Electrophysiological Correlates of Specific Feature Binding in Remembering – Introducing a Neurocognitive Model of Human Memory

Ullrich K. H. Ecker, Christian Groh-Bordin & Hubert D. Zimmer

Brain & Cognition Group, Department of Psychology, Saarland University, Saarbruecken, Germany

Abstract: In our neurocognitive model of long-term memory, we distinguish at least three kinds of memory representations. These are: (a) type-traces – gradual changes in activation of (semantic) long-term memory subserving implicit memory effects, (b) object tokens – consolidated object files representing the perceived features of an object, and (c) episodic tokens – representations of items in their spatiotemporal context. On the background of this model we investigated whether these memory representations differ in their binding of perceptual features of a study episode. We report data from experiments in which the sensory congruency of stimuli was manipulated between study and test. The effects of this manipulation on behavioural and electrophysiological measures serve as a basis for our inferring distinguishable representation formats. The distinction between types and tokens is supported by the differential sensitivity of implicit and explicit tests towards perceptual specificity in behavioural and ERP data. The distinction between object and episodic tokens is supported by the result that changes of intrinsic (object-) and extrinsic (context-) information influence reaction times and ERPs differentially. This suggests that sensory features are bound into these memory representations in different ways. The possible contribution of the hippocampus and other neuroanatomical structures to these processes is discussed, as is the potential impact of our model on future research in the field.

1 Outlining the model

Let us first consider step by step what happens if one - deliberately or not - encodes some information, stores it and at some time-point in the future reactivates it.

As Zimmer has proposed many years ago (Zimmer, 1988, 1993), and as studies from the field of neuroscience have shown, different features of objects or events are processed by different domain-specific modules. For instance, information about 'what' an item is and information about 'where' an item is are processed independently at some stage (Ungerleider & Haxby, 1994; Mecklinger & Pfeifer, 1996; Goodale & Humphrey, 1998). The same holds true for different perceptual object features, such as colour and shape (Livingstone & Hubel, 1988; Corbetta & Miezin, 1990). Objects are therefore represented as distributed entities in perception – and also in semantic knowledge (Kellenbach et al., 2001). In order to form a coherent representation, the single features of an event are mutually bound together, whereby some are more strongly interconnected than others, forming units or chunks. These chunks are the origin of memory.

Exactly what these chunks are and what binds them together is still uncertain. One important aspect for the constitution of a unit is probably the task processed during encoding. For instance, when learning a list of words, a word tends to be a unit, when watching a movie a scene reflects a unit, and so on. As far as the binding mechanism is concerned, attention might be a crucial factor. Following Reinitz (2003), all features that are simultaneously attended to might become a chunk. Using fMRI, O'Craven et al. (1999) found that attending to one feature of an object enhances the neural representation not only of the attended feature, but also of other features of that object. This implicates that whole objects are preferably selected by attentional processes, and therefore objects are likely units of memory. On a more basic neurophysiological level, the mechanism mostly discussed is phase synchronisation, meaning that different neural populations processing to be bound information

oscillate synchronously at the same pace, mainly in a frequency range of about forty Hz (Tallon-Baudry et al., 1996; Herrmann et al., 1999).

When feature information is processed by domain-specific modules (input modules in Figure 1), it leaves traces of its processing behind. Memory traces, in our view, can then be considered the persistently available after-effects of these encoding processes, or in other words, consolidated representations. This goes well together with an idea recently put forward by Nyberg (2003), Paller (2000) or Cycowicz and colleagues (Cycowicz & Friedman, 2003; Cycowicz et al., 2001), namely that information is generally stored where it is processed in the first place, in functionally specialised regions of the cortex. In the latter studies, using the ERP method, late parieto-occipital old/new effects were found in source memory tasks when subjects tried to recapitulate colour information, but not in mere item memory tasks. This is paralleled by an equivalent fMRI finding, i.e., higher occipital activation in an associative colour recognition task than in a mere old/new decision task (Yonelinas et al., 2001). These studies indicate that access to stored visual perceptual information activates extrastriate cortex.

Turning to the retrieval side, it now becomes clear that memory retrieval requires – to a variable degree – the reintegration of the encoded feature-ensemble. We can distinguish two *retrieval modes*: *intentional* and *automatic*. In our view, when successfully *trying* to remember an episode, memory retrieval is holistic[1], i.e., all bound (and available) features will be involuntarily reactivated, no matter if they are task-relevant or not. Phase synchronisation is again (as in encoding) discussed as a mechanism by which this could be achieved (e.g., Klimesch et al., 2001). Depending on the retrieval experience one can distinguish *recollection* and *familiarity*. These differ in the information one can access, meaning that basically no contextual features are retrieved in familiarity based retrieval. Anyway, memory activation can also occur involuntarily, i.e., when one is not trying to remember anything. This is called automatic retrieval. Here, a very different scenario arises - reactivation of a (part-) representation occurs while the subject is trying to solve some non-mnemonic task. This may or may not lead to a subjective retrieval experience. The performances, however, are independent of this experience, but only dependent on the task demands.

Generally, what kinds of processing take place is of course dependent on the task. Thinking of functions a perceived object could have, for example, requires other cognitive processes than thinking of other objects that bear some physical resemblance to it. This is the viewpoint of the so-called task appropriate processing (TAP) approach (Roediger et al., 1989). That is, a task requires certain processes every time it is faced, which results in higher efficiency if processing is repeated. Hence, better performances are observed if study- and test-tasks of a memory test require similar processes. This is how advocates of the TAP approach explain repetition priming in implicit- or depth of processing effects in explicit memory tasks.

However, the task is not the only factor to be taken into account. It is known, for instance, that explicit memory tests are influenced by task irrelevant manipulations such as changes in size, colour or orientation between study and test. The very same perceptual (and still irrelevant) manipulations do not, however, affect perceptual implicit memory tests, although these are obviously a lot more 'perceptual' in nature than explicit tests (e.g., Zimmer, 1995; Zimmer & Steiner, 2003). This is a fact not easily explained within a pure TAP framework. So there has to be something else determining what processes will take place. We argue that the cognitive or neural architecture places constraints on which processes can (or rather, must) and cannot take place when the system is facing a certain task in a certain input modality, a position we refer to as a **'constrained task appropriate processing'** (cTAP) approach. Referring again to the differential effects of perceptual specificity on implicit and explicit memory performance, a verisimilar explanation in this vein seems to be that there are multiple memory entries, some of which comprise specific sensory information and some of which do not. In

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[1] Since not all features of an object or episode will typically be available at the time of retrieval, this does not imply that performance will take place in an all-or-none fashion, but will only be stochastically dependent (at least when considering recollection as opposed to familiarity, cf. Meiser & Bröder, 2002).

other words, the multimodal nature of the memory system gives rise to a situation where different representations are addressed dependent on the task.

The main point of our model can then be summarised as follows: The representation of an event can be described as a set of distributed feature representations, and the retrieval of this episode requires the reintegration of these distributed pieces of information. But we are not talking of a unitary representation here – in order to explain the range of findings in human memory research, our proposal is that there are at least three different types of representations that cause memory effects.

2 The past in our head - Types and tokens

2.1 Types vs. tokens

Firstly, and as stated above, we need to distinguish between a kind of representation that codes for the invariant features of objects and a kind of representation that codes for the specific features of particular objects. The invariant, non-accidental features of objects are used for identification and for the sake of 'understanding' a stimulus. The generic feature representations (types) are relevant in all kinds of semantic tasks; in contrast, the specific feature representations (tokens) are relevant in episodic tasks.

The generic, prototypical representation is what we refer to as a **sensory type**, binding the invariant sensory features of an object category to the semantic representation of this category. This is a slow-changing representation, because huge changes would result in catastrophic difficulties especially in the learning of new concepts (cf. Elman et al., 1996). Accidental features irrelevant for identification are not included in types. It is also a modality-specific representation, meaning that in a visual type only visual information is included. In order to access the according auditory information when presented the picture (e.g., seeing an animal and imitating its sound), the object has to be conceptually identified first (Engelkamp & Zimmer, 1994). In this vein, the type can be considered an entry point into the conceptual system. The activation of a type in the course of perception temporarily changes the state of bound features, and this is what we call **type-traces**. These changes are likely to be the foundation of perceptual implicit memory effects. As far as processes of study- and test-tasks overlap, the whole cascade of processes will become faster at test (as indicated by the dashed arrows in Figure1), making the re-use of the same type easier. The notion that types bind features relevant for identification explains why priming is exemplar-specific (Biederman & Cooper, 1992). On the other hand, the assumption that only invariant features are represented explains why manipulations of accidental features like size, orientation or arbitrary colour do not affect implicit memory effects.

