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The Relationship Between Episodic Memory and Context: Clues from Memory Errors Made While Under Stress

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In a series of studies in the late 1950s and early 1960s, Jan Bures introduced cortical spreading depression to the field of behavioral neuroscience (eg. Bures 1960). This technique offered a unique way to study the role of cortex in learning and memory, and attracted the attention of many who began their graduate studies at that time, including one of us (LN, cf. Nadel 1966).

An NIH postdoctoral fellowship to study with the master himself brought LN to Prague in September 1967. Thus began a relationship that included science, politics, and personal life, and has lasted over 30 years[1,2].

The first scientific exchange began with Jan pulling a piece of paper from his desk with a long list of possible experiments written on it -- "pick one", he said. This led to a series of studies on interhemispheric transfer of learning under conditions of monocular input, demonstrating, amongst other things, that such transfer is not a uniform process. Depending on the kind of trials given with both hemispheres intact, and the eye which remained open to input, transfer can either be non-specific, likely involving some kind of procedural knowledge, or highly specific, likely involving knowledge about the trained discrimination itself (Nadel and Buresova, 1970). These studies anticipated LN's future work on multiple memory systems, a research enterprise pursued in the following decades by many labs (including LN's: e.g. Nadel and O'Keefe 1974, O'Keefe *et al.* 1975).

In this paper we focus on several scientific issues that Jan has been thinking about for the past 25 years. In particular, we consider spatial learning, the hippocampus, and memory. To this mix we add stress, something well known to anyone living in Prague in 1968.

LN left Prague after the 1968 invasion and stayed in London for seven months, during which time arrangements were made for an eventual return to the Medical Research Council Cerebral Functions Research Group in 1970. Thus it was that LN happened to be down the hall when John O'Keefe and Jonathan Dostrovsky discovered place cells (O'Keefe and Dostrovsky 1971) and began the program of research leading to the cognitive map theory of hippocampal function (O'Keefe and Nadel 1978).

Cognitive Maps, Memory, and Context

Originally formulated on the basis of research with animals, cognitive map theory started with detailed proposals about spatial memory in rats and ended with suggestions about episodic memory in humans. We reasoned that the hippocampus had a special role in episodic memory because cognitive maps represented spatial *context*, and such context was an essential part of memory for events. In two subsequent papers (Nadel and Willner 1980, Nadel *et al.* 1985) the notion of spatial context and its role in various learning phenomena was fleshed out in considerable detail, but the relation between context and episodic memory was not. Those reports attempted to clarify the conceptual confusion surrounding the notion of context, with only modest success. In the intervening years, the notion that the hippocampus somehow mediates context has gained much support (eg. Penick and Solomon 1991, Phillips and LeDoux 1992, Honey and Good 1993), but confusion about context itself remained. Not much has changed in the years since.

The word context derives from the Latin *contexere*, which means "to join together". We suspect

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that this origin reveals a central role of spatial context -- namely, that it serves to join together, or bind, the disparate elements that make up a given episode. This role in binding is one of the reasons why a neural system concerned in the first instance with spatial context is crucial to episodic memory.

In this paper we describe the beginnings of an experimental program aimed at elucidating the mechanisms of “false memory”, or the inaccurate remembering of past events. Retrieving an episodic memory is largely a reconstructive act (Schacter and Tulving 1994), and under some conditions this reconstruction can go awry. We suppose that correctly reconstructing an episode requires binding together the different elements of that episode (what was seen, heard, etc.), and that context plays a critical role in this binding process. Failure to bind properly leads to the possibility of incorrect retrieval and consequently, false memory. Our research starts from this set of assumptions and targets context, via its role in episodic binding, as an important element in the understanding of memory distortions.

The Hippocampus and Stress

We argue that manipulations adversely affecting contextual encoding and retrieval should interfere with veridical remembering. Stress could be one such factor. The hippocampus has a dense concentration of receptors for glucocorticoids, hormones released during stress (eg. McEwen *et al.* 1986). Human and animal studies firmly establish that the high levels of glucocorticoids released during stress impair the function of the hippocampus, weakening or completely disrupting those aspects of contextual and episodic memory subserved by this structure (De Quervain *et al.* 2000,Diamond and Rose 1994, Lupien *et al.* 1998, Nadel and Jacobs 1998, Newcomer *et al.* 1999).

