

Objects in Context

The Neurocognitive Representation, Binding, and
Processing of Object and Context Features in
Recognition Memory – An Electrophysiological Approach

Dissertation zur Erlangung des Grades eines
Doktors der Philosophie
der Philosophischen Fakultäten der Universität des Saarlandes

vorgelegt von

Ullrich K. H. Ecker

aus St. Ingbert

Diplom-Psychologe

Saarbrücken, 2007

Dekan:

Prof. Dr. Rainer Krause, Universität des Saarlandes

Berichterstatter:

Prof. Dr. Hubert D. Zimmer, Universität des Saarlandes

Prof. Dr. Axel Mecklinger, Universität des Saarlandes

Tag der Disputation: 20.07.2007

*i seem to recognize your face, haunting, familiar, yet i can't seem to place it
cannot find a candle of thought to light your name, lifetimes are catching up with me
all these changes taking place, i wish i'd seen the place, but no one's ever taken me
hearts and thoughts they fade away*

*i swear i recognize your breath, memories like fingerprints are slowly raising
me you wouldn't recall, for i'm not my former, it's hard when you're stuck upon a shelf
i changed by not changing at all, small town predicts my fate, perhaps that's what no one wants to
see*

*i just want to scream...hello, my god it's been so long, never dreamed you'd return
but now here you are, and here i am
hearts and thoughts they fade away*

Eddie Vedder (pearl jam) – elderly woman behind a counter in a small town

*do you remember me
i was the giver of eternity
will you surrender to me
i scream repress repress repress
you won't get rid of me*

Ullrich Ecker (raindog) – dr zhivago

*memory is who we are, yet memory is also dependent on whom we've chosen to be [...it] holds us
together and can break us apart*

Chris Oricchio

you can't put your arms around a memory

Johnny Thunders

To my wife, best friend, and sharer of dreams, Birgit: Thanks for your support, I love you.

underneath that smile lies everything

Eddie Vedder (pearl jam) – inside job

To my beloved sons, Toby Jonah & Daniel James: The world is yours. Go for it.*

*when he was six he believed the moon overhead followed him
by nine, he had deciphered the illusion, trading magic for fact
no tradebacks*

if he only knew now what he knew then

Eddie Vedder (pearl jam) – I'm open

** as you made your way to Earth (still equivalent to your mum's belly at this stage) around the same time as this thesis, the name is preliminary... ☺*

Overview

1 Introduction.....	1
2 Objects in Our Head - Types and Tokens	6
2.1 Types vs. Tokens	6
2.2 Object Tokens vs. Episodic Tokens	9
2.2.1 Familiarity vs. Recollection.....	9
2.2.2 Object & Episodic Tokens & the Binding of Intrinsic & Extrinsic Information	15
2.2.3 Support for the Token Distinction	18
3 Synopsis	25
4 Experiments I.....	28
4.1 Experiment 1	28
4.1.1 Design and Hypotheses	28
4.1.2 Methods	30
4.1.3 Results and Discussion	33
4.2 Experiment 2	36
4.2.1 Design, Hypotheses and Methods.....	36
4.2.2 Results and Discussion	38
4.3 Experiment 3	52
4.3.1 Design, Hypotheses and Methods.....	52
4.3.2 Results and Discussion	53
5 Interim Discussion.....	59
5.1 Summary	59
5.2 Effects of the Intrinsic Feature Manipulation	61
5.3 Effects of the Extrinsic Feature Manipulation	64
6 Experiments II.....	67
6.1 Experiment 4	67
6.1.1 Design, Hypotheses and Methods.....	67
6.1.2 Results and Discussion	69

