intriguing evidence that, although emotional events may not be immune to distortion, negative emotion may nevertheless provide some benefits in terms of memory accuracy.

Corroborating evidence for beneficial effects of negative emotion on memory accuracy has come from laboratory investigations. In one of the first studies to examine the effects of emotion on memory accuracy, participants were presented with lists of words that were orthographically associated to nonpresented lure words. Some of the lists were associated with emotional lures (e.g., cape, nape, nape all are associated with rape) whereas other lists were associated with neutral lures (e.g., book, look, cook all are associated with hook). After studying these lists of orthographic associates, participants were less likely to falsely recall or to falsely recognize the emotional lure words than the nonemotional ones (Kensinger & Corkin, 2004a; Pesta, Murphy, & Sanders, 2001).

These data provided suggestive evidence for an effect of emotion on memory accuracy. However, in the orthographic-list paradigm, the majority of the studied items always were neutral. Thus, the emotional lures may have been rejected due to their conceptual incongruence with the studied items rather than because of specific effects of emotion. In other words, participants may have been able to reject that rape had been on the study list because the word was not consistent with the types of (nonemotional) words that had been presented during the study phase. More direct evidence for effects of emotional salience on memory distortion has come from examinations of the effect of emotion on reality monitoring ability (the ability to distinguish what has been perceived from what has been imagined; Johnson & Raye, 1981).

Accurate assignment to an external or internal source typically can be made by remembering the types of information associated with an event: memories that originate from perception or experience usually are remembered with more perceptual detail (e.g., color, sound) and with more contextual information about the time and place of presentation. In contrast, memories originating from introspection or imagination include more detail about the cognitive operations that guided the generation of the information (Johnson, Hashtroudi, & Lindsay, 1993; Johnson & Raye, 1981). It has been proposed that participants rely on the types of information retrieved in order to decide whether an item has been perceived or imagined, and recent neuroimaging evidence has confirmed that individuals tend to believe that an item was perceived if its retrieval is associated with enhanced activation in sensory cortices, whereas they are likely to attribute an item to imagination if the item's retrieval is associated with enhanced activity in regions thought to support self-generated reflection and self-referential processing (Kensinger & Schacter, 2006b). Although remembering these characteristics typically allows accurate memory attributions, reality-monitoring errors sometimes can occur.

Kensinger and Schacter (2006d) investigated the effect of emotion on reality-monitoring performance, adapting a paradigm that had been shown to elicit high levels of reality-monitoring errors (see Gonsalves & Paller, 2000). We asked participants to view words, half of which were negative (e.g., snake, grenade) and half of which were neutral (e.g., barometer, blender). Participants formed a mental image of the named object. Half of the time, the name was followed by its photo, whereas the other half of the time it was followed only by a blank square. At retrieval, participants listened as words were pronounced over a headset, and they were instructed to indicate whether or not they had seen the corresponding photo. The critical finding from this study was that reality-monitoring errors occurred less frequently for negative arousing items compared to nonemotional ones. This enhanced discrimination for negative arousing items existed whether or not participants were informed about the memory task that would follow, and the effect was present for both verbal stimuli and single objects.

This finding is consistent with evidence indicating that emotional content enhances the linking or binding of many types of item and event details. For example, emotionally arousing items are more likely to be remembered with details such as the color of font in which a word was written or the location of a word on a screen (D'Argembeau & Van der Linden, 2004; Doerksen & Shimamura, 2001; Kensinger & Corkin, 2003; MacKay et al., 2004; MacKay & Ahmetzanov, 2005). Enhanced binding could combat

reality-monitoring errors in a number of ways. It could increase the likelihood that participants remember the critical event details needed to distinguish presented from imagined events (e.g., sensory, perceptual, semantic details; Johnson et al., 1993). It also could prevent stimulus confusion. For example, after studying a picture of a tomato, a person may later falsely believe that they saw a picture of an apple if they remember only general information about that object (e.g., a red, round food). In contrast, this confusion may result less frequently for emotional items if they tend to be remembered with more detail, allowing them to be distinguished from other items.

To directly examine whether individuals are more likely to remember the specific visual details of a negative item's presentation, Kensinger, Garoff-Eaton, and Schacter (2006) presented participants with colored objects at study, some of which were negative and some of which were neutral. At retrieval, we used the previously described procedure from Garoff et al. (2005), and showed participants three different types of exemplars: "same" exemplars that were identical to the studied exemplars, "similar" exemplars that shared the same verbal labels as studied objects but that differed in any number of visual features (e.g., color, size, shape, or orientation), and "new" exemplars that were unrelated to studied objects. The data revealed that participants were better able to discriminate the "same" from "similar" exemplars when the objects were negative than when they were neutral.

These behavioral studies demonstrate that items with negative emotional content can be remembered with more detail than items lacking emotional meaning. But they leave open the question of whether this increased memory accuracy for the negative arousing information is specifically related to the processing of the emotional information, or whether it stems from engagement of the same processes that reduce memory distortion for neutral information. In other words, do the effects of emotion on memory accuracy result from increased engagement of domain-general processes that serve to boost memory accuracy for emotional and nonemotional information, or do they arise from engagement of emotion-specific processes?

This question is difficult to answer behaviorally, and so recent research has turned to neuroimaging to examine the neural processes that are engaged during the accurate encoding and retrieval of emotional and nonemotional information. Kensinger and Schacter (2005a, 2005b) asked participants to perform the reality-monitoring task, described earlier, while in the MRI scanner. As in the behavioral studies discussed above, reality-monitoring errors occurred less frequently for the negative items than for the neutral items. The critical question was whether distinct

neural processes influenced the frequency of reality-monitoring errors for the two types of items.

