

Chapter 6

Slow Potentials During Long-Term Memory Retrieval

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Almost half a century ago, Karl Lashley summarized his decade-long effort on the localization of the engram with the following, somewhat pessimistic statement: "it is not possible to demonstrate the isolated localization of a memory trace anywhere in the nervous system. Limited regions may be essential for learning or retention of a particular activity, but ... the engram is represented throughout the region" (Lashley, 1950). As far as neocortical structures are concerned, this position seems to be still valid. Neither experimentally induced lesions in animals nor those which occur naturally in human subjects support the idea that specific mnemonic contents can be narrowly localized anywhere in the cortex. A localization of memory functions could be established only insofar as that specific anatomic structures were found to be essential for the *process* of storage and retrieval but not for the engram itself. Moreover and surprisingly, these structures, which may be seen as relay stations within larger functional circuits, are for the most part not localized in the neocortex but in more ancient regions of the brain, for example, in the diencephalon, the basal forebrain, the hippocampus or the amygdalae (see, for example, the summarizing theories of (Mishkin and Appenzeller, 1987, or Markowitsch, 1985)). How these relay stations communicate with neocortical regions during storage and retrieval and where in the neocortex specific memory contents are held are still open questions.

In the light of these circumstances it may sound hubrical if someone

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claims that it is possible to monitor the contribution of neocortical structures to memory functions by means of the electroencephalogram. Nevertheless, the data that we summarize in this chapter do indeed suggest a close relationship between neocortical structures and memory retrieval processes. Moreover, these data also suggest that some neocortical structures are specifically related to the processing of particular mnemonic codes.

The methodological basis of our studies are the so-called slow event-related potentials (slow ERPs). ERPs can be classified along the continuum of their temporal extension: At one end there are the short-lived, transient shifts that have a clear peaklike appearance; at the other end there are slow deflections which may prevail for a couple of hundred milliseconds or more. The latter can show either a short rise and fall time and a more or less constant amplitude between on- and offset or a more gradual, ramplike increase and resolution. In any case these slow potentials have not a well-defined peak but a broad temporal extension. The best known slow wave phenomena are the processing negativity (Nd; Hansen and Hillyard, 1983), the readiness potential (RP; Kornhuber and Deecke, 1965) and the contingent negative variation (CNV; Rohrbaugh and Gaillard, 1983; Walter et al., 1964) and all three are manifestations of longer lasting functional states of the brain: attention to particular stimulus "channels," preparation for motor performance, and event anticipation, respectively.

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These three, however, are not the only slow wave phenomena that can be related to particular cognitive states. Scanning through the literature reveals that slow negative waves have been observed in a wide variety of tasks, among others during short-term memory scanning and perceptual scanning of displays (Horst, Ruchkin, and Munson, 1987; Looren de Jong, Kok, and van Rooy, 1987; Wijers et al., 1989), during planning and execution of motor responses (Deecke et al., 1987; Lang, M. et al., 1988), during more conceptual tasks as mental arithmetic (Rösler and Heil, 1991; Rösler, Schumacher, and Sojka, 1990; Ruchkin et al., 1988), picture naming (Stuss et al., 1984; Stuss, Picton, and Cerri, 1986), mental rotation (Farah and Peronnet, 1989; Rösler, Schumacher, and Sojka, 1990), concept formation (Lang, M. et al., 1987; Uhl et al., 1990) or anticipation and processing of feedback stimuli (Brunia and Damen, 1988; Delisle, Stuss, and Picton, 1986; Grünwald et al., 1984; Rösler and Heil, 1991). For summaries, see Birbaumer et al. (1990); Haider, Groll-Knapp, and Ganglberger (1981); McCallum and Curry (1993).

A closer look at these data suggests that slow waves may be of particular interest for monitoring "higher" cognitive functions. First, slow waves seem to have a task-specific topography. Tasks with semantic material are accompanied by slow waves that have a maximum over more frontal regions of the brain, while tasks which require the processing of nonsemantic material, for example, mental rotation of images, evoke slow negative shifts with a more parietal maximum. Second, slow waves seem to have an amplitude that is related to task difficulty or processing effort. For example, the negativity

that can be observed during short-term memory scanning shows a systematic increase of amplitude with increasing memory load (Wijers et al., 1989). Likewise the negativity that accompanies mental rotation tasks increases with the angular disparity between the two objects to be compared (Peronnet and Farah, 1989; Rösler, Schumacher, and Sojka, 1990). Finally, some studies provide evidence that the duration of these slow waves is related to the duration of particular processing stages. Nd is a convincing example; it persists as long as the evidence of a particular channel has to be analyzed and discriminated against the evidence of another, competing channel (Hillyard and Hansen, 1986). In summary, these psychophysiological findings suggest that slow waves, in particular negative slow waves, seem to be a manifestation of longer lasting cognitive states. Their topography may reveal differences in task quality; their amplitude, differences in the amount of effort that has to be invested to solve a task, and their duration may be related to the duration of particular processing stages.