The claim that type-traces are the basis for implicit memory effects, and that they should be distinguished from tokens used in episodic memory, is supported by findings of relatively intact priming in amnesic patients in the context of impaired episodic recognition (Verfaellie et al., 1996; Cave & Squire, 1992). This suggests that different brain structures underlie these effects. It also suggests that the hippocampal formation does not seem to be involved in type activation and priming. If medial temporal structures are necessary for binding, as we will discuss later, this implies that there is no active binding in the literate sense taking place in type activation (integrating information across widely distributed part-representations), but that we are rather dealing with more local changes[2]. Whether one refers to these changes as weight-, synaptic-, or state changes depends on one's frame of reference. Probable candidates for the maintenance of types lie in the posterior neocortex. In an fMRI-study, Buckner et al. (1998) found multiple regions exhibiting less activation for repeated items, including extrastriate visual cortex and inferotemporal cortex. The latter region, constituting the end of the 'what'-pathway, was already considered a plausible region for the storage of type-like representations by Schacter (1992), and also by Wiggs & Martin (1998), who labelled the decreased

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[2] This is not to say that effects relying on binding processes will not occasionally appear in implicit tests.

activation 'repetition suppression', meaning improved processing due to the sharpening of cortical stimulus representations.

One problem with sensory types is that they can not be addressed if something has to be identified for which no representation exists. But priming effects have also been reported in studies using novel stimuli such as nonobjects (Schacter et al., 1990). Of course part components of these stimuli can already have representations stored in memory (cf. Bowers & Schacter, 1993), but our model yields a clear cut prediction: Priming with *truly* novel stimuli can not rely on type-traces. This is not to say that such effects do not exist, but rather that they would have to rely on a different kind of representation or mechanism. Perhaps processes of 'repetition enhancement' as for instance described by Henson et al. (2002) come into play here, as they may correspond to the formation of cortical stimulus representations. This dichotomy of sharpening vs. formation is consistent with our model. Of course, types are not only addressed in implicit memory tasks, but every time an object has to be identified. It therefore will also be addressed in episodic recognition tasks. However, they do not constitute the basis for explicit memory phenomena – in our model, episodic memory performance relies on what we refer to as tokens.

Tokens are representations that code for the specific features of particular objects encountered, or more generally, of events experienced in the past. The negative effects of perceptual manipulations on episodic object recognition prove that information used in these tasks is not purely conceptual, but includes sensory information about (ideally) all perceived attributes of the specific object (see Figure 1). The fact that these effects are generally not present in more perceptual implicit memory tasks speaks strongly in favour of two different representation formats. Even if effects of perceptual specificity (beyond basic shape manipulations, e.g., colour manipulations) do appear in implicit tasks, it is very likely that they are based on explicit contamination, i.e., they rely on episodic representations (Zimmer et al., 2002; Schacter et al., 1995; Kinoshita & Wayland, 1993). Because tokens include (perceptual) information about the specific features of a perceived stimulus, they are considered episodic memory entries which can be reactivated by automatic or intentional retrieval processes. Therefore, tokens have to be distinguished from types.

As already mentioned, studies of amnesic patients have demonstrated many times that implicit and explicit memory performances can be dissociated and almost definitely rely on different brain structures (cf. McCarthy & Warrington, 1990; Paller, 2000). Interestingly, amnesic patients do show deficits in implicit learning if the task is concerned with associative information (Chun & Phelps, 1999), and they do not show indirect effects healthy people do if relational information in visual scenes is manipulated (Ryan et al., 2000). This points to an understanding of amnesia as a binding (or consolidation-of-binding) deficit (Curran & Schacter, 1997) and to the brain regions damaged in amnesia as structures relevant for binding. Strengthening the case, Gabrieli et al. (1995) described a patient with an occipital lesion showing the opposite pattern of intact explicit memory and impaired perceptual priming. Using an inclusion-exclusion procedure, Wagner et al. (1998) demonstrated that this patient showed absolutely normal contributions of recollection and familiarity processes to recognition, adding weight to the validity of the distinction between priming and both recollection and familiarity.

Further support for a distinction between types and tokens comes from studies in the context of attention and perception. For example, attentional blink studies (cf. Treisman & Kanwisher, 1998) showed that the second of two target items presented in rapid succession is often not recognised but still gives rise to semantic priming (Shapiro et al., 1997), even potentially altering the N400 ERP-component (Luck et al., 1996). This indicates that objects can activate their types before an object file (the precursor of the object token in perception) is even compiled and stable to allow for conscious access.

Finally, implicit and explicit memory processes seem to be reflected in different ERP components. Rather early occipital effects have been reported and linked to differences in early visual processing for new and repeated items, although different polarities are reported across studies (Johnson et al.,

1998; Paller & Gross, 1998; Paller et al., 2003). On the other hand, frontal and parietal old/new effects have been associated with explicit memory processes in episodic recognition.

2.2 Object tokens versus episodic tokens

We propose, though, that the concept of tokens can be further subdivided. We have mentioned earlier that episodic recognition can rely on two different processes, namely familiarity and recollection. We will argue that these two processes operate on different kinds of representation within episodic memory. One major difference between familiarity and recollection lies in the amount of information accessible at the time of retrieval. This factor is often used when explaining to subjects the concepts of a 'remember' vs. a 'know' response (Tulving, 1985). Thus, if subjects remember any specific details about a study episode (or report that they do) a response is supposed to rely on recollection, while a response is supposed to rely on familiarity if no details are retrievable. Although the amount of information is a crucial factor, there are several reasons for assuming that this distinction is not a quantitative, but a qualitative one (cf. Yonelinas, 2002a, 2002b).

First, familiarity and recollection are functionally dissociable. This has been shown for a number of variables such as processing depth (affecting recollection; e.g. Gardiner et al., 1996) or study-test-lag (mainly affecting familiarity; Yonelinas & Levy, 2002). Furthermore, amnesic patients occasionally show the ability to recognise objects above chance level without recollecting anything specific about an earlier encounter (Aggleton & Shaw, 1996; Mayes et al., 2002). Srinivas & Verfaellie (2000) examined some of these rare cases of amnesics with intact familiarity-based recognition. Using a picture recognition task, they showed that these patients were sensitive to manipulations of perceptual attributes such as orientation, and argued convincingly that these effects were neither based on recollection nor priming. This speaks in favour of the type-token distinction in general, but it is also a strong argument for distinguishing an episodic representation that includes specific accidental object features, supporting familiarity, from an episodic representation that allows for recollection. The highly influential work of Vargha-Khadem et al. (1997) has shown that children can acquire a fair amount of semantic knowledge about the world even though they suffer from dense developmental amnesia. These children also exhibit a pattern of quite intact familiarity-based recognition without recollection although their recall performances are amiss (Baddeley et al., 2001). In recognition, they even show the expected pattern in studies using the ERP method (Düzel et al., 2001), which leads us to the second point.

Namely, the two processes of recollection and familiarity are correlated with different ERP effects (cf. Friedman & Johnson, 2000; Mecklinger, 2000). Familiarity gives rise to the reduction of an anterior component known as the FN400 effect (intact and even accentuated in developmental amnesia). Recollection processes are reflected in a later left posterior old-new effect (LPC, absent in developmental amnesia); additionally, there are two later components, a late right frontal effect which has frequently been linked to retrieval effort and/or –success, and a late posterior negative slow wave (LPN) occurring in memory tasks which demand for the binding of item- and contextual information, discussed by Johansson & Mecklinger (2003).

The FN400 effect is prominent over midfrontal areas at around 400 ms post stimulus and usually lasts for about 200 ms. It has been linked to familiarity because its amplitude and topography are the same regardless of whether items are 'remembered' or 'known' (Smith, 1993). Curran examined the effects of study-test-manipulations that hardly affect stimulus familiarity. He changed the number of words from singular to plural or vice versa (Curran, 2000), or mirror-reversed pictures (Curran & Cleary, 2003) and reported that the FN400 effect is unaffected by such changes. Current source density analyses indicate that the surface potential of the effect partly emanates from subcortical regions (Johnson et al., 1998), a likely neural generator being the perirhinal cortex (cf. Mecklinger, in press).