6.1.3 Discussion	80
6.2 Experiment 5	84
6.2.1 Design, Hypotheses and Methods.....	86
6.2.2 Results.....	89
6.2.3 Discussion	99
7 General Discussion	104
7.1 Summary	104
7.2 Familiarity is Perceptually Specific. Is it also Associative?	105
7.2.1 Associative Familiarity.....	105
7.2.2 Intrinsic versus Extrinsic Binding	108
7.2.3 Types of Context	110
7.3 Episodic versus Semantic (Familiarity) Memory.....	114
7.4 One Dual Process out of Control?	118
7.4.1 Where is Control – or – A Neuroanatomical Peculiarity	118
7.4.2 Global Match and Dual Processing Models	119
7.4.3 Resolution: Iteration. Interaction. Integration.	125
8 Conclusion	132
9 Appendix	134
10 Zusammenfassung	136
10.1 Einleitung.....	136
10.2 Experimente	139
10.3 Diskussion	144
11 References	147
Abbreviations.....	168
Annotation	169
Danksagung	170
Curriculum vitae.....	171

Figure Index

Figure 1. Illustration of the binding problem; figure adapted from Cer & O'Reilly (2006).....	2
Figure 2. Stimuli used by O'Craven et al. (1999).....	3
Figure 3. Results of Srinivas & Verfaellie (2000).....	12
Figure 4. ERP old-new effects reported by Smith (1993)	12
Figure 5. FN400 effects of Curran & Cleary (2003).....	13
Figure 6. Schematic diagram depicting the MTL's interface role.....	15
Figure 7: Schematic depiction of sparse representation in the hippocampus	17
Figure 8: A schematic depiction of the neurocognitive type-token model	17
Figure 9. Results of Davachi et al. (2003).....	20
Figure 10. Results of Groh-Bordin et al. (2005)	26
Figure 11. Examples of items used in Experiment 1	31
Figure 12: Object (old-new) decision data, Experiment 1	33
Figure 13: Feature decision data, Experiment 1.....	34
Figure 14: ERPs, Experiment 1	35
Figure 15. Examples of items used in Experiment 2	38
Figure 16. Object (old/new) decision data, Experiment 2	39
Figure 17. Feature decision data, Experiment 2.....	40
Figure 18. ERPs, object decision, Experiment 2, Colour group.....	41
Figure 19. ERPs, object decision, Experiment 2, Context group	42
Figure 20. Topographic ERP maps.....	43
Figure 21. Mean ERP voltages, object decision, Experiment 2.....	44
Figure 22. Topographic CSD maps, object decision, Experiment 2.....	47
Figure 23. ERPs from frontopolar electrodes, object decision, Experiment 2.....	49
Figure 24. ERPs, feature decision, Experiment 2, Colour group	50
Figure 25. ERPs, feature decision, Experiment 2, Context group.....	50
Figure 26. Recognition data, Experiment 3	54
Figure 27. ERPs, Experiment 3	55
Figure 28. Topographic ERP maps, Experiment 3	57
Figure 29. Topographic CSD maps, Experiment 3.....	57
Figure 30. Sample items used in Experiment 4.....	68
Figure 31. Recognition memory performance, Experiment 4	70
Figure 32. RT data, Experiment 4	70
Figure 33. ERP data, Experiment 4, Intrinsic condition	71
Figure 34. ERP data, Experiment 4, Extrinsic condition	72

Figure 35. ERP data, Experiment 4, Intrinsic condition, Standard group	74
Figure 36. ERP data, Experiment 4, Intrinsic condition, Inverse group.....	74
Figure 37. ERP data, Experiment 4, Extrinsic condition, Standard group.....	75
Figure 38. ERP data, Experiment 4, Extrinsic condition, Inverse group	75
Figure 39. RT data, Intrinsic & Extrinsic conditions, Standard & Inverse groups, Exp. 4 ..	79
Figure 40. Items and test conditions of Experiment 5.....	88
Figure 41. Performance data, Experiment 5	90
Figure 42. RT data, Experiment 5	90
Figure 43. ERP data, Experiment 5	91
Figure 44. Topographic ERP maps, Experiment 5	91
Figure 45. Mean voltage amplitudes, frontal ROI, time window 1, Experiment 5.....	93
Figure 46. ERP data, Experiment 5, right parieto-occipital ROI.....	96
Figure 47. Topographic ERP maps, Experiment 5	96
Figure 48. Australian Estuarine (Saltwater) Crocodile (<i>Crocodylus porosus</i>).	133
Figure 49. An unfamiliar face – familiarity reduced by hairstyle.....	134
Figure 50. A familiar face.....	135