This functional hypothesis is further corroborated and extended by neurophysiological findings about the generating mechanisms of slow waves. There is convincing evidence that slow waves originate predominantly from cortical structures (Creutzfeldt, 1983; Speckmann, Caspers, and Elger, 1984). According to the present knowledge, slow waves seem to reflect changes of the basic activity level of cortical tissue, that is, synchronized changes of the resting potentials of cortical neurons at their apical dendrites. Moreover, the polarity of slow waves provides clues about the type of change. In general, it seems to hold that slow negative potentials result from an increase of excitatory postsynaptic potentials (EPSPs) in the upper layers of the cortex; thus, they indicate an increase of activity or an increase of the responsiveness of the underlying cortical areas. Slow positive potentials, on the other hand, go together with a decrease of EPSPs or even an increase of inhibitory postsynaptic potentials (IPSPs). Therefore, they indicate a relative decrease of activity or a relative inhibition of particular cortical areas. Elbert and Rockstroh (1987) suggested that slow waves are manifestations of a threshold regulating mechanism that adjusts cortical areas according to expected actual processing demands.

Considering these presumed generating mechanisms of slow waves the hypothesis about their functional significance can be extended toward a neuropsychological dimension. A particular slow wave pattern being evoked during a particular cognitive task may reveal which cortical areas are in a relatively higher or lower state of activation. Thus, monitoring slow waves during cognition may provide an online method for a functional differentiation of cortical areas. This neuropsychological hypothesis is corroborated by studies in which regional cerebral blood flow and slow waves were monitored in the same task conditions. These studies revealed that negative potentials appear with substantial amplitude selectively above those cortical areas which also show a high metabolic activity (Lang, M. et al., 1988).

In this chapter, we report some recent studies in which slow waves were

monitored during long-term memory (LTM) retrieval. To overcome some limitations of traditional LTM retrieval tasks, we made use of a special experimental paradigm, the so-called FAN-effect paradigm that was introduced into memory research by Anderson and colleagues (e.g., Anderson, 1974; Reder and Anderson, 1980; Reder and Ross, 1983). The empirical basis of this paradigm is the following observation: The time to decide whether two memory representations have an episodic link or not depends on the total number of links that branch out from each representation. If each representation has connections to many other representations, the decision will be very difficult and time-consuming; if, on the other hand, there are only very few other connections, the decision will be easy and fast. An example may help to illustrate this fact: Consider you have to decide whether two researchers, authors A and B, ever published a paper together. Assume that both authors published only two papers in their total career. In that case you would be pretty fast with retrieving the necessary fact. But now consider that both authors were very active, that they published about 50 papers, and that you are familiar with all. In that case it would need a very thorough search through all the entries that exist in your memory about the publications of these two authors until you come up with the correct conclusion. And this more extensive search would result in a considerably longer decision time.

It is easy to conceive how the FAN-effect may be used to manipulate memory retrieval processes systematically. What is necessary is an experimentally established memory structure in which the FAN of different representations varies in a well-controlled manner. Retrieval tasks can then be constructed that activate different subsets of an associative structure and which therefore vary in difficulty. The paradigm can also be used to study differences in the quality of retrieval processes. For example, an associative network can be elaborated for different types of material, semantic entities as words or concepts, and nonsemantic entities as spatial positions or colors, respectively. Within one type of material the quality of associations can be manipulated as well, for example, associations can be elaborated between elements that belong either to the same or to a different level of an hierarchically ordered set.

Experiment 1: Associations Between Semantic Concepts

In our first experiment of this series (Rösler, Heil, and Glowalla, 1993), subjects had to learn associations between semantic concepts. The items to be learned were nouns that were presented as elements of distinct lists. Each list comprised seven elements: a list title, three specific concepts or tokens, and three general concepts or types. The general concepts were always superordinates of the specific concepts (see Table 1 for examples). One particular specific concept appeared either in only one, in only two, or in

Table 1. Design of Experiment 1.*

List #	Label	Token	Type
1	STATION	furniture island fruit	<u>table</u> Malta banana
2	LAWYER	sports car dog	<u>football</u> Porsche beagle
3	SCHOOL	furniture car vegetables	<u>table</u> Porsche <i>carrot</i>
4	RESTAURANT	furniture city dog	<u>table</u> Berlin <i>dachshund</i>
5	LECTURE	sports city fruit	<u>football</u> Berlin orange
6	APARTMENT	sports island vegetables	<u>football</u> Malta beans

*The table shows a subset of the memory structure that was established by means of an extensive learning procedure. Ss had to learn associations between a particular list label, category names (tokens) and category exemplars (types), respectively. In the example probes of exemplars with FAN 1 are given in italics, probes with FAN 3 are underlined. See text for further explanation.

three different lists. If it appeared in only one list (e.g., as carrot or dachshund in Table 1) it was episodically linked to the elements of only one list. Thus it had a FAN of one. In case a specific concept appeared in two different lists it was episodically linked to the other elements of both lists and it had a FAN of two (e.g., Porsche or Berlin in Table 1). Finally, a specific concept appeared in three lists it had a FAN of three. It was episodically linked to all other elements of the three lists.