The other highly consistently found old-new effect, the LPC, typically has a slightly left lateralised topography, onsets at about 500 ms post-stimulus and lasts for about 300 ms. Many factors have led to its association with recollection, including that it is more pronounced for remember vs. know

responses (Smith, 1993), and that it is larger for items whose study context is additionally retrieved (Trott et al., 1997) or for congruently vs. incongruently repeated items (Ranganath & Paller, 1999), respectively. Intracranial ERP data supports the notion that the LPC at least partially relies on MTL activity (Grunwald et al., 1999).

As far as the remaining effects are concerned, the functional significance of the late right frontal effect is still under debate (cf. Ranganath & Paller, 1999), and so is that of the LPN discussed by Johansson & Mecklinger (2003) Although these highly interesting components point to the complexity of processes underlying recollection, for present purposes we will leave them aside.

Finally, recent neuroimaging studies have shown that familiarity and recollection processes rely on at least partially independent brain regions. For example, using the remember-know procedure, Eldridge et al. (2000) studied memory for words. The fMRI scans revealed increased hippocampal activity only for recollected words as opposed to words recognised on the basis of familiarity, or new words. Yonelinas et al. (2001) found stronger activation in bilateral hippocampal and parahippocampal regions when subjects were retrieving associative information (the study-colour of objects) as opposed to the retrieval of item information alone. Fan et al. (2003) found more left frontal activation in a similar comparison, but, however, no differences in hippocampal activity.

Based on these results we propose that there are two different kinds of representation underlying these two processes: Object tokens and episodic tokens. An **object token** can be thought of as a consolidated object file, a concept introduced by Anne Treisman (e.g., Treisman, 1992). An object token contains information about structural, accidental and non-accidental attributes of specific encountered objects, but no information about the context the object was originally encountered in. It allows for episodic object recognition without the retrieval of any additional contextual information. This is the representation supporting familiarity processes, allowing healthy people and some amnesic patients to base their old/new decisions on a signal devoid of context. We argue that the hippocampus proper is not essential for the binding processes involved in the (re-) construction of this component, but that instead regions of the posterior neocortex in conjunction with the parahippocampal gyrus, in particular the perirhinal cortex, serve this purpose (see Figure 1).

The claim that accidental object features are represented in the object token and that object tokens underlie the familiarity signal seems to contradict the finding of Curran & Cleary (2003) mentioned earlier, where a change of an accidental feature like orientation did not affect the familiarity ERP component. However, a similar change in orientation was used in the Srinivas & Verfaellie (2000) study reported above. In that study, the episodic object recognition performance of amnesic patients was reduced by a change in orientation, even though performance was obviously familiarity based. Seemingly, changes of sensory features sometimes do and sometimes do not influence familiarity-based recognition. We assume this to be the case because the familiarity signal is a graded one. If the magnitude of mismatch caused by changed features is minor compared to the magnitude of matching features, the change of the familiarity signal, and hence impairment, will be small or even absent. Familiarity is therefore an ineffective mechanism to detect slight semantic or sensory stimulus variations (Holdstock et al., 2002; Mayes et al., 2002).

The second kind of token in our model is what we call an episodic token. An **episodic token** integrates the object information already part of the object token with multimodal contextual information, enabling subjects to retrieve the 'how', 'where' and 'when' they encountered an object or person, i.e., recollection. The (re-)construction of such a complex representation, integrating information dispersed across multiple cortical regions, requires sophisticated binding mechanisms. It is widely accepted that the hippocampus is essential for this purpose (see Figure 1).

Apart from the cases of human amnesic patients with relatively intact recognition (Aggleton & Shaw, 1996; Srinivas & Verfaellie, 2000; Baddeley et al., 2001; Mayes et al., 2002), other findings speak in favour of this conclusion, as well. In rats, for instance, Mumby et al. (2002) demonstrated that after lesioning the hippocampus the animals still showed a certain preference for new (vs. familiar) objects, but no longer exhibited any preference for familiar objects in new (vs. old) contexts or places. Using an immediate early gene technique, Wan et al. (1999) showed that the CA1 field in the rat's

hippocampus is activated if familiar objects are presented in a novel arrangement, while the perirhinal cortex is activated when single novel objects are presented. This might point to the perirhinal cortex being an essential structure in creating a familiarity signal. Compatibly, single cell recordings indicate that the perirhinal cortex is particularly rich in novelty sensitive cells (Brown & Aggleton, 2001). Even in studies where amnesic patients with relatively confined hippocampal lesions show deficits in episodic object recognition, patients with confirmed additional perirhinal lesions do even worse (Buffalo et al., 1999). Turning to the encoding side, Ranganath and colleagues (Ranganath et al., 2004) were able to show in a very recent fMRI-study that activity in the rhinal cortex during encoding predicted familiarity-based recognition, whereas activity in the hippocampus and posterior parahippocampal cortex predicted recollection.

Studies comparing item- and source memory, like the ones by Yonelinas or Fan already mentioned, offer some compelling evidence in favour of two different representation formats underlying these processes. Cansino et al. (2002) found more right hippocampal activation when subjects correctly retrieved spatial source information as opposed to mere item information. Slotnick et al. (2003) found more parahippocampal activation when subjects only retrieved item information compared to spatial source information. These data fit nicely with the proposed functions we attribute to these regions (but see Fan et al., 2003). Prefrontal activation was also reported in both studies, however, inconsistently across conditions[3]. Assumed prefrontal activation is also a major difference in ERP studies comparing item- and source memory (e.g., Trott et al., 1997). Using pictorial stimuli, Van Petten et al. (2000) found a larger and longer lasting old/new effect in an item plus spatial source recognition task than in a plain item recognition task over prefrontal scalp locations. This effect was independent of source retrieval success, whereas a later posterior effect was sensitive to the accuracy of the source judgement. The delay of this effect (700-900 ms) relative to old/new effects (400-700 ms) suggests two processes operating in succession: An item recognition based process and a source recognition process. This idea is consistent with data from an intracranial ERP study conducted by Fernandez and colleagues (Fernandez et al., 1999). Examining subsequent memory effects, they found evidence for interrelated and sequentially occurring processes in the MTL, namely an early onsetting (300 ms) rhinal process and a subsequent hippocampal process onsetting at around 500 ms. In terms of our model, these could reflect the construction (the Fernandez study) and later reconstruction (the Van Petten study) of an object- and an episodic token, respectively.

Advocating for a distinction between *intrinsic item-* and *extrinsic context-information* analogue to our distinction between object- and episodic tokens is a study presented by Troyer & Craik (2000). They argue that incidental item information, tightly bound to the item, is automatically encoded, whereas richer, multimodal event information requires more attentional resources and intentional processing at encoding and retrieval. They demonstrated that divided attention at encoding and retrieval leads to worse recognition only of extrinsic context information. This is consistent with our assumption that item- and contextual information are potentially bound by different structures - namely that the hippocampus is essential for the integration of contextual information but not for the binding of intra-item information. Furthermore, it also points to more fundamental differences in the processing of these different types of information. A similar view is promoted by Wilding (2004), who proposed that there are different types of information that differ in underlying binding mechanisms. Intrinsic information is integrated so well that one 'just can't help remembering' it. In contrast, the retrieval of other, extrinsic information is more under the control of subjects (Herron & Rugg, 2003).

In summary, we propose three different kinds of memory representation underlying different memory tasks: Type-traces, object tokens and episodic tokens (cf. Figure 1). The first contribute to implicit memory, the second to familiarity in explicit recognition, and the third to recollection.

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[3] As far as the much debated role of the PFC in episodic retrieval is concerned, these findings do not offer conclusive evidence. It is still uncertain whether prefrontal activation mainly reflects the attempt to retrieve source information or whether it mainly reflects evaluation processes if source information is successfully retrieved. A review of the literature suggests that both viewpoints might be right. Our model, however, remains silent in this debate.