Table Index

Table 1. ANOVA Results, Time window 1, Experiment 2	45
Table 2. ANOVA Results, Time window 2, Experiment 2	46
Table 3. ANOVA Results, Time window 1, Experiment 3.	56
Table 4. ANOVA Results, Time window 2, Experiment 3	56
Table 5. Planned comparisons, Time window 1, Experiment 4	72
Table 6. Planned comparisons, Standard/Inverse groups, Time window 1, Exp. 4.	76
Table 7. Planned comparisons, Standard/Inverse groups, Time window 2, Exp. 4	77
Table 8. Planned comparisons, Time window 1, Experiment 5	94
Table 9. Planned comparisons, Time window 2, Experiment 5	95
Table 10. Planned comparisons, Time window 0a, Experiment 5.	97
Table 11. Planned comparisons, Time window 0b, Experiment 5	98
Table 12. Planned comparisons, Time window 3, Experiment 5.	99

1 Introduction

Aristotle was famous for knowing everything. He taught that the brain exists merely to cool the blood and is not involved in the process of thinking. This is true only of certain persons. (Will Cuppy)

We experience the world as consisting of coherent entities. Things we see and interact with are physically separated in space, episodes we have experienced and which we communicate with others are separated in time and/or space, and we seldom face difficulties in these basic interactions with the world. Yet, this is actually not what the world is like. Our environment at any given point in time consists of dozens or hundreds of visual objects which are superimposed, and even basic speech is by no means physically univocal. Nevertheless, we manage to find important notes on a chaotic desk (well, most of the times) and we can make conversation at the much cited cocktail party. If this is noteworthy, even more impressive is the fact that we can represent and maintain structured and perceptually rich information over time, and can more or less accurately recall long-gone episodes and recognise people and objects we have seen only once before. Sometimes we even remember something without even knowing that we are remembering at all.

To fully appreciate our ability to identify and remember objects, one needs to consider processes of attention and feature binding in perception and memory. A main question is how our cognitive system manages to create a meaningful and neatly structured experience from a "sensational mess" and especially, for the purpose of the present thesis, how it preserves this structured experience. How does the system separate an object or item from contextual information, and is item and context information represented differentially in memory? How can one recognise an object or face encountered in the past and thereby retrieve and utilise both features of this "item" itself and – potentially but not necessarily – of the environmental context present at encoding? And actually, what is an item? What is context? Before tackling these fundamental questions, 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 Hubert 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 in-

stance, information about "what" an item is and information about "where" an item is are processed independently at some stage (Goodale & Humphrey, 1998; Mecklinger & Pfeifer, 1996; Ungerleider & Haxby, 1994). The same holds true for different perceptual object features, such as colour and shape (Corbetta & Miezin, 1990; Livingstone & Hubel, 1988). Objects are therefore represented as distributed entities in perception – and also in semantic knowledge (Kellenbach, Brett, & Patterson, 2001). In order to form a coherent representation, the single features of an event are mutually bound together (see Figure 1), whereby some are more strongly interconnected than others, forming units or chunks. These units are the origin of memory.

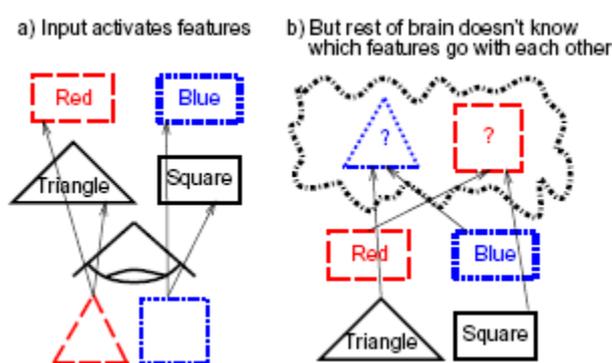


Figure 1. Illustration of the binding problem; figure adapted from Cer & O'Reilly (2006).