If the subject is now asked to decide whether two concepts belong to the same list or not a different subset of the associative structure has to be activated and searched. This subset increases systematically from concepts having FAN 1 to those having FAN 3. The retrieval times for negative probes, that is, pairs of test words that are not elements of the same list and on which the subject has to decide with "no, there is not a common link," are given in Figure 1. It can be seen that there is an almost linear increase of the retrieval/decision time with increasing FAN for specific concepts. This supports the claim that the retrieval process varies in difficulty, if specific concepts with a different FAN have to be checked for their connectedness.

For general concepts, the story is different. If one considers how the material is constructed, one has to conclude that these general concepts always have an explicit FAN of three. Thus it is not too surprising that the

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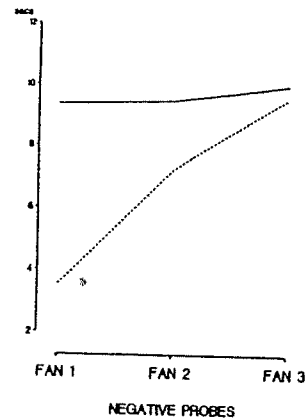


Figure 1. Average retrieval times obtained in the semantic FAN experiment. Subjects had to decide whether two concepts shared a common episodic link (belonged to the same list) or not. Shown are the retrieval times for negative probes, i.e., pairs of concepts for which the correct decision was "no, they do not share a link."

waves, and (2) qualitatively different retrieval processes should be associated with topographically different slow wave patterns.

Methods

Nine healthy subjects (students of the Philips-University of Marburg) came to the lab on two consecutive days. On the first day they had to learn the material by heart. This was a set of 18 lists constructed as outlined in Table 1. Knowledge about these lists was 100% at the end of the training session (see Rösler, Heil, and Glowalla, 1993, for details). On the second day the retrieval test took place with the EEG recorded; 400 test trials were presented in five blocks with 80 trials each. Subjects initiated trials by briefly lifting one of two fingers. After a delay of 1 sec two test words appeared in the center of the screen and remained visible for a total of 15 sec, independently from whether or not the subject responded within the 15 sec. The subjects were instructed to respond as quickly and as accurately as possible. A bonus was paid depending on the percentage of correct responses. The two responses (*yes*: "the two concepts are elements of the same list", or *no*: "they are not") were given by lifting either the index or the middle finger of either the right or the left hand. The responding hand was varied across subjects.

The EEG was recorded monopolar from left, central, and right frontal cortex (F3, Fz, F4), from the vertex (Cz), and from left, central, and right parietal cortex (P3, Pz, P4) with linked mastoids as reference. Eye movement and blink artefacts were monitored with one electrode pair placed right to the upper canthus and left to the lower canthus of the left eye. Blinks were corrected according to Gratton, Coles, and Donchin (1983); epochs with other artefacts were rejected. Low-frequency cutoff of the recording system was set to -3 dB at 0.0013 Hz ($\tau_c = 120$ sec) and upper-frequency cutoff was set to -3 dB at 35 Hz. Electrode impedance was kept below 1 k Ω in all cases. The activity of all channels was AD converted with 12-bit resolution and a rate of 64 samples/sec.

Results and Discussion

The experiment revealed several systematic slow wave effects that seem to be related to search in long-term memory. First, the overall topography reveals a pronounced, DC-like negativity over the left frontal cortex (Fig. 2). This negativity appeared in all retrieval conditions irrespective of a particular type of probe (general or specific), a particular level of FAN, or a particular response (yes or no). As the following experiments reveal, this negativity seems to be specific to retrieval processes that have to be performed on semantic contents. A left frontal negative slow wave was also observed by Lang, M. et al. (1987), while subjects had to learn paired associates of words. Similarly, Stuss, Picton, and Cerri (1986) described a kind of slow wave that appeared during object naming and which was also

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retrieval times for general concepts do not vary in dependence of whether they are associated with a specific concept having a FAN of one, two or three respectively. A closer analysis of the retrieval process itself, however, suggests that retrieving associations between general concepts does not involve exactly the same processes as retrieving associations between specific concepts (Heil, Rösler, and Hennighausen, 1993). The difference concerns the route how the particular links are accessed. With specific concepts this access is straightforward. The system checks whether there is a common episodic link or not. With general concepts this access is indirect; it is accomplished via the specific links. The general concepts are in a certain sense redundant to the specific ones; they have not to be learned explicitly. If a subject has to decide whether an island and a car belongs to the same list, he or she can retrieve this fact by first activating the specific counterparts (e.g., Malta and Porsche). And this seems to be what subjects actually do in this situation. One can conclude, therefore, that the retrieval process varies in difficulty for specific concepts having a different FAN but that it varies also in quality, if one compares access to specific and to general concepts, respectively. With general concepts an additional process has to be assumed that first generates specific instances.