The two experiments reported below served to test some specific hypotheses derived from our model. Experiment 1 aimed at the type-token distinction. The idea was that the differential sensitivity of explicit and implicit tests towards perceptual specificity should also be reflected in ERPs. If so, this would constitute another piece of evidence supporting our type-token distinction. Experiment 2 was concerned with the notion of two different representations subserving episodic recognition. The hypothesis tested was that the manipulation of intrinsic object features and extrinsic context features should yield differential results in both behavioural and electrophysiological data. If so, this would speak in favour of our distinction between object- and episodic tokens.

Fig.1: A schematic depiction of our neurocognitive model of long-term memory.

3 Testing the model – Some experiments

3.1 Experiment 1

3.1.1 Aim

According to the above argumentation the main goal of our first experiment was to examine whether event-related potentials (ERPs) recorded in an explicit and implicit memory task under otherwise comparable task conditions provide evidence that different memory representations underlie both types of task.

As illustrated in the introduction, we assume that explicit memory entries (tokens) include perceptual details, whereas the representations responsible for perceptual implicit memory (types) include only perceptual information relevant for identification. Performance in implicit memory tasks should thus be independent of changes of sensory stimulus attributes irrelevant for the task to be

performed. We therefore expected equal ERP repetition effects – mainly over posterior electrodes – for both types of repeated stimuli. Recognition memory, on the other hand, should be affected by such feature manipulations even if they are irrelevant for the decision or if subjects are unaware of it. This suggests that in the episodic recognition task participants access an integrated token that binds all features. We were interested if ERPs were able to reflect these indirect influences of our perceptual manipulation. Given what we know from ERP studies about explicit memory (cf. Friedman & Johnson, 2000; Mecklinger, 2000) we expected modulations of the mid-frontal and the (left) parietal effect, both of which should differ from the ERP effects in the implicit memory task.

3.1.2 Method

We therefore conducted an experiment in which two groups of subjects (an implicit and an explicit group) incidentally learned 60 visually presented objects by performing a living-nonliving task. Each picture was presented for 500 ms. During test, all subjects were presented 120 objects, 60 of which had been seen previously in phase 1, and 60 that were new. Half of the repeated items was presented identically and half as mirror-reversals. In order to enhance the contribution of sensory information to memory processes, we used stimuli that were hard to identify. They were similar to the items of 'Ishihara's Test for Colour Blindness' (see Figure 2).
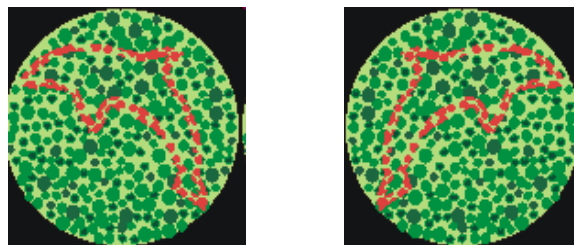

Fig. 2: Example of items used in Experiment 1. The same item in standard and mirror-reversed orientation is depicted.

Subjects from the implicit group again had to perform the living-nonliving task, whereas subjects from the explicit group were given an unexpected recognition memory test. In the latter condition, old objects presented in the same orientation (congruent) as well as mirror reversed objects (incongruent) had to be accepted as old, and new items had to be rejected. In the implicit condition there was a third experimental phase (phase 3), in which subjects saw those 60 objects again that had been new (i.e., presented for the first time) in phase 2. Hence, these items were now (in phase 3) seen for the second time (30 identically repeated, 30 repeated as mirror-reversals). Again, subjects performed the living-nonliving task. This procedure resulted in a total of 120 first presentation items (60 from phase 1 and 60 from phase 2) and 120 second presentation items (60 from phase 2 and phase 3, respectively).

Since the data will be reported elsewhere, we will only give an overview, for any further (e.g., statistical) details please see Groh-Bordin, Zimmer, and Mecklinger (in review). All reported results were significant in α-adjusted comparisons.

3.1.3 Results and discussion

We observed a behavioural as well as an electrophysiological dissociation between type of task and perceptual specificity. Reaction times for incongruent items in the explicit test were decelerated relative to congruent ones, whereas both types of items caused identical repetition priming in the implicit test (see Figure 3).
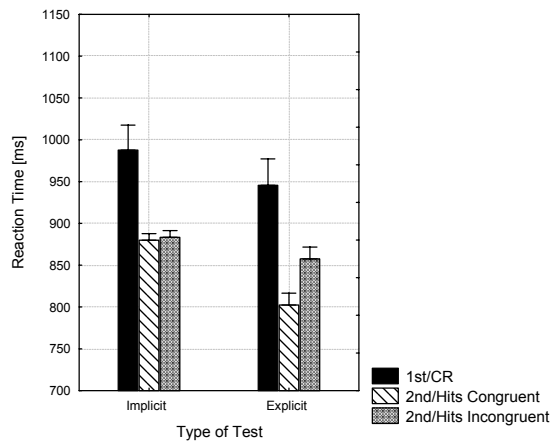
Fig. 3: Average response times for correct answers in the implicit and explicit test as a function of item status; 1st refers to first presentations in the implicit test, 2nd to congruent or incongruent second presentations; CR and Hits refer to correct answers in the explicit test for new, old congruent and old incongruent items; error bars indicate within subjects standard errors of mean.

Electrophysiological data revealed converging evidence for this dissociation. In the *implicit memory* test, ERPs showed a more pronounced positivity for repeated stimuli relative to new items mainly over centro-parietal recording sites in a time interval from 500 to 800 ms, and this effect was independent of perceptual congruency (see right-hand side of Figure 4). ERPs in the *episodic recognition* condition showed a positive deflection resembling the previously described mid-frontal old/new effect (FN400 effect) in its spatial and temporal characteristics, but only for identically repeated stimuli, not for reversed ones. The parietal proportion of the old/new effect, on the other hand, differentiated between old and new items but did not dissociate identical repetitions and reversals (see left-hand side of Figure 4).

These results provide further evidence for the independence of perceptual priming from variations of accidental sensory features. ERPs in the implicit condition showed similar characteristics for congruent and incongruent stimuli during the whole recording epoch. In contrast, waveforms in the explicit condition highlighted the influence of perceptual specificity by differentiating congruent and incongruent items in an early time interval (250-450 ms). We suggest that this dissociation can be explained by different forms of memory representations accessed by implicit and explicit memory tests. Our findings support the view that the memory representations implicit memory relies on do not include information about arbitrary perceptual features. Rather, they reflect a representation of features relevant for identification (type) which includes the visual object form. Temporary changes to this representation may cause an implicit old-new effect, because these types are automatically accessed during identification. Explicit memory, on the other hand, is based on object tokens that bind all stimulus features of an item independently of their relevance for identification. When people are in a retrieval mode they try to access these tokens, leading to familiarity or recollection-based recognition judgements. Incongruent features hinder the reactivation during episodic retrieval even when they are irrelevant, because they mismatch information represented by the token. The ERP as well as the behavioural data in our first experiment are in good agreement with this suggestion.

The finding that sensory manipulation affected the frontal but not the parietal old-new effect is in contradiction to the result of Curran and Cleary (2003). This can possibly be explained by some characteristics of our study, namely the emphasis on sensory processing due to the nature of the stimuli, and the fact that study was incidental. These factors might have reduced binding processes relying on the hippocampus at encoding (and hence also at retrieval), and might have increased the contribution of object tokens (as opposed to the hippocampally dependent episodic tokens) to recognition caused by a stronger reliance on sensory information. At the same time, the perceptual conditions enhanced the magnitude of non-matching sensory information in early processing in the incongruent case. To put it simply, all pictures appeared to be new at first glance and only after some processing did they match their object token. Additionally, in contrast to Curran and Cleary, in our