The study revealed some overlap in the neural processes that were related to successful encoding and retrieval for the negative and neutral items. Most notably, activity in the left posterior hippocampus showed a relation to accurate encoding for both item types (i.e., greater activity during the encoding of items later correctly attributed to a presented or nonpresented source than during the encoding of items later misattributed; Kensinger & Schacter, 2005a), and activity in the anterior hippocampus showed a relation to accurate retrieval for both item types (Kensinger & Schacter, 2005b). These data suggest that there are some mnemonic processes that are broadly engaged during the successful encoding and retrieval of all items, regardless of their emotional content.

However, there also were distinctions in the neural processes that were related to accurate memory for the emotional and neutral items: Enhanced activity in the amygdala and the orbitofrontal cortex corresponded with a reduction in the likelihood of memory misattributions specifically for the negative items. Activity in these regions showed a strong relation to memory accuracy for the negative items both during encoding (Kensinger & Schacter, 2005a) and during retrieval (Kensinger & Schacter, 2005b), but neither region showed a relation to memory accuracy for the neutral items. Both the amygdala and the orbitofrontal cortex are regions that frequently are engaged during the processing of emotional information (Bechara, Damasio, & Damasio, 2000; Kensinger & Schacter, 2006c; Phan et al., 2002; Zald, 2003). Thus, it appears that the way in which emotional information is processed can result in a memory accuracy advantage.

Part of the effect of these emotion-specific processes appeared to be exerted via their interactions with regions that promote accurate encoding of both emotional and nonemotional items. Activity in the amygdala was highly correlated with activity in the hippocampus during the encoding of emotional items later accurately attributed (Kensinger & Schacter, 2005a), consistent with a number of other studies that have found evidence for interactions between the amygdala and the hippocampus during the encoding on emotional information (Dolcos, LaBar, & Cabeza, 2004; Kensinger & Corkin, 2004b; Kilpatrick & Cahill, 2003; Richardson et al., 2004).

The results provide strong evidence that the enhancement in memory accuracy for emotional items does not stem solely from the additional engagement of domain-general processes that enhance accuracy for all items. Rather, domain-specific processes (in the amygdala and orbitofrontal cortex), engaged during encoding, serve to enhance memory accuracy for

the emotional items. Nevertheless, the results also suggest that items with emotional content are not remembered because of engagement of processes that are entirely distinct from those that support memory for nonemotional information. Rather, there seems to be some overlap in the medial temporal-lobe mnemonic processes that support memory for information with and without emotional content (see also Kensinger & Schacter, 2006a).

Taken together, these studies demonstrate that information with negatively emotional content is more likely to be remembered accurately and specifically than is information lacking emotional salience. This boost in memory accuracy occurs across a range of behavioral paradigms and appears to result from the engagement of emotion-specific processes, particularly in the amygdala and the orbitofrontal cortex, during both encoding and retrieval.

CONCLUDING COMMENTS

In this chapter, we have reviewed evidence from several domains of individual memory in which issues regarding the specificity of memory have been salient. We discussed evidence showing the stimulus and response specificity of priming effects, and considered the relation of such specificity to memory encoding. We then discussed the role of the self in memory encoding, focusing on recent data from neuroimaging studies that suggest that self-reference encoding may constitute a specific, specialized type of memory process, rather than simply reflecting the operation of general processes that operate across a numbers of domains. Finally, we considered evidence highlighting the specificity of emotional memory.

Although we cannot say very much about how research concerning the specificity of individual memory is related to collective memory, it seems likely that specificity is a relevant dimension for collective memory research: whether a society remembers its past in a specific or general manner should have important consequences for how that society views itself. Societal differences in values and orientations to the world could dictate which dimensions are distinct and valued in memory. For example, cultures differ in the extent to which they consider the self to be an independent entity that is separate from the group, and this can also guide the expression and experience of emotion (Markus & Kitayama, 1991). It may be the case that cultures vary in the degree to which emotional and self-referential memory engage specific and special processes. Moreover, it seems to us that an important challenge would be to develop a means of assessing specificity in collective memory. Although individual memory researchers have developed a

variety of techniques for assessing memory specificity in several domains, we are unaware of analogous research in the area of collective memory.

Although we have focused on specificity as an important dimension of how individuals remember their personal pasts, there is also evidence that specificity is relevant to how individuals envisage their personal futures. For example, Williams et al. (1996) gave word cues to depressed patients and healthy controls, and instructed them to recall an episode from the past or imagine a future episode. Depressed patients showed reduced specificity in their retrieval of both past and future autobiographical events – that is, they retrieved or imagined vaguer, more general events than did the controls. Furthermore, Williams and colleagues demonstrated that they could induce healthy individuals to retrieve more general events through task instructions that encouraged them to adopt a general retrieval style. Such instructions produced a comparable reduction in the specificity of subsequently generated future events. These findings, along with much other evidence from both behavioral and neuroimaging studies, suggest that remembering the past and imagining the future depend, to a large extent, on shared cognitive and neural processes (for recent review and discussion, see Atance & O'Neill, 2005; Buckner & Carroll, in press; Schacter & Addis, in press; Suddendorf & Busby, 2005).

It is intriguing to consider whether such a link in specificity of past and future events holds within the domain of collective memory. It seems only reasonable to assume that the specificity with which societies remember their pasts is related to how, and how specifically, they envisage their futures. Further examination of the specificity of remembering past events, and envisaging future events, would appear to be a promising possible link between research on individual and collective memories.

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