We reasoned that if stress interferes with the normal functions of the hippocampus, and the hippocampus is central to context effects in memory, then stress might interfere with those forms of memory depending on context and the binding it supports. To test this idea, we designed a set of studies aimed at assessing the effects of stress on several kinds of binding. This was important because binding itself (like context) is a notion that has been used in multiple ways. For example, vision scientists talk about the binding of features such as shape and color leading to object perception, which is rather different than the kind of binding discussed in the memory literature. We predicted that if binding involves spatial context, then stress might disrupt it. However, if spatial context is not involved, stress should be without effect.

Psychological Stress and False Memory

To date we have completed the first study in this program, and already the results are not coming out exactly as expected. In this study, we focused on a kind of false memory that has been extensively investigated in recent years. We induced false memories in our subjects using the Deese (1959), Roediger-McDermott (1995), or “DRM” paradigm. In brief, subjects study numerous lists of semantically associated words (e.g. candy, sour, sugar, bitter, chocolate, cake, etc.). Each list is followed by a recognition task that consists of three types of words: words that were actually presented (e.g. sugar), unrelated distractor words that were not presented (e.g. hat), and words that are highly related to the theme or ‘gist’ of the list, but that were not presented (e.g. sweet), called “critical lures”. Perhaps not surprisingly, subjects routinely falsely remember many of these critical lures in DRM experiments. In fact, the typical pattern of results reveals high rates of false recognition that under some conditions can equal or even surpass hit rates for correctly identified words (see Roediger *et al.* 1998).

We wondered about the fate of false memories in this paradigm if participants were subjected to stress before performing the task. Stress was induced in half of our subjects using the Trier Social Stress Test (TSST), a procedure that reliably elicits moderate psychological stress in a laboratory setting (Kirschbaum *et al.* 1993). Subjects were required to give a speech in front of a one-way mirror. They were told that three trained investigators were located behind this mirror, ready to evaluate their performance. Speeches are stressful in and of themselves, but to make the experience even more unsettling, the speech was delivered in front of a microphone, and in the presence of two tripod-mounted 1000-watt stage lights. Subjects also believed they were being audio and videotaped for later analysis. The speech lasted for a full 5 minutes and was followed by a moderately difficult 5-minute math task (subjects serially subtracted 13 from the number 1022 aloud and without stopping). The experimental procedure was identical for non-stressed control subjects, except that controls did not have to endure the stress manipulation. Rather than giving the speech, control subjects performed a non-

Komentář:

stressful spatial memory task for an equal amount of time.

Given the typical findings of DRM experiments (a high rate of falsely recognizing critical lures), we predicted no effect of stress on false memory rates. We reasoned that the kind of memory involved in recognizing words from a recently experienced list need not involve spatial context. Indeed, we initially considered this task as a control condition for another manipulation involving false memories in narrative recall, which we believed stress would impact.

In spite of this prediction, we found that stress significantly increased false memory in the DRM paradigm. Stressed subjects falsely recognized more critical lure words than did non-stressed subjects. This result could reflect either a specific increase in false memory under stress, or it could reflect a general increase in overall responding -- a "criterion shift". If the latter were the case, we would expect to see a difference in the rate at which subjects accurately identified presented words, and/or the rate at which subjects falsely recognized unrelated distractor words. However, stressed and non-stressed subjects responded similarly to both types of words; that is, they correctly recognized roughly the same number of presented words and falsely recognized the same number of unrelated distractor words. We concluded, therefore, that the stress effect was specific to false memory for the related lure words.