case the sensory change was not relevant and it was not mentioned during encoding. We will come back to this aspect in the general discussion.
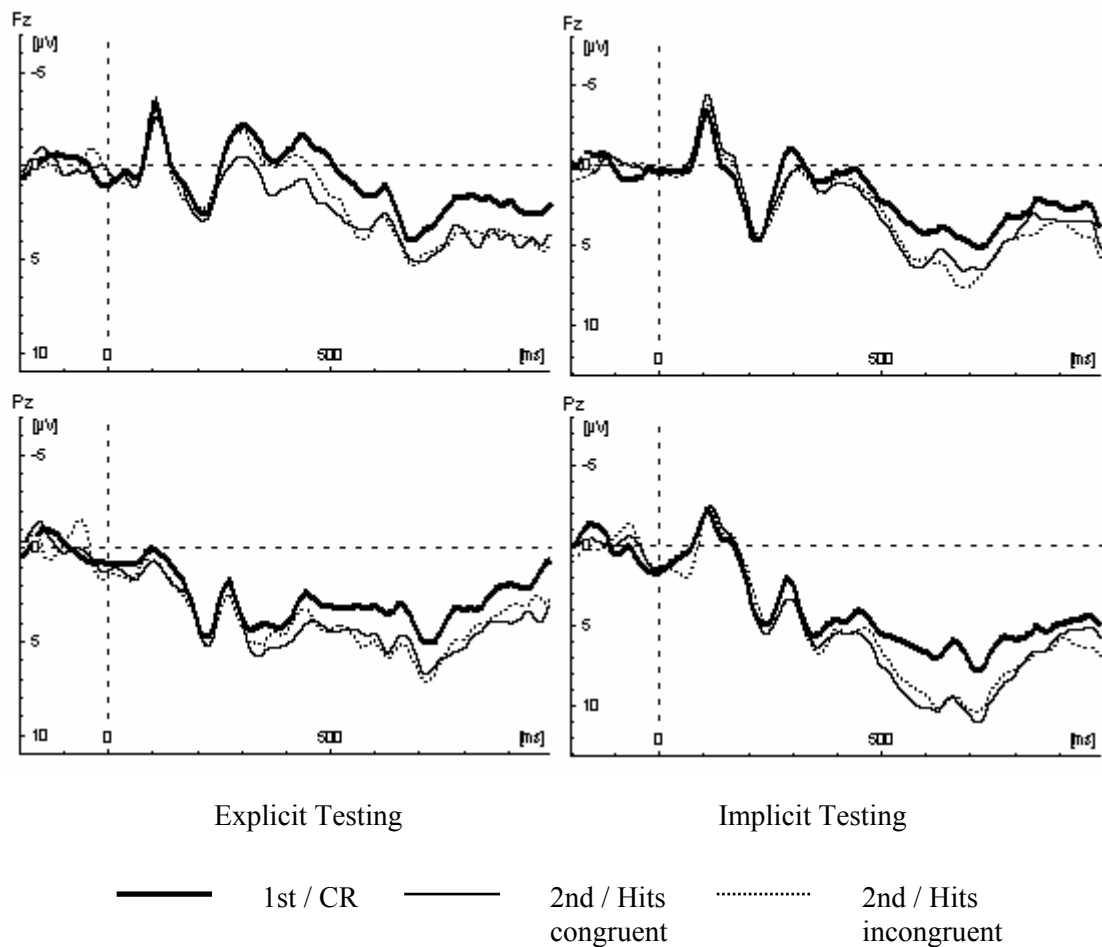

Fig. 4: Grand average waveforms (linked mastoids referenced) at Fz and Pz electrodes in the explicit (left-hand side) and implicit (right-hand side) test as a function of item status (1st refers to first presentations in the implicit test, 2nd to congruent or incongruent second presentations; CR and Hits refer to correct answers in the explicit test for new, old congruent and old incongruent items); time scaling ranges from –200 to 1000 ms after stimulus onset; stimulus offset is at 500 ms; positive deflections are displayed downward.

3.2 Experiment 2

3.2.1 Aim

As pointed out in the introduction, we think that there are two different kinds of representation concerned with object- and episodic recognition. The object token comprises information about individual items and their incidental features and is necessary for item recognition via familiarity processes. Richer, contextual information is included in the episodic token, which enables recollective experience.

Changing an irrelevant feature of an object should have detrimental effects on recognition performance in terms of longer reaction times, because the object token will be automatically reactivated in whole when the cue is presented. According to Troyer and Craik (2000), contextual

information should rely more on controlled processes, and therefore subjects should be able to mask out the irrelevant context information. Thus, changing only the background should not impair object recognition. As far as the ERP data from the object decision phase is concerned, we hypothesised that the incongruency of colour should become apparent in a modulation of the frontal old-new-effect. However, colour information is potentially also bound into the episodic token by more controlled processes. As we explicitly instructed subjects to encode colour and context and to elaborate these features, we expected that the incongruency of colour might also modulate parietal effects. Incongruency of context, however, should only (if at all) become apparent in the parietal old-new effect, because in this case object information has to be actively bound to extrinsic context information (i.e., into an episodic token) in order to produce an effect of incongruency – a process for which the hippocampus should be vital.

3.2.2 Method

We conducted an experiment in which an object feature (colour) and the shape of an arbitrary grey background (context) were manipulated between study and test. In the study phase, subjects were presented 80 images of everyday objects which could appear in one of four different arbitrary colours and on one of four different arbitrary backgrounds (see Figure 5). Every item was presented twice in succession to enhance encoding. Instructions were to intentionally memorise the specific combination of object, colour and background. At test, the 80 old items were intermixed with 80 new items and, more importantly, 40 old items were presented incongruently, i.e., either in a different colour or on a different background (i.e., in a new context). The colour-context factor was varied between subjects. Subjects had to make two succeeding decisions concerning every item. First, they had to decide whether or not the object had been presented before, independently of colour or background (old-new decision). Then a cue was presented and participants were to indicate whether or not the colour or the context of the object, respectively, had changed (feature decision). Twenty-seven subjects took part in this experiment, but eleven had to be excluded due to bad performance (object recognition at chance level) or technical problems, leaving 16 subjects that entered the analysis. For Experiment 2, we will report parts of our data in more detail, because they are not published elsewhere.
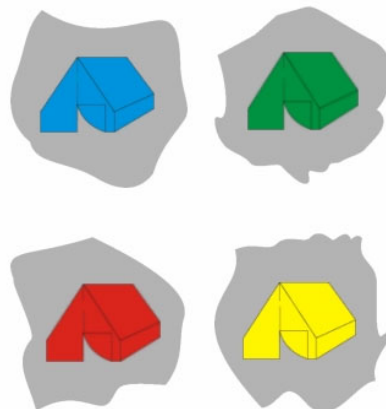

Fig. 5: Examples of items used in Experiment 2. Note: Only colour or context was changed at test in incongruent cases, both features were never altered at the same time.

3.2.3 Behavioural results and discussion

As in other experiments (Zimmer & Steiner, 2003), the incongruency of colour produced costs in episodic object recognition, i.e., colour incongruent objects were recognised more slowly even though colour was irrelevant (1121 ms vs. 1040 ms; $F(1,14)=7.73$, $MSE=3401$, $p=.015$). Context incongruency, however, had no effect on reaction times (1077 ms vs. 1059 ms; $F<1$). There were also

no effects in the relative frequency data in either case (see Figure 6). The behavioural results therefore confirmed our expectations.

That this is a genuine effect of the manipulated features and not an effect caused by different strategies in the two groups of participants is proved by the results of a control group. These subjects (13 persons) were given the same task in a behavioural test, but in this experiment the manipulation of colour and context was a within subject factor, so strategy changes were unlikely. In this experiment, a post-hoc analysis (Fisher's LSD) revealed that colour and context congruent trials (1271 ms) differed from colour incongruent (1373 ms; df=24, MSE= 12998, p=.04) but not from context incongruent (1288 ms) trials.
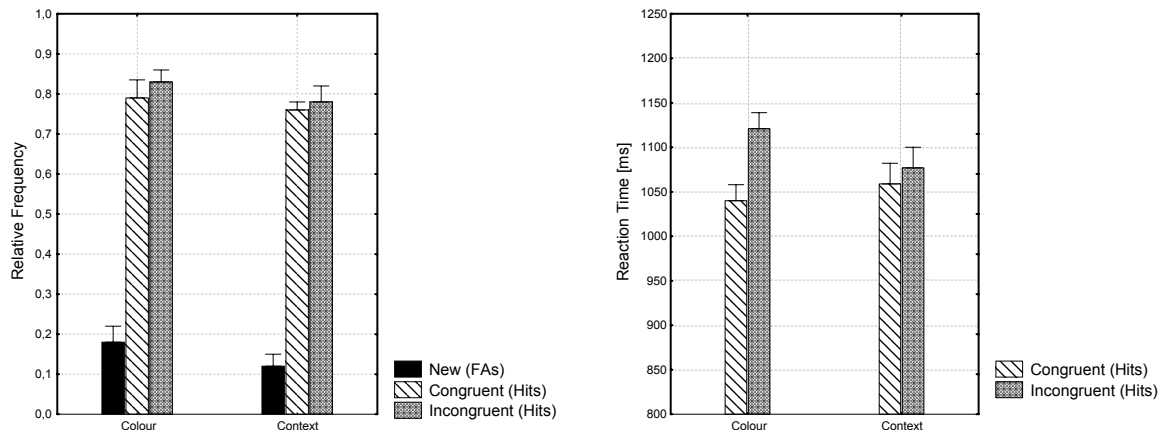

Fig. 6: Object (old-new) decision data. Relative frequencies for all 'yes'-responses as a function of item status (left-hand side) and average response times for hits as a function of item status (right-hand side); FAs refers to false alarms; error bars indicate within subjects standard errors of mean.