Exactly what these units 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 functional magnetic resonance imaging (fMRI), O'Craven, Downing, and Kanwisher (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. They let subjects view stimuli consisting of transparent and superimposed images of a face and a building, with one of them moving (Figure 2). Subjects attended to the face, the building, or the movement. The magnetic resonance signal of respective processing areas (fusiform area, parahippocampal place area, and area MT/MST for processing of faces, buildings, and visual movement, respectively) indicated that attending to the movement of a stimulus also led to increased activation in the area relevant for processing the identity of

the stimulus, despite all stimuli occupying the same spatial location. Thus, task-irrelevant attributes of an attended object will be selected along with task-relevant attributes, even when these attributes are independent. 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 (Herrmann, Mecklinger, & Pfeifer, 1999; Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996).



Figure 2. Stimuli used by O'Craven et al. (1999).

When feature information is processed by domain-specific modules (input modules in Figure 8), 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 put forward by Damasio (1989; Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996), Squire (1992), Haxby et al. (2001), Nyberg (2002), Paller (2000), or Cycowicz and colleagues (Cycowicz & Friedman, 2003; Cycowicz, Friedman, & Snodgrass, 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 event-related potential (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 tasks¹. 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

¹ I assume the reader to be familiar with basic key concepts of memory research, including "item" vs. "source memory", "implicit" vs. "explicit memory", "recognition" vs. "recall", "episodic" vs. "semantic memory", etc., as for instance detailed in Ecker (2002). Also, I will not attempt to outline basic principles of the ERP (or fMRI) method, as this has been extensively done elsewhere (see Handy, 2005; Picton et al., 2000; Rugg & Coles, 1996).

(Yonelinas, Hopfinger, Buonocore, Kroll, & Baynes, 2001). These studies indicate that access to stored visual perceptual information activates extrastriate cortex. Accordingly, occipital lesions may lead to amnesia for visual detail (Ogden, 1993). In a similar vein, Woodruff, Johnson, Uncapher, and Rugg (2005) demonstrated content-specificity effects (differential activity associated with retrieval of words vs. pictures) within left fusiform cortex. Guo, Voss, and Paller (2005) demonstrated that the binding or association of information can be made tangible in event-related potentials already at encoding. They reported ERPs predicting later retrieval of associative information (face plus name) to differ from the sum of subsequent memory potentials predicting item memory (i.e., face or name, respectively).

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. As we shall see, behavioural cognitive research has suggested that when successfully trying to remember a unitised chunk of information, memory retrieval is rather holistic², that is, all bound (and available) features will be involuntarily reactivated, no matter if they are task-relevant or not (we shall also see that this probably only applies to some features but not others). 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. Performances, however, are not necessarily dependent on this experience, but depend more 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

² 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 (see also Meiser & Bröder, 2002).

processing (TAP) approach (Roediger, Weldon, & Challis, 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 other words, the multimodal nature of the memory system gives rise to a situation in which 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 Objects in Our Head - Types and Tokens

Make everything as simple as possible, but not simpler. (Albert Einstein)

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 Figure 8), 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 sup-

ported by findings of relatively intact priming in amnesic patients in the context of impaired episodic recognition (Cave & Squire, 1992; Verfaellie, Gabrieli, Vaidya, Croce, & Reminger, 1996). 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 changes³. 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 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, Cooper, & Delaney, 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, Shallice, Gorno-Tempini, and Dolan (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.

³ This is not to say that effects relying on binding processes will not occasionally appear in implicit tests.

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 8). 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 (Schacter, Church, & Bolton, 1995; Kinoshita & Wayland, 1993; Zimmer, Steiner, & Ecker, 2002). 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; Verfaellie, Martin, Page, Parks, & Keane, 2006), and they do not show indirect effects healthy people do if relational information in visual scenes is manipulated (Ryan, Althoff, Whitlow, & Cohen, 2000). In conditioning, hippocampally lesioned animals do not show the typical decreased rates of responding when conditioned stimuli are presented in a different context (Penick & Solomon, 1991) or the temporary dip in responding when a CS predictive of a US is suddenly accompanied by another stimulus (Allen, Padilla, Myers, & Gluck, 2002). This points to an understanding of amnesia as a contextual 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, Fleischman, Keane, Reminger, and Morell (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, Stebbins, Masciari, Fleischman, and Gabrieli (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, Driver, Ward, & Sorensen, 1997), even potentially altering the semantically sensitive N400 ERP-component (Luck, Vogel, & Shapiro, 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, Kreiter, Russo, & Zhu, 1998; Paller & Gross, 1998; Paller, Hutson, Miller, & Boehm, 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 vs. Episodic Tokens

I propose, though, that the concept of tokens can be further subdivided, based on a distinction I have mentioned earlier, namely that recognition memory can rely on two different processes, familiarity and recollection.