We expected that these two experimental manipulations should become manifest in distinct slow wave effects. In particular, we hypothesized: (1) a variation of the difficulty of retrieval processes should produce either different amplitude levels or different durations of retrieval-related slow

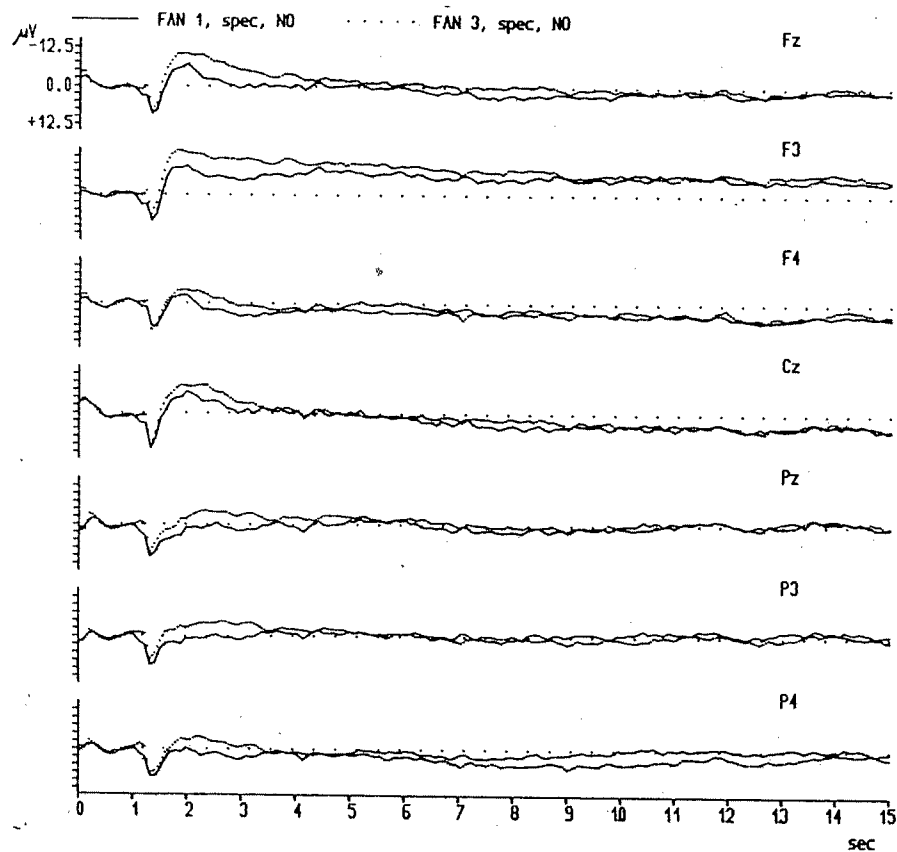


Figure 2. Event-related activity during retrieval of associations between semantic concepts. Grand averages were obtained with negative probes having either a FAN of one (continuous line) or a FAN of three (dotted line). Probe onset was at 1 sec. Notice pronounced sustained negativity at F3.

substantially negative over frontocentral regions. Considering the functional interpretation of negative slow waves given earlier, all these findings agree on the hypothesis that the left frontal cortex is particularly involved when semantic material has either to be stored into or retrieved from LTM. This would also be in line with neuropsychological evidence provided by lesion studies (e.g., Risse, Rubens, and Jordan, 1984).

The second finding of this study concerns the experimental manipulation of retrieval difficulty. The amplitude of the negative potential that was observed over the frontal cortex varied systematically with different FAN; it was largest with FAN 3, intermediate with FAN 2, and less pronounced but still substantial with FAN 1 (see Fig. 2). This result suggested that the overall negativity over the frontal cortex is modulated by task difficulty.

Moreover, the fact that the main experimental manipulation became manifest exactly at those locations where the overall negativity had its maximum substantiates the assumption that this frontal negativity is specifically related to the process of retrieval or activation of permanently stored semantic associations.

Finally, the experimental factor type of concept general versus specific became also apparent as a slow wave effect. Decisions on the relatedness of general concepts were always accompanied by a more pronounced negativity than decisions on the relatedness of specific concepts. However, this amplitude difference had a more parietal distribution, and it emerged later in time than the amplitude difference observed between the different FAN conditions. The difference from factor FAN was already present 500 msec after probe onset, while the difference from type of concept emerged no earlier than 1000–1500 msec after probe onset.

In summary, the first experiment in which the FAN paradigm was employed revealed that slow waves seem to be systematically related to memory retrieval processes. The slow wave pattern had a specific topography, and two topographically distinct amplitude variations were found to be related to particular retrieval conditions. Both effects were associated with a modulation of a negative slow wave pattern in such a manner that the always more demanding condition evoked a more substantial negative-going amplitude. This is in line with our general working hypothesis, which assumes a systematic relationship between the amplitude of negative waves and the amount of effort that has to be invested to solve a task. The topographic difference between the two effects, that is, that factor FAN had a more frontal expression and factor type of concept a more parietal one, is in line with the psychological analysis of the task. It has to be assumed that both experimental manipulations tap different mechanisms of the involved retrieval processes. Factor FAN concerns a difficulty manipulation; it relates to the fact that a different number of associations has to be searched. The factor type of concept, on the other hand, concerns a manipulation of retrieval strategy. When subjects had to decide on the relatedness of general concepts, they activated specific instances before they searched these for common links. Subjects had reported during debriefing that they often accessed or generated these specific instances by means of imagery. This nonsemantic strategy would explain why the effect had its maximum expression over the parietal cortex.