Looking at performances regarding the feature decision, however, showed that subjects had only learnt the object-colour associations, but not the object-context associations. The difference between the proportion of 'yes'-responses in congruent (hits) and colour-incongruent (false alarms) trials was highly significant (.59 vs. .17; $F(1,14)$=58.85, MSE=.012, p<.001) while there was no difference between congruent and context-incongruent trials (.57 vs. .52; F<1). The analysis of reaction times for the feature decision yielded no significant results (see Figure 7). In other words, we could show that the colour associations had been learnt, and that incongruency of this intrinsic feature produced indirect costs on object recognition, just as predicted. Unfortunately, however, we were unable to show that subjects had learnt the context associations. Hence, we can take this result as support for the notion that the learning of colour and context features, respectively, differ in some respect, but we cannot take the result as support for the stronger assumption that the mismatch of colour at test results in different effects than the mismatch of context if both features are part of a memory trace (i.e., have been learnt). This result thus does not directly contradict our hypothesis, but it does not allow appropriately testing it, either.

3.2.4 Electrophysiological results and discussion

Turning to the ERP data recorded during the object decision phase, we analysed the data basically in the same way as described in Groh-Bordin et al. (in review). We found a centroparietal old-new effect with a slightly left-lateralised topography from about 400 to 600 ms (maximal at midcentral ROI; $F(1,15)$=6.51, p=.02). This is the expected pattern associated with recollection. There was no significant circumscribed frontal old-new effect, however. Nevertheless, we did find an early onsetting (200 to 800 ms) congruency effect at left- and midparietal electrodes in the colour group (midparietal ROI; $F(1,7)$=5.97, p=.04), and a rather broad and late (700 to 900 ms) congruency effect in the context group, maximal at midcentral electrodes (midcentral ROI; $F(1,7)$=5.92, p=.045) (see Figure 8).
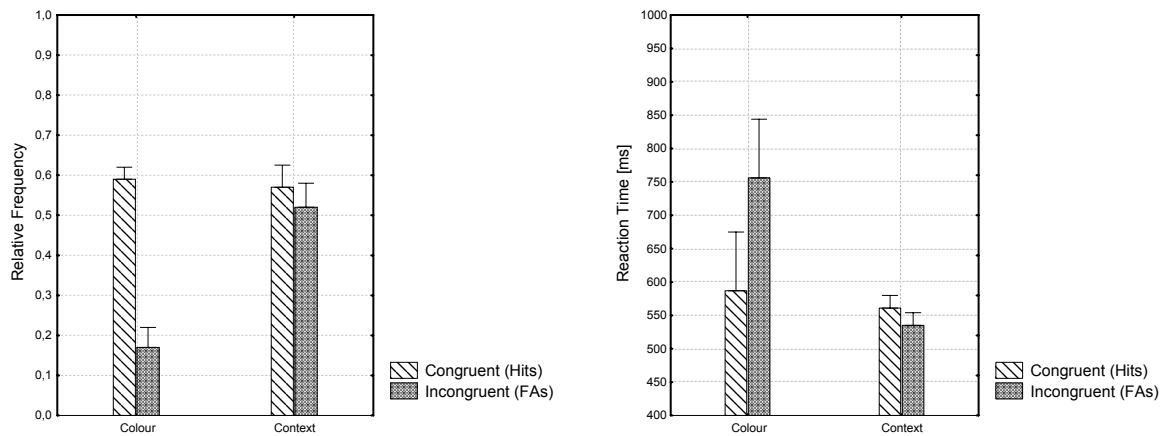
Fig. 7: Feature decision data. Relative frequencies (left-hand side) and average response times (right-hand side) for all 'yes'-responses as a function of item status; FAs refers to false alarms; error bars indicate within subjects standard errors of mean.

Colour group   Context group

——— CR   ——— Hits   ·········· Hits
                              congruent   incongruent
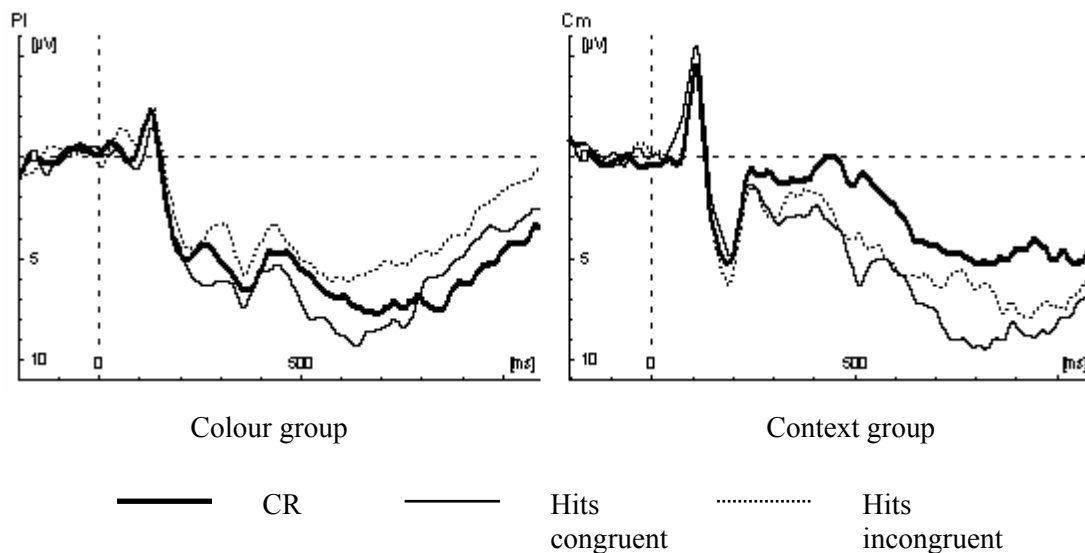
Fig. 8: Grand average waveforms (linked mastoids referenced) from the object (old-new) decision at left parietal ROI for colour (left-hand side) and mid central ROI for context (right-hand side) as a function of item status; time scaling ranges from –200 to 1100 ms after stimulus onset; positive deflections are displayed downward.

It was unexpected that the congruency effect in the colour condition only occurred at centro-parietal sites. However, the very early onset and long duration of the colour-congruency effect might indicate that this effect reflects two components. The early portion – starting at around 200 ms – might be related to an automatic access of colour information, while the later portion might reflect a modulation of the parietal old-new effect due to intentional colour processing. This is speculative but consistent with the notion that in the case of explicit feature encoding, colour information is integrated into an episodic token, and is henceforth processed differently compared to remembering following incidental encoding. We do not know, however, whether this explicit colour encoding is also responsible for the absence of the expected frontal modulation. Two further factors are potentially relevant. First, the easy identification of objects might have reduced the contribution of incongruent sensory feature information to the familiarity signal of stimuli (cf. Curran & Cleary, 2003). A second reason is that we did not introduce totally new context backgrounds in the test phase. Therefore, even new objects were displayed on highly familiar backgrounds. Thus, the base line for the familiarity component might not have been assessed properly.