2.2.1 Familiarity vs. Recollection

Familiarity may be described as a general feeling of prior occurrence, of having encountered a person or specific object before, without conscious access to contextual details, such as the time or place of the encounter. Recollection, on the other hand, refers to the conscious retrieval of specific details related to the encoding episode. These specifics are not limited to spatiotemporal context, but may as well consist in thoughts one had at the time of first encounter, or other items present at encoding. While introspectively appealing, the validity of this distinction has been experimentally supported by a wealth of findings from cognitive psychology and neuropsychology (see Mecklinger, 2000, 2006, 2007; Yonelinas, 2002a, 2002b; Zimmer, Mecklinger, & Lindenberger, 2006a, for reviews), although it is not unchallenged, as will be elaborated on in the General Discussion (e.g., Dunn, 2004; Humphreys, Bain, & Pike, 1989; see also Clark & Gronlund, 1996).

Functionally, findings do in fact suggest that familiarity is a rather fast and automatic process sufficient for mere item memory, whereas recollection is a rather controlled process needed for contextual integration (source memory; cf. Cabeza, 2006; also see Curran, Tanaka, & Weiskopf, 2002, for a similar claim). For instance, using a response deadline procedure, Gronlund and Ratcliff (1989) have demonstrated that item information is usually available before associative information can be accessed, arguing for a different time course of integration, an issue that will be elaborated on below and in the General Discussion. The ERP method employed throughout this thesis offers the potential for fine-grained analyses of cognitive processing, so this is an important point. Familiarity has been described as a standard signal-detection process with overlap between target and lure distributions, whereas recollection is assumed to be mnemonically more diagnostic (due to the hippocampus' ability to assign distinct representations even to similar stimuli, i.e. pattern separation, see below), although it is probably not truly an all-or-none high-threshold process (Norman & O'Reilly, 2003). I will later argue that these two processes of familiarity and recollection 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, but see Dunn, 2004).

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, Java, & Richardson-Klavehn, 1996) or study-test lag (mainly affecting familiarity; Yonelinas & Levy, 2002). Dobbins, Kroll, and Yonelinas (2004) have recently demonstrated that while recollection profits relatively more from elaborative encoding, rote rehearsal under divided attention benefits familiarity more than recollection. 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, Holdstock, Isaac, Hunkin, & Roberts, 2002). Srinivas and Verfaellie (2000) examined some of these

rather 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 (i.e., they showed congruency effects in reaction times), and argued convincingly that these effects were neither based on recollection (patients were severely impaired in a direct orientation test, there was no correlation between direct feature memory and indirect congruency effects, and congruency effects were still present in a subset of patients that showed chance-level feature memory), nor priming (see Figure 3). This speaks in favour of the type-token (fluency-familiarity) distinction in general (see also Habib, 2001; Nessler, Mecklinger, & Penney, 2005; Snodgrass, Hirshman, & Fan, 1996), 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. Verfaellie, Cook, and Keane (2003) argued that amnesics showed a stronger deficit in recollection as opposed to familiarity. Yet, this was based on the finding that (a) healthy subjects showed size congruency effects mainly in "Remember"-responses, and that (b) amnesics did not show size congruency effects even when overall performance level was matched. Although the conclusion is in line with the type-token model, from our point of view size congruency effects should be based on familiarity (and recollection) in healthy subjects. Whether or not familiarity is more affected than recollection in amnesics almost certainly depends on the exact extent of the lesion and is still highly debated. In this vein, 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, Vargha-Khadem, & Mishkin, 2001; but see Squire & Zola, 1998). In recognition, they even show the expected pattern in studies using the ERP method (Düzel, Vargha-Khadem, Heinze, & Mishkin, 2001), which leads us to the second point.