Further analysis revealed two additional interesting patterns in the data. First, non-stressed subjects appeared to retain some ability to distinguish presented words from critical lure words . For stressed subjects, however, this was not the case, as their rate of correct recognition of presented words was almost identical to their incorrect recognition of critical lure words. Thus, it appears that stressed subjects were entirely unable to distinguish actually presented words from non-presented words that are merely related to the theme of the list. Moreover, when control subjects falsely recognized related lure words, they took an unusually long time to do so – because we presented words on a computer, and recorded responses on the computer as well, we had a measure of reaction time. Control subjects hesitated on the falsely recognized lure words, indicating some level of differentiation between presented words and lures. The stressed subjects, conversely, responded just as quickly when they falsely recognized related lure words as they did when they correctly recognized presented words. Apparently, something about psychological stress makes it difficult, if not impossible, to distinguish between "true" and "false" memory in this paradigm.

This research suggests that stress increases at least one type of false memory -- the false recognition of non-presented semantic associates in the DRM paradigm. Perhaps more importantly, it demonstrates that while non-stressed subjects retain some ability to distinguish between presented items and related critical lures, stressed subjects appear to lose this ability entirely. The question, of course, is why? Given our initial assumption that context would not play a role in this kind of memory task, and hence that stress should not influence false recognition rates, we needed to think more carefully about the potential role of context in the DRM task.

Why False Recognition? The Role of Context

We started by considering why there is such a prominent rate of false recognition in normal, non-stressed subjects, both in this study and elsewhere (Roediger *et al.* 1998). In a recognition experiment of the sort conducted here, correct performance is not a matter of remembering whether or not one has ever seen the words on the recognition tests; most, if not all, these words are quite common and are undoubtedly familiar to the subjects. Rather, correct performance requires remembering that one heard particular words in the specific experimental context. In practice, this means that subjects must experience some form of specific recollection that they heard the target words, and by contrast, fail to have such recollections for the critical lures they correctly discard. We think context plays an essential role in this recollection process.

What we mean by context in this study can be defined as follows: First, there are the features that are specific to the experimental space. This includes not only the objects occupying the space but also their location in relation to each other. For instance, the laboratory consisted of two desks on opposite walls, a computer which sat atop one of them, a curtain that separated the speech area from the testing area, and so on. In addition to the features defining the experimental space, there are other features that define the experimental episode. These features include where one was (in a psychology laboratory), the purpose one had in being there (to participate in an experiment), what one was instructed to do (to listen to lists of words), what one's goal was (to indicate whether or not certain recognition words had appeared on the lists), the words actually presented for study (cake, candy, sugar, sour), the order in which these words were presented (cake came before sour), what the words sounded like (all presented words were spoken in a female voice), and so on. This information, in all its detail, is what renders the various features of our experiment a specific episode.

Some of the above-mentioned contextual features are quite distinctive and clearly unique to the episode of participating in the experiment (e.g. what the experimenter looked like, the spatial layout of the lab, what one's goal was). However, the features that are specific to the task itself *lack* this distinctiveness. Aside from information about the serial position of various words in the lists and the sound of these words as they are presented, there is little information that places the common words that are heard in this particular episodic context. The word lists themselves are highly similar (i.e. each list consists of exactly 15 words, which are all nouns, etc.), and within each list, all words are semantic associates of each other. On the subsequent recognition test, using critical lures that are drawn from the same semantic categories, there is little distinctive information available to subjects as they attempt to decide which words were and which words were not on the lists. This lack of distinctive detail linked to the specific context in the DRM task could be one of the reasons why it is extremely difficult to perform, and why false recognition errors are common, even when subjects are not exposed to stress.

Consider the two currently prominent theoretical explanations of false recognition in the DRM paradigm. The first of these accounts draws on the concept of spreading activation, while the second involves the concept of gist. Spreading activation theories of false recognition assert that exposure to a word causes the activation of semantically related words (e.g. Collins and Loftus, 1975; Underwood, 1965). Presentation of an entire list of related words virtually guarantees that the critical lure will undergo considerable activation. This activation of a nonpresented word may result in a sense of familiarity, or even the recollection that one actually encountered the word on the list. This leaves subjects with the difficult task of deciding whether they really heard the word on the list, or merely thought of it as they were listening to the list. This difficulty is commonly described as a "source-monitoring" problem (Johnson *et al.* 1993).