Experiment 2: Associations Between Semantic Concepts Revisited

The first study was performed with limited equipment. There were only a few electrodes and moreover the EEG was not recorded with genuinely DC- but with AC-coupled amplifiers having a time constant of 120 sec. To

test for the reliability of the effects just mentioned and to get a more complete picture about the topography, we repeated the experiment.

Methods

Another sample of 11 healthy students were trained and tested with the same semantic material as used in experiment 1. Training and testing were accomplished as previously outlined. However, apart from the recording equipment there were some other minor methodological changes. A test trial was no longer initiated by the subject but presented in a computer-controlled mode with a varying intertrial interval of 2 sec. A trial began with the presentation of a fixation point. After a baseline recording epoch of 3 sec, there was an acoustic warning stimulus, which was followed by the test words 1 sec later. The test words were visible for 14 sec. The EEG was recorded with proper DC characteristics from 17 locations: from F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, O1 and O2. The EOG was monitored for artifact control by means of three channels, which recorded the vertical, lateral, and radial vector component, respectively, of eye movements and blinks. The DC recordings were corrected for drift artifacts by a method suggested by Hennighausen, Heil, and Rösler (1993). Trials with other artifacts, as substantial eye movements or blinks, were rejected by inspection of all single trials. Slow wave activity was measured by means of average amplitudes for consecutive intervals of 500 msec. All effects were tested by means of MANOVA, and only those with a reliability of at least $p(F) < .01$ are reported.

Results and Discussion

The overall topography observed with this replication was very similar to the one already described with the limited set of electrodes. There is again a clear left frontal preponderance of a negative slow shift that is switched on after probe onset and which gradually resolves with progressive time, that is, with increasing likelihood that a decision about the relatedness of the two probe words had been achieved (Fig. 5, top row). There is also some negative activity going on over the occipital cortex, a phenomenon that we were not able to observe in Experiment 1. This negativity is not too surprising, because the probe was presented throughout the total recording epoch and subjects could process the visual stimuli permanently.

The slow wave amplitude difference resulting from different levels of FAN could also be replicated. Again FAN 3 evoked the most pronounced negative amplitude and FAN 1 the least pronounced. This difference appeared immediately after probe onset and again had its maximum expression over frontocentral locations with a preponderance to the left hemisphere (see Fig. 3).

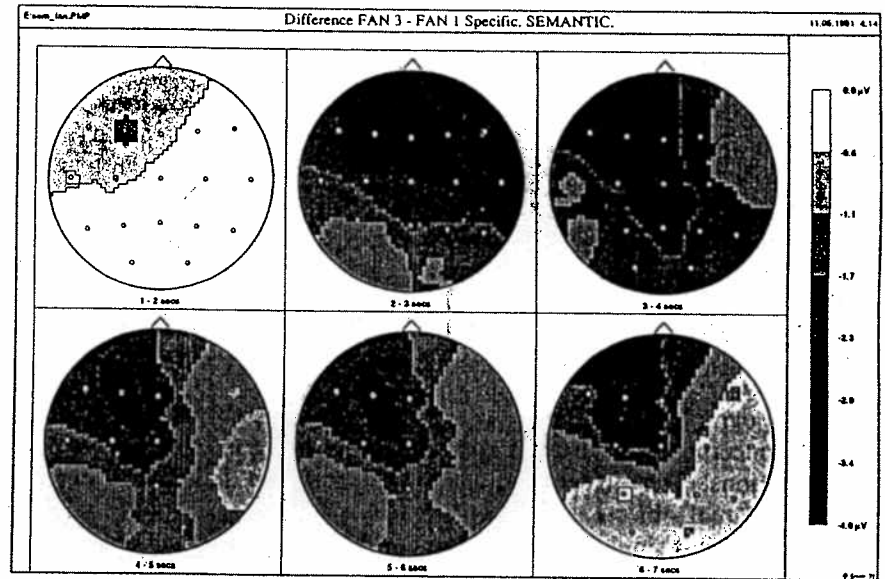


Figure 3. Difference maps of event-related activity during retrieval of associations between semantic concepts show the difference between the grand averages obtained with negative probes having a FAN of three and a FAN of one. More negativity in condition FAN 3 results in a larger difference amplitude. The maps show the average amplitude difference of consecutive time intervals after probe onset beginning with interval 1, 2 sec (top left) and ending with interval 6, 7 sec (bottom right). Notice pronounced sustained negativity over left frontocentral cortex.

The slow wave difference from the factor type of concept was not as pronounced as in Experiment 1. The overall topography of this effect when expressed as a difference wave (general specific) revealed as before a maximum that was more posterior and later than the maximum observed in the difference wave obtained from subtracting the potentials of FAN 1 from those of FAN 3. However, the effect extended more toward frontal sites than in Experiment 1. One explanation for this different outcome of the two experiments may be found in interindividual differences. As outlined earlier, the effect from factor type of concept seems to be a correlate of a specific strategy that is employed when links of general concepts are retrieved. This strategy, which says that specific instances are activated on the presentation of general probes by means of imagery, is very likely not used by all subjects to the same extent. Debriefing revealed that there were also some subjects who had actually learned the general concepts explicitly. In addition, the ability to make use of the process of imagery may also vary across subjects. Unfortunately, we did not control these factors explicitly. Therefore, it could be that our second sample included fewer subjects who used this particular retrieval strategy.