Namely, the two processes of recollection and familiarity are correlated with different and distinct 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 (late positive component- or LPC effect, 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).

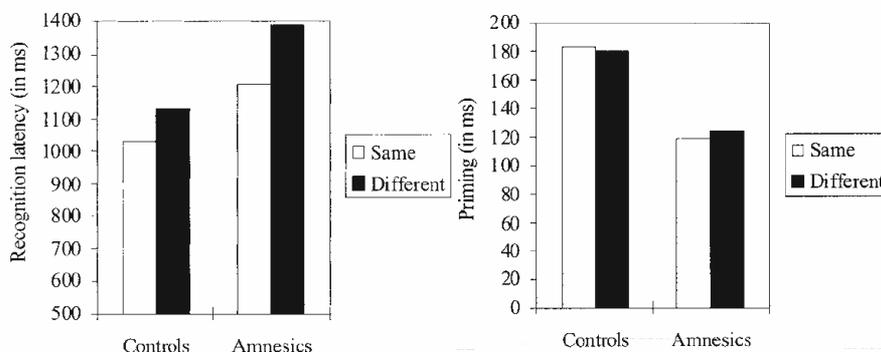


Figure 3. Results of Srinivas & Verfaellie (2000).

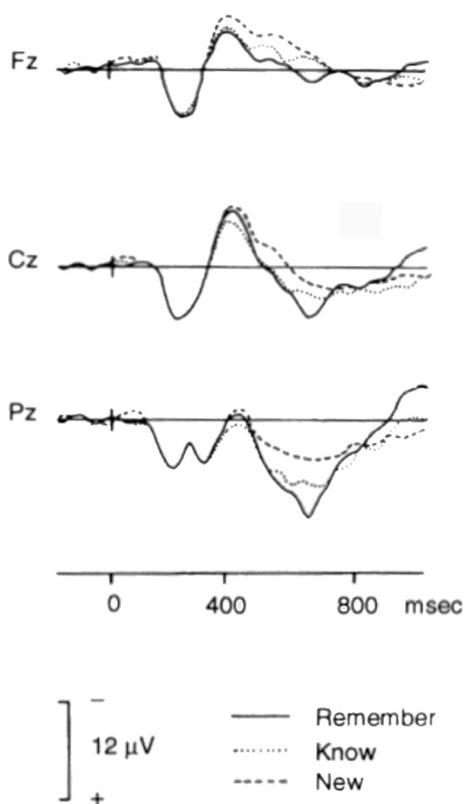


Figure 4. ERP old-new effects reported by Smith (1993).

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" (Curran, 2004; Smith, 1993; Wolk et al., 2006; see Figure 4). Moreover, it is insensitive to depth of processing manipulations (Rugg, Walla, et al., 1998), and is still present when recognition performance can no longer rely on recollection – in a patient with focal hippocampal damage (Düzel et al., 2001). 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, 2006).

The other highly consistently found old-new effect, the LPC effect, typically has a slightly left lateralised parietal topography, onsets at about 500 ms post-stimulus and lasts for about 200-300 ms. Many factors have led to its association with recollection, including that it is more pronounced for "Remember" vs. "Know" responses (Düzel, Yonelinas, Mangun, Heinze, & Tulving, 1997; Smith, 1993; see Figure 4), and that it is larger for items for which study context is additionally retrieved (Trott, Friedman, Ritter, & Fabiani, 1997) or for congruently vs. incongruently repeated items (Ranganath & Paller, 1999), respectively. Also, it is sensitive to depth of processing manipulations (Paller & Kutas, 1992; Rugg, Walla, et al., 1998).