In the context condition, there are seemingly two consecutive processes taking place, consistent with an idea expressed above (cf. Van Petten et al., 2000): An early recognition of the object disregarding context reflected in the old-new effect, and a late process reflecting retrieval of contextual detail and affected by congruency. This late congruency effect either occurs after subjects have made their feature decision, or reflects a process too weak to affect either the object or the feature decision (remember that there were no behavioural signs of such an effect in either the object or the feature decision). This would indicate that subjects made their feature decision quite early – already during the object decision phase. One point speaking in favour hereof is that ERPs from the feature decision phase showed no process specific effects whatsoever. The fact that the congruency effect in the context group extended to frontal sites might correspond to higher demands on retrieval control while attempting to retrieve detailed contextual information, or to the retrieval of detailed contextual information itself[4] (cf. Rugg et al., 1999; Ranganath et al., 2000).

The conclusion to be drawn, however, is that congruency effects seem to differ markedly in onset and topography for intrinsic and extrinsic features, assumingly reflecting differences in necessary (controlled) retrieval effort, or, in our terms, differential access to stored representations. Thus, although we didn't observe the expected distinct effects on familiarity and recollection components, these differences in onset and topography indicate differences in the processing of intrinsic and extrinsic features.

3.3 Experiment 2a

3.3.1 Aim and method

One major drawback of Experiment 2 was the fact that subjects obviously failed to learn the object-context associations. We speculated that this was due to the insufficient discriminability of the backgrounds used. However, a good deal of participants even failed to recognise the objects above chance level, so the task might have generally been too difficult. We therefore designed a follow-up study (Ecker & Zimmer, in preparation) in which we introduced a number of changes in experimental material and procedure to enhance performances. Namely, we now used nameable, more distinct geometrical backgrounds (see Figure 9) and we introduced two separate study-test blocks. Additionally, all items were presented twice in one study block and we announced a performance feedback to motivate subjects. Altogether subjects were presented 2 (repeated presentation of same items in one study block) x 40 (number of individual items per study block) x 2 (dual study-test-blocks) study items. At test, we presented each item during the object decision *and again* for the feature decision task and we emphasised the need for quick responses in subjects' instructions. This supposedly enhanced the likelihood of subjects indeed postponing their feature decision until the item reappears, enabling us to analyse ERPs from this second phase as well (in the first experiment only a cue had been presented for the feature decision, but the item had not been shown again). The data of 32 subjects were entered into the analysis.

3.3.2 Results and discussion

From this study only the behavioural data is already available, the ERP data is preliminary. First of all, the newly introduced changes to experimental procedures were successful: No subject had to be excluded due to bad object recognition performance, which was near ceiling overall (>.9 in all conditions). Replicating the behavioural findings from the two already mentioned studies, the incongruency of colour again produced costs in object recognition, i.e., colour incongruent objects were recognised more slowly even though colour was irrelevant (1057 ms vs. 962 ms; $F(1,30)=20.02$, $MSE=3539$, $p<.001$). Again, context incongruency had no effect on reaction times (1089 ms vs. 1081 ms; $F<1$). Although there was a significant interaction in the frequency data compatible with our hypotheses – more 'yes' responses to colour congruent items (.98) compared to the other 3 conditions (.93-.94); $F(1,30)=11.02$; $MSE=.001$; $p=.002$) – this effect has to be interpreted with caution due to

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[4] Note that this effect has nothing to do with the well studied but earlier onsetting familiarity component mentioned above.
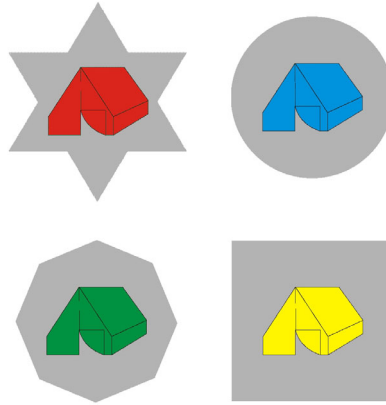
Fig. 9: Examples of items used in the follow-up study of Experiment 2 (Exp. 2a). Note: Only colour or context was changed at test in incongruent cases, both features were never altered at the same time.

ceiling effects. Turning to the feature decision, the difference in relative frequencies between congruent and incongruent trials was now significant and of about the same size for both groups (.81 vs. .18 in the colour group, $F(1,30)=119.78$, $MSE=.03$, $p<.001$; and .76 vs. .25 in the context group $F(1,30)=79.70$, $MSE=.03$, $p<.001$. There was no significant difference in discrimination scores (Pr-score .64 vs. .52; $t(30)=1.43$, $p>.1$). This means that we can now state that the incongruency of an intrinsic feature causes indirect costs on object recognition, whereas the incongruency of an extrinsic feature causes no such costs, even though both kinds of information were learnt and associated with object information to the same degree. This outcome is what we had predicted (see Figure 10).

As far as the ERP data of the episodic object recognition phase is concerned, we found the expected frontal and parietal old-new effects, and we were able to replicate the modulation of the parietal old-new effect by congruency in the colour condition. There were no congruency effects in the context group, though. The fact that congruency effects in the colour group *only* appeared parietally and not frontally as well replicates Experiment 2, but is inconsistent with our hypotheses.
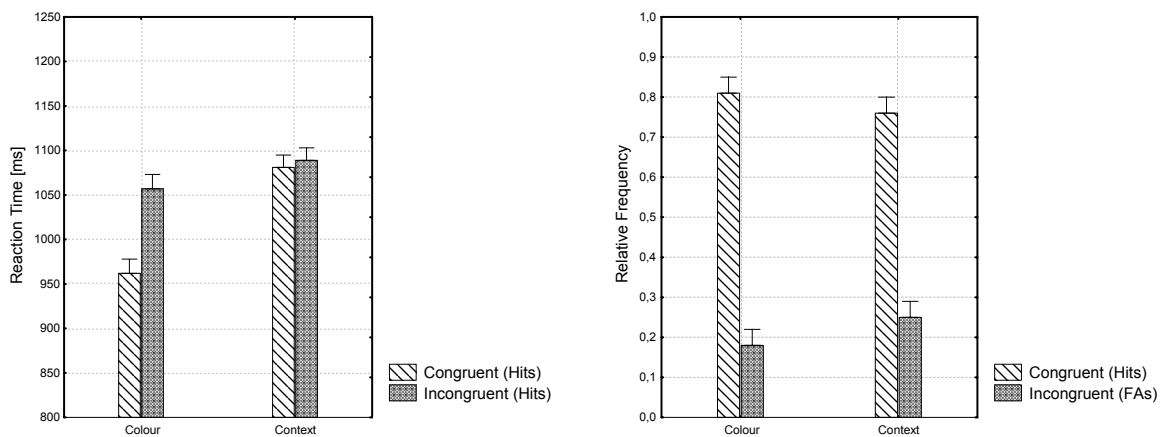

Fig. 10: Average response times for hits as a function of item status in the object (old-new) decision (left-hand side); relative frequencies in the episodic object recognition test are given as figures in the text. Average proportions of 'yes'-responses as a function of item status in the feature decision (right-hand side); FAs refers to false alarms; in this case response times are given as figures in the text. Error bars indicate within subject standard errors of mean.

4 General discussion

Concentrating on the main results, we observed four effects. In a **perceptual implicit test**, we found clear old-new effects in behavioural and electrophysiological data (Exp. 1) which were *independent* of sensory congruency (a change of the picture's orientation). In the **episodic object recognition** test of Exp. 1, using the same material (unusual pictures difficult to identify), the same incongruent and still irrelevant sensory feature impaired recognition and modified the early *frontal* old-new effect. *Incongruent* pictures elicited an early *FN400* component comparable to the one elicited by new items. The parietal old-new effect was not influenced by sensory congruency. In Exp. 2, we contrasted **intrinsic** (colour) and **extrinsic** (context) **feature** manipulation. We adopted a sequential test procedure, with an old-new object recognition test followed by a feature recognition test. An *incongruent colour* impaired episodic object recognition, and it modulated the *parietal* old-new effect. A changed *context* did *not* influence episodic object recognition, neither in the behavioural nor in the electrophysiological data (Exp. 2a). However, in Exp. 2, a very late parietal effect of congruency could be seen.

These data demonstrate that our distinction of different memory entries is reasonable. Consistent with our expectations, the implicit test was unaffected by sensory congruency and context did not influence episodic object recognition. We attribute the first outcome to type-traces, and the second to episodic tokens deliberately used *after* the object token has been addressed. We had predicted these results from our model. However, we had not expected the ERP effects in episodic object recognition to vary dependent on the experimental procedure. In Experiment 1 we observed an early midfrontal congruency effect in the explicit test, yet in Experiment 2 we observed a parietal congruency effect. The reasons for this are not quite clear, however, there are some critical differences between the two paradigms that might be crucial.