Nevertheless, the replication revealed two very reliable effects. The clear left frontal maximum of the negative slow wave was found in both studies, and the variation of retrieval difficulty became apparent in both studies with the same topography and the same polarity: the left frontal negativity increased with increasing difficulty.

Experiment 3: Associations Between Pictures and Spatial Locations

The objective of this study (Heil, Rösler, and Hennighausen, 1990; Rösler, Heil, and Hennighausen, 1993) was to investigate whether and how the overall topography of the slow wave pattern changes, when the retrieval process concerns associations between completely nonsemantic memory representations. To this end, subjects had to learn links between line drawings of real objects and locations in a checkerboard-type grid (Fig. 4). The situation is similar to that created in the children's game "Memory."

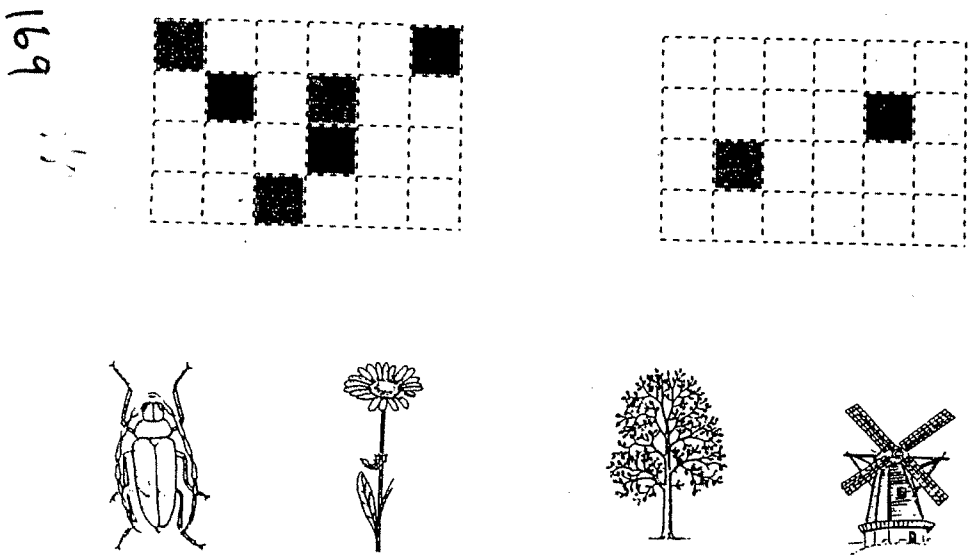


Figure 4. Construction principle of material used in Experiment 3. Subjects learned associations between locations in a grid and linedrawings, the latter showing either animate or inanimate real objects. The left panel presents two objects that had a FAN of three, i.e., they were each associated with three different locations in the grid (e.g., the beetle was associated with the locations shown in light grey, the flower with the locations shown in dark grey). In the right panel, two objects are presented that both had a FAN of one. See text for further explanation.

The grid pattern had three rows and six columns of uniformly gray squares. During learning, a line drawing was presented below the grid and one square of the grid was specified by a brightness change. The subject had to memorize the associations between the line drawing and the particular location in the grid. The material was constructed according to the same principles as outlined in Experiment 1, that is, there was a systematic variation of FAN and a variation of the type of object. FAN was varied as follows. A particular line drawing could be associated with only one location, with two locations, or with three, respectively. The type of object manipulation concerned the concreteness of the object that was depicted by the line drawing. Specific objects were realized by pictures of actually existing and prototypical objects (e.g., a tower windmill, a post windmill, a modern windmill motor). General objects were more abstract pictures that represented no details but just the typical features of an object category.

Methods

A sample of 11 healthy students, who had not participated in Experiments 1 or 2, was recruited. Again, they were trained with the material extensively until they had a complete command of it. On the next day they were tested and the EEG was recorded. A test trial always included two line drawings that were presented side by side without the grid. The subject had to decide whether both objects shared a common grid position. The response was given by lifting one of two fingers. The test trials were constructed such that the two items were either both of type specific or of type general, and that both had either a FAN of one, two, or three, respectively. In addition, there were some filler trials. These showed two line drawings that had either a different FAN or which were of a different type. (These filler trials were not analyzed.) The EEG was recorded from the same 17 locations as in Experiment 2. Likewise, the EOG was recorded with three channels. Artifact handling and statistical analysis was as in Experiment 2.