Second, gist-processing accounts of false recognition (Brainerd and Reyna 1998, Schacter *et al.* 1998) assert that subjects remember the gist of what they have experienced (i.e. the 'theme' of the word-list), rather than the specific details (i.e. the individual words). This reliance on gist leads naturally to false recognition of similar, but non-presented, words because of the high degree of semantic-relatedness between lures and presented words.

Both theories offer an account of why (non-stressed) subjects have such high rates of false recognition, but neither offers an obvious explanation for the effects of stress observed in our study. We suggest that taking the role of context into account might help. For example, it has already been demonstrated that experimental manipulations that increase distinctive, contextually-specific information typically *decrease* false recognition errors. Schacter and colleagues, for instance, presented subjects with pictures in addition to the to-be-remembered words. Studying the words with accompanying pictures, as opposed to studying the words alone, dramatically reduced the number of false recognition errors to critical lures (Israel and Schacter 1997, Koutstaal *et al.* 1999). Similarly, asking subjects to focus on source information (e.g. to attend to the specific voice in which words were presented) also reduced false recognition in a DRM experiment (see Mather *et al.* 1997).

Schacter has argued that the decrease in false recognition rates stems from increased distinctiveness, and from subjects' metamemorial belief that they should be able to remember the distinctive pictorial information. We agree that distinctiveness is involved in the explanation, and point out that this is because it allows subjects to distinguish words they heard in the specific experimental context from words that are related but were not heard in this context. The pictorial information tags the words as being specific to the experimental context. The same argument can be made for manipulations that encourage subjects to attend to source information.

It is reasonable to assume that under normal conditions, subjects in a DRM study can utilize some context information to support their limited ability to distinguish presented words from critical lures. When this information is made more distinctive, performance is enhanced, as we have just noted. However, when access to contextual information is disrupted by stress, even a minimal level of differentiation between presented and non-presented words becomes impossible.

With limited, or no, access to information specifying where the words were learned, the order and voice in which they were presented, etc., our stressed subjects rely on gist-processing and hence are susceptible to the influence of spreading activation. In either case, the result would be the same; an increase in false recognition errors and an inability to differentiate critical lures from presented words under stress. And this is precisely what we found. Stressed subjects in our experiment false alarmed to critical lures over 80% of the time. In addition, because of their disrupted contextual memory and concomitant binding deficits, stressed subjects were unable to remember the contextual details that would otherwise have helped them distinguish between lures and presented words.

Some Caveats

At this stage of our research program it is critical to note a few caveats, having to do with the results themselves, and our interpretation of the results.

In our study we followed widely-used procedures in choosing the words for presentation, the critical (non-presented) lures, and the unrelated distractors. These materials have a number of obvious advantages, but also one disadvantage that might bear on our findings. Because the unrelated distractors were not semantically related to the presented words and critical lures, it proved relatively easy for all our subjects, stressed or not, to correctly reject them. The possibility exists, therefore, that what we have characterized as a selective effect of stress on false memory is really a more general effect on memory overall, but that a floor effect with the distractors prevented us from detecting it. We are inclined to reject this possibility, partly because of our reaction time data, which go beyond the standard false memory result to distinguish normal and stressed subjects in ways unrelated to any such floor effects.

We have chosen to interpret our results as reflecting a direct effect of stress on the hippocampus, and through that, on the availability of contextual information that would allow subjects to reject at least some of the critical lures. We might have included an impact of stress on the prefrontal cortex, which is also known to have a dense concentration of glucocorticoid receptors (McEwen etal. 1986), and to play an important role in certain aspects of contextual coding. In a more general vein, we might have argued that our stressful manipulation had affected performance by interfering with proper allocation of attention by our subjects. We hope to explore both of these possibilities in future research.

Context and Episodic Memory

What do these results tell us about context and the role it might play in episodic memory? Earlier in the paper we defined context as consisting of two different levels of information. One level contains features that are specific to the environmental space in which an episode occurs. This information seems to be best captured by the title “spatial context”, and represents what one of us (LN) has discussed at some length in the past (Nadel and Willner 1980, Nadel *et al.* 1985). The other level contains distinctive features or details that happen to be contained within this space. They are specific to the episode but are not inherently spatial in nature. Nevertheless, these details, such as the voice in which the words are spoken, contribute to the context in the sense that they help to define a particular episode and distinguish it from similar events. What we mean by these two levels of contextual information should become clear in the following examples.