The first is study intention: In Experiment 1 participants were not instructed to memorise the items, whereas an integrative learning instruction was explicitly given in Experiment 2. Furthermore, subjects knew that the manipulated sensory attribute was to become relevant in Experiment 2, whereas it was irrelevant throughout Experiment 1. These inconsistencies are similar to those reported above when we compared the Curran and Cleary with the Srinivas and Verfaellie study. Noticeably, congruency effects were observed frontally (or in familiarity based recognition) when learning was incidental, but parietally when learning was intentional and subjects' attention was focussed on the relevant feature. We assume that the instruction to memorise the colour of the objects may have led to more explicit colour processing, and consequently to a hippocampally mediated integration of colour information into the episodic token at study. Similarly, at test, the required feature judgement in the second decision might have enhanced the tendency to base the object decision on the episodic token, too. According to our cTAP approach, the study task together with the constraints of the neural architecture are the key factors for all further processing, including the construction and reconstruction of representations. In other words, what is consciously and intentionally bound (by the hippocampus) will be consciously reactivated (via the hippocampus) when subjects are in the respective retrieval mode (cf. Moscovitch, 1992).

Another point is the nature of the stimulus material used[5]. Items in Experiment 1 were designed to enhance perceptual processing. This may have led to more sensory information being integrated into the object token. On the other hand, the incidental nature of study reduced constructive processing of the episodic token. Both effects together may have rendered congruency effects in familiarity more likely. The exact contribution of these factors and their interaction are not well understood yet, so under what circumstances congruency effects will appear frontally or parietally, and why they do not occur together, is still unclear. Further studies manipulating study intention, the amount of necessary

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[5] The reader might have noticed that we had also manipulated different sensory features in these two experiments. We do not consider this to be relevant, because sensory congruency effects are reported for both types of features. However, this factor should be controlled in future research.

sensory processing, and also looking at subsequent memory effects at encoding are urgently needed in order to clarify these issues.

Finally, we would like to comment on some aspects our model does not, or only marginally, address. As far as semantic memory is concerned, we have only stated that sensory types can be considered entry points to the 'semantic system', as they carry some conceptual information themselves (what does a rubber duck look like?) and are an important step along the processing route from basic visual analysis to object identification and usage. Obviously there is a lot more to semantic memory. According to Treisman, semantic information is part of an object file. We have focussed on the sensory information represented in an object token. The relationship between these types of representation and its consequence on binding have to be clarified more thoroughly. The already mentioned studies of developmental amnesia (Vargha-Khadem et al., 1997; Baddeley et al., 2001; Brizzolara et al., 2003) have suggested that conceptual knowledge can be acquired without an intact episodic memory system. In terms of our model it seems as if object tokens can be sufficient to encode information into the semantic memory system. Episodic tokens would then be confined to spatio-temporal and other contextual information[6]. An interesting question would be what happened if not only the hippocampus, but also the perirhinal cortex was damaged in early childhood? Anyway, the topic of how and under what circumstances adult amnesics can acquire semantic knowledge remains unsolved (Tulving et al., 1991; Hamann & Squire, 1995; McKenna & Gerhand, 2002; Bayley & Squire, 2002), and so is the role of higher brain plasticity, more efficient learning strategies, environmental support and personality traits in the performance of developmental amnesics.

Furthermore, we have discussed the role of some brain structures (the hippocampus, perirhinal cortex, domain-specific modules in the posterior neocortex), but not others, also highly relevant for human mnemonic processing (the diencephalon, the prefrontal cortex). Diencephalic lesions commonly lead to dense amnesia, and hence must subserve some crucial function (Aggleton & Brown, 1999). However, there seems to be no consensus yet about exactly what that function is (for some interesting ideas, see Burgess et al., 2002). Apart from that, a wealth of memory studies has reported prefrontal activation in different conditions (cf. Lepage et al., 2000; Cansino et al. 2002, Slotnick et al., 2003). As mentioned above, the role of the PFC in episodic encoding and retrieval is highly debated but still far from resolved. Its functions are probably manifold. We agree with a thought brought forward by Foster (2003), however, that key 'hotspots' such as the hippocampus mediate key memory processes (such as binding) while other structures like the PFC serve more modulatory functions. The finding that prefrontal lesions typically do not lead to dense amnesia (Alexander et al., 2003) underscores this argument.

Some studies, however, report evidence that contradict our model to a certain degree. For example, Stark and Squire (2003) presented data from some experiments in which patients with hippocampal lesions showed impaired recognition memory without any hint of especially impaired associative memory (but see Kroll et al., 1996). This shows that there is probably no strict dichotomy in a sense that the hippocampus is *only* relevant for associative learning while the parahippocampal gyrus is *only* relevant for non-associative learning, even though there certainly are functional differences. For example, even single item learning is associative inasmuch as the environment is co-encoded to a variable degree. Taking a connectionist perspective, differences in learning rate and sparseness of representation lead to differential aptitudes for certain tasks. This makes evolutionary sense because multiple, differently fast learning mechanisms enable us to extract information from the environment in a highly flexible way (cf. McClelland et al., 1995). These functional differences arise from architectural differences, which most likely fall along a continuum and are not dichotomous (Norman & O'Reilly, 2003). To us this means that the rhinal cortex also takes part in binding processes, e.g., 'associative' intra-item binding, but that the hippocampus is necessary for 'higher-level binding'. As

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[6] In fact, spatiotemporal information is seemingly not included in this process of decontextualisation, as the patient Jon studied by Vargha-Khadem et al. (1997) is still highly desoriented even in highly familiar surroundings. He also exhibited selective deficits in memory for spatial information and the temporal order of events in a virtual reality setting (Spiers et al., 2001). This points to the hippocampus playing a crucial role in spatial learning and the representation of temporal order.

already stated for the prefrontal cortex, even the small regions of the MTL we are talking about probably all subserve different functions. For example, the perirhinal cortex is not only relevant for familiarity in the sense of recent occurrence, but apparently also codes for the long-term familiarity of stimuli (Hölscher et al., 2003). Another point with regard to the Stark and Squire paper is that the medial temporal region rarely 'sleeps', meaning that it is often active even during non-associative tasks (baseline problem). This might be a reason why not all studies find hippocampal activation during associative retrieval (Fan et al., 2003) and some studies even find activation in both the hippocampus and the parahippocampal cortex (Yonelinas et al., 2001). A further problem in ERP studies is the cylindric orientation of hippocampal neurons which hinders the detection of field potentials at the surface of the head. Hence, for a strong test of our model we will have to combine ERP and fMRI methods.

One more fundamental objection to the approach presented here is a study by Yovel and Paller (2004), who recently called the link of FN400 and familiarity into question. According to them, the FN400 effect is actually more closely tied to conceptual priming processes due to reading or subvocal naming of stimuli. They argue that this ERP component has only been associated with familiarity because verbal material was used in most studies, and found no according effect in their studies using unfamiliar faces. Our studies, however, are not able to clarify this dispute, although we did observe frontal old-new effects using pictorial stimuli in two out of three experiments. Concerning the one experiment in which no significant FN400 effect was found, it is unclear why pictorial stimuli should be subvocally named in some studies (Exp. 1, Exp. 2a; Curran & Cleary, 2003; Tsivilis et al., 2001), but not others (Exp. 2). More experiments using non verbalisable material need to be done, and future studies should aim at carefully disentangling familiarity and conceptual priming processes.

In conclusion, our model shares some resemblance to other models presented by Aggleton & Brown (1999), Paller (2000, in review), Murre (1999), or Eichenbaum (for an update of his relational representation model see Eichenbaum, in review), but it has some important properties in its own right. Namely, it fills a gap between more processing oriented models like the classic TAP-approach and more neuroanatomical models that mainly assign function to structure. Our model is more concerned with an intermediate level of representations - representations that guide processing on the one hand, while themselves relying on (partly) different brain structures on the other hand. Types and their temporary changes, object tokens, and episodic tokens are three types of memory representations representing different information, serving different purposes and provided by different brain structures. The properties of these representations are the focus of our research, and the model we have proposed offers clear-cut hypotheses regarding these properties.

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