Results and Discussion

For brevity only the overall topography obtained with this variant of the FAN paradigm is reported here (for a full account of this study see Rösler, Heil, and Hennighausen (1993)). There was again a very pronounced negative slow wave that emerged shortly after the presentation of the test trials and which gradually resolved toward the end of the recording epoch. The topography of this slow wave, however, was completely different from that observed with the semantic FAN (Fig. 5). The maximum was now found over the parietal cortex while there was hardly any negativity over frontal areas. The frontal sites were even somewhat positive. This supports our hypothesis that the slow wave pattern being observed during memory retrieval has a code-specific topography. Moreover, the topography evoked

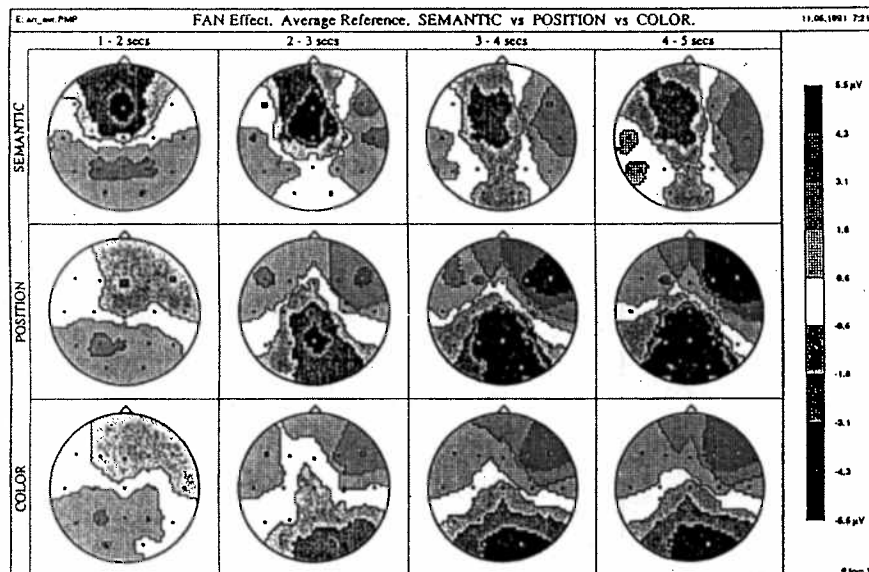


Figure 5. Event-related brain activity observed during retrieval of different types of associations from long-term memory. Top row: data from experiment 2, retrieval of semantic associations; middle row: data from Experiment 3, retrieval of associations between pictures and spatial locations; bottom row: data from experiment 4, retrieval of associations between pictures and color patches. Presented are grand averages of the overall topography observed within consecutive intervals of 1 sec after probe onset. Maps were computed by means of spline interpolations. To permit a comparison across experiments, data were rescaled with respect to an "average reference." Relative negativity is presented as a densely stippled pattern; relative positivity as a coarsely stippled pattern.

by this nonsemantic retrieval condition is in line with neuropsychological findings on the functional division of the cortex. The negativity was most pronounced exactly above those cortical areas that are functionally related to the processing of spatial representations (e.g., Kosslyn, 1987).

Experiment 4: Associations Between Pictures and Color Patches

With our final experiment (Heil, Rösler, and Hennighausen, 1990; Rösler, Heil, and Hennighausen, 1993) we wanted to test more thoroughly the material-specific topography of memory-related slow waves. An obvious question concerns the functional distinctiveness of the topography: is it only related to gross functional differences, as semantic versus nonsemantic, or is

the functional resolution possibly much finer such that also more subtle differences can be detected? As far as the sensitivity of the method is concerned, the results of Experiment 1 were already promising. They had revealed a topographical difference within the domain of semantic material alone. This difference was found to be related to the strategy employed for retrieving specific versus general concepts. On the other hand, this effect was very likely also bound to a semantic versus nonsemantic distinction, because, as it was argued, the presentation of general concepts may have induced a nonsemantic strategy for generating specific instances. With the current experiment, we pursued a more direct approach to determine functional differences. We used another nonsemantic type of material, color-picture associations, and hypothesized that the retrieval processes should evoke a slow wave pattern topographically different from that observed in Experiment 3.

Methods

The same line drawings as in Experiment 3 were used, but instead of spatial locations they were paired with different color patches. During learning each line drawing was presented above a grid with three rows and six columns of color patches. A color patch to be associated with a particular picture was flashing throughout the presentation of a trial. To exclude any positional clue the color patches were rearranged in the grid on the presentation of each new learning trial. Thus the subject had indeed to learn associations between pictures and colors, not pictures and locations. All other details of the material were as in Experiment 3: there was the same variation of FAN—one, two, or three colors could be associated with one particular picture, and there were again the specific line drawings showing real objects and the general ones showing abstract category representations. All other methodological and procedural details were the same as in Experiment 3. Eleven healthy students who had not participated in any of the former experiments were recruited for this study.

Results and Discussion

Again we report only about the overall topography. (For more details see Rösler, Heil, and Hennighausen (1993)). As before, the retrieval process is associated with a well-pronounced negative slow wave. The time course is similar to Experiment 3; it has a short rise time and a gradual resolution. However, as expected, the topography is different. Compared to the topography observed with the spatial locations the maximum of the negativity has now moved more toward occipital sites (see Fig. 5). This result clearly demonstrates once more that the topography of the slow wave pattern observed during memory retrieval is code specific. However, it is not just the gross distinction between semantic and nonsemantic codes that becomes

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manifest in a distinct topography. Obviously, differences within the domain of nonsemantic codes can be detected by means of this approach as well. It is important to note that the overall topography observed in this study is also in agreement with neuropsychological findings on the cortical representation of color-processing mechanisms. As summarized by Meadows (1974), all types of color agnosias are caused either by lesions within areas 18 and 19 or by a disconnection of these areas from other functional units.