Imagine that you enter the residence of a family friend and are immediately escorted to the living room. Imagine further that an important event transpires in this room; perhaps you have a life-changing career discussion with your friend. The living room is beautifully furnished, with expensive-looking leather armchairs in two corners and ornate tapestries hanging on the far wall. A fire burns in a decorative fireplace located on the wall to your left and, to your right, snow falls outside a large bay window. These are the spatial-contextual features of the room. The most distinctive thing about the living room, however, is the couch, which is deep maroon in color and embroidered with golden suns. It sits in the middle of the room, and is by far the biggest couch you have ever seen. Sitting on it, you also realize that it is the most comfortable sofa you have ever sat upon. There is a good chance that when you call this episode to mind in the future the couch will be included in the memory. Because the couch is so ornate and distinctive, it can be referred to as ‘contextual detail’. We call it a contextual detail, because it helps to define the living room as a unique space and distinguishes it from other living rooms you have been in. Moreover, it may be one of the more richly represented features in the memory for the episode. As distinctive as this feature may be, however, the couch by itself is merely a detail, and a single detail by itself usually cannot define a spatial context. [3]The couch is an important detail in that it likely enriches your memory of the episode involving a career discussion, but it is only one of many details linked or “bound” to the spatial context in which it was contained. Because it is distinctive, however, the representation of the couch perhaps has a better chance of being encoded as part of the spatial context than other, less distinctive features, and thus may serve as a better retrieval cue for the episode. In this sense, spatial context plays a critical role in episodic binding, as the superordinate representation to which the various details (distinctive and otherwise) composing an episode are attached..

Fundamental to all episodes is the fact that they occur in a particular location in space. Given the well-known role of the hippocampus in spatial learning and memory (O'Keefe and Nadel 1978), its involvement in episodic memory is not surprising. Although the specifics of this involvement are still unclear, most researchers agree that the hippocampus plays a specific role in binding together the various bits and pieces of information that make up an episodic memory . That is, it provides a mechanism by which various disaggregated features of a given memory (stored in different neocortical systems) are kept in touch with each other. This organization lends itself to a special role for spatial context in anchoring the various features that comprise an episode, with the hippocampus acting as a kind of spatial scaffold onto which the elements of an episode are attached. This combination gives rise to a comprehensive and accurate episodic memory, complete with spatial context and specific content. The reconstruction of any episode, then, involves a fundamental interaction between elements in hippocampus and elements in cortex.

In sum, we believe that the hippocampus is directly concerned with coding the spatial features of an episode, and suggest that the additional details or distinguishing features of that episode are represented in cortical regions of the brain. Further, representations of gist, based as they are on similarities among presented items or details, are also to be found in cortex rather than hippocampus. Context reflects an interaction among several brain regions, with the hippocampus contributing the spatial information that is critical for reconstructing an episode, and the cortex contributing the details that flesh out the specifics of any particular episode.

To return to our example, the various details associated with the career decision episode (e.g. what one said, what one thought about, who was present during the discussion, what time of day it was, etc.) would be bound together by a hippocampal base, the job of which is to anchor and provide an index to these dispersed neocortical features. In a similar way, the hippocampus binds the numerous fragments comprising a subject's participation in the DRM experiment, including the representations associated with individual words. Presented words, which we assume are stored in cortex, are bound by the hippocampus, thereby providing them with a unique spatial-contextual tag that non-presented lures do not have. Spatial-contextual binding makes it more likely that words that really were a part of the episode will be distinguished from critical lures that overlap with the gist of a list and merely result in a feeling of familiarity.

Stress, The DRM Task, and Episodic Memory

We did not expect stress to affect false memory in the DRM paradigm because we overlooked the important role of context in this task. The DRM task promotes two different types of processing. First, it promotes gist-processing (and/or spreading activation) because of the high degree of semantic similarity amongst the words on the list. Second, it promotes contextual processing because these word lists are part of a larger experience. Thus, the DRM task engages the hippocampus and episodic memory as well as the cortex and gist-based memory. Gist-processing emphasizes the theme of a list, or what the various words have in common, whereas contextual processing emphasizes what makes the words distinct. Contextual processing is what allows non-stressed subjects some degree of success in correctly rejecting critical lure words when they are presented for recognition.