Summary and Conclusions

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The set of experiments reported here proves that it is possible to monitor long-term memory functions by means of slow event-related brain potentials. All four experiments revealed a pronounced negative slow wave that is temporally related to the process of retrieval. In each case this negativity emerged immediately after the presentation of a memory probe, and it resolved at about the same time when an overt response indicated the end of the search process. The topography of the negative slow wave was found to be closely related to the quality of the retrieval process; it changed when different memory codes were accessed. The maximum of the plateau-like negativity was found over frontal areas with semantic material, over parietal areas with spatial material, and over occipital areas with color material. Moreover, the topography was also affected when distinct retrieval strategies were induced by different probes belonging to one type of material. Finally, the amplitude of the negative slow wave was found to be systematically related to the difficulty of the retrieval process. Probes that induced a more extensive search, as indicated by response times, were always associated by a larger negative amplitude. This amplitude modulation was most pronounced at those electrode locations where the negativity had its absolute maximum. Taken together, these findings suggest that the observed slow wave effects were indeed specific to the memory retrieval task.

The topography of the three slow wave patterns was congruent with the functional division of the cortex as it is suggested by lesion studies. For a particular material, the negative maximum was always found exactly over those cortical areas that are known as functionally specific for processing the related code. This close correspondence supports the assumption that the neuropsychological generators of slow negative shifts are actually located in the underlying cortical tissue. The finding is also consistent with the idea that the negative maximum of a slow wave pattern indicates which cortical areas are in a relatively higher state of activity than others during particular steps of human information processing.

If this interpretation of a slow wave pattern proves to be correct, it will open an interesting perspective for the field of neuropsychological diagnos-

tics. Slow waves could then become a very sensitive tool for monitoring the functional division of the cortex. The method could be used quasi online and it would also allow studying functional distinctions in healthy subjects. Moreover, as slow waves have a much higher temporal resolution than other noninvasive methods, for example, rCBF or PET scans, they could help to disclose very subtle differences of cognitive processes.

The data presented here are already convincing in this respect. If one looks at the behavioral data that were collected in the four experiments—response times and error rates, respectively no material-specific effect would have been detected at all (see Heil, Rösler, and Hennighausen, 1993). Retrieval times were virtually the same irrespective of the kind of associations tested—semantic, spatial, or color associations, respectively. For one thing, this was intended. We wanted to create tasks that were equivalent as closely as possible. There should be no difference in the difficulty of the retrieval processes, just the type of code should be manipulated. However, from a theoretical point of view these behavioral data could also be taken as evidence for the fact that the retrieval processes were exactly the same in all three conditions. Adherents of a theory that assumes a uniform propositional code for all entities stored in long-term memory would be delighted with this finding (e.g., Anderson and Bower, 1973). However, our psychophysiological findings cast some doubt on such a unifying position. Although the retrieval processes may in fact be equivalent with each kind of material, the topographic differences indicate nevertheless that these processes seem to operate on different structures. These structures may constitute different subsets of long-term memory representations. This still leaves open the possibility that everything is transformed into a propositional code, but on accessing this code different transformations seem to be involved.

Of course, monitoring slow event-related brain potentials during memory retrieval does not solve the riddle of the engram: how mnemonic contents are coded, where they are stored and how they are reactivated. However, the findings reported here give at least some clue about the functional role of cortical structures during memory retrieval. Obviously the cortical structures involved during explicit memory retrieval are also those necessary for perception. The engram may be distributed across these structures and, as proposed by Markowitsch (1985, p. 214) “for retrieval to occur, limbic system-related structures, (...) may act as an organ of resonance which induces the (primarily) cortical neuronal network with the particular information to fire in a way which represents the mnemonic event”.

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Chapter 7

Event-Related Potentials Dissociate Immediate and Delayed Memory

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Evidence from human amnesia suggests that immediate or working memory and long-term memory involve activation of two distinct neural systems, with a transfer of information from immediate to long-term memory occurring from 15 to 60 sec post encoding. Amnesiac patients can correctly repeat six or seven items and carry on apparently normal conversations. This immediate memory process has a limited capacity, so that the addition of new items will impair performance on old items in these patients (Squire, 1986). Further, if they are distracted for a few minutes, the patients will not recall the items or their conversation. Conversely, amnesiac patients are able to recall events that occurred before they sustained hippocampal system damage (Scoville and Milner, 1957). This suggests that while their working memory, long-term memory storage, and recall mechanisms are intact, the hippocampal damage has impaired their ability to transfer information from immediate memory to long-term storage. This transfer problem is referred to as a deficit in short-term memory or anterograde amnesia.

Endogenous event-related potentials (ERPs) have been used to study the chronometry of cognition since it was discovered that these electrophysiological measures were responsive to the psychological state of the subject. First reports of this phenomenon showed that a late positive component of the ERPs was generated at 300 msec after stimulus delivery of unexpected or deviant tones in a tone sequence (Desmet, Debecker, and