Under non-stressful conditions, two things happen in the DRM task. Gist processing and/or spreading activation occur and the words are bound into a specific memory trace for the experimental episode, anchored by the specific spatial location in which they were encountered. When it comes to deciding whether or not lure words were presented for study subjects could override the sense of familiarity associated with the lures by comparison with the experience of correctly identifying presented words. Recollecting a presented word should entail memory for distinguishing details (voice information, etc.) that are not associated with lure words, thus increasing the likelihood that a subject will be able to distinguish between presented words and lures.

Under stress, however, the scenario changes. While not interfering with memory for the individual words, which are represented in cortex, stress impairs the ability of the hippocampus to code the spatial context, and to bind the words and specific details associated with the words into a contextually-specific episode. Thus, in the presence of stress one loses the ability to use critical distinguishing information – not because the details themselves are necessarily lost, but because of an impaired ability to link the details together as belonging to a specific context. Stressed subjects cannot say that a particular word was presented on a list in a particular experimental context, which in turn makes it nearly impossible to distinguish between a word that really was presented during the experiment and a word similar in meaning that merely feels familiar. Without the hippocampus acting as a spatial-contextual anchor, veridical details (such as the words themselves) are more easily confused with 'false' details (such as critical lures) of a similar appearance and nature.

This account of the tendency towards considerable false recognition in the DRM paradigm has implications for the broader issue of false memory. However, we will have to defer discussion of those implications to another time and place, except for the following analysis of the episode memories lodged permanently in the brain of LN concerning his time in Prague with Jan Bures. The unusual stress of living in Prague in the late 1960s may have rendered the details of these episodic memories somewhat suspect, but their gist remains intact. Jan (and Olga) provided numerous examples not only of how to function as a scientist, but also how to live as a person in a complicated moral and political universe. Such examples may have been derived from particular events in a very unique context, but they have survived as general rules, and have found application in a variety of settings ever since. In this complex interaction between specific experience, and the residues left behind, lie answers to many questions about memory, true and false.

Appendix

[1] Jan and LN's first political exchanges took a while to unfold, given the climate in Czechoslovakia at that time. However, within several months the Prague Spring had started, Dubcek was in power, and a fascinating but ultimately very distressing year had begun. During that year, Jan (and Olga) were constant sources of interpretation, speculation and education. It was a thrilling time, but it all came to a crashing halt on August 20, 1968 with the uninvited arrival of Warsaw Pact troops, first noticed by LN at about 7 AM when tanks came rumbling up the road outside his house in the countryside on the outskirts of Prague (located near the Physiology Institute housing the Bures/Buresova lab).

[2] Personal exchanges began with the "adoption" by Jan and Olga of LN's two young children, whose mastery of Czech far exceeded his own, and whose romps through the lab showing off their knowledge remain as memories in the minds of all observers (except those of the now-grown kids, who of course remember not a single thing from a time when they spoke Czech and quoted Marxist slogans inculcated in them in materska skola [nursery school]). In that first year Jan and Olga's personal advice culminated in the strong suggestion that for the sake of the children's safety LN leave the country shortly after the invasion and occupation. Which he did. Some eight months later, when he returned with the children (now minus their mother), Jan and Olga helped him through 16 months of single fatherhood in a strange land -- paradoxically perfect for that situation given the very good arrangements for childcare in Prague.

[3] The exception is in very impoverished environments where a single detail may be enough to define the spatial context. More typically, spatial contexts are riuchly embroidered, and the removal of any single detail leaves them intact. In our example, removing the couch would certainly be noticed, but it would not lead to the conclusion that one was in a different context. It is a critical, but unsolved, empirical question just how many details, or what proportion of detail, must be altered before one concludes that one is in a new, rather than changed, context. Recent studies of "re-mapping" of hippocampal places cells are beginning to address this issue.

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