Some relevant ERP work stems from behavioural response signal studies showing a nonmonotonic course of false alarm rates to similar lures in exclusion tasks, which has been taken as evidence for two successive retrieval operations (Hintzman & Curran, 1994, but see Brockdorff & Lamberts, 2000, and Rotello & Heit, 1999). Tim Curran (2000; Curran & Cleary, 2003) has repeatedly demonstrated that for almost equally familiar but slightly modified lures (i.e., changing words from singular to plural or vice versa, mirror-reversing pictures), the FN400 effect is more or less unaffected, whereas the LPC effect is largely reduced or absent. Note, however, that despite nonsignificant interactions in overall analyses, there is a tendency for perceptual specificity of the FN400 effect in some of Curran's results (see Figure 5, and also Curran & Dien, 2003). In Curran (2004) it was shown that divided attention at study selectively diminishes the LPC effect, leaving the FN400 effect uninfluenced, although behavioural data from the Remember/Know paradigm suggest there is also a small effect of divided attention on familiarity. For present purposes, it is important to note that ERP old-new effects allow for the examination of familiarity and recollection processes in recognition memory experiments.

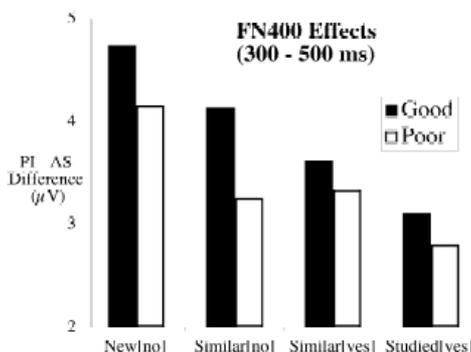


Figure 5. FN400 effects of Curran & Cleary (2003; manipulating object orientation) showing a tendency for perceptual sensitivity in the group of good performers.

Intracranial ERP data basically support the notion of distinct contributions of anterior medial temporal lobe cortices (MTLCs) and the hippocampus and their association with the mentioned scalp ERP effects (Grunwald et al., 1999; Trautner et al., 2004), showing also that memory formation is associated with differential MTLC and hippocampus activity (Elger et al., 1997; Fernández et al., 1999; Fernández, Klaver, Fell, Grunwald, & Elger, 2002).

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 and Mecklinger (2003). Although these highly interesting components point to the complexity of processes underlying recollection, for present purposes we will leave them aside.

Finally, as adumbrated above, recent neuroimaging studies have suggested that familiarity and recollection processes rely on at least partially independent brain regions. Although evidence is still mixed, the prevalent view seems to be that only recollection relies on the hippocampus proper, whereas familiarity may rely on medial temporal lobe cortices, especially the perirhinal cortex (see Figure 6). For example, using the Remember-Know procedure, Eldridge, Knowlton, Furmanski, Bookheimer, and Engel (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 cortex (PHC) regions when subjects were retrieving associative information (the study-colour of objects) as opposed to the retrieval of item information alone. Fan, Snodgrass, and Bilder (2003) found more left frontal activation in a similar comparison, but, however, no differences in hippocampal activity. Henson, Cansino, Herron, Robb, and Rugg (2003) reported evidence from a series of imaging studies for decreased activation in anterior MTLC for old versus new items across different materials and independent of task aspects such as demand for contextual retrieval and retrieval intention, strongly arguing for a differential contribution of anterior MTLC – encompassing perirhinal cortex – to familiarity versus recollection. More evidence from the imaging literature will be presented below, when discussing studies of item- versus source memory.

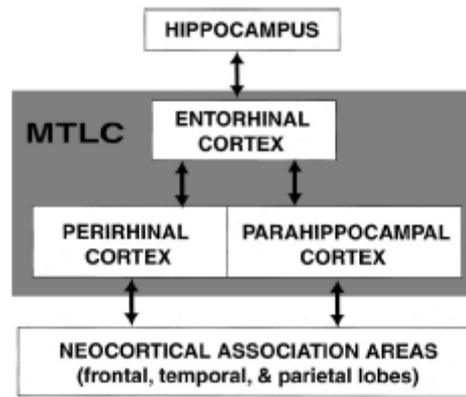


Figure 6. Schematic diagram depicting the MTL's role as an interface between neocortex and the hippocampus; figure adapted from Norman & O'Reilly (2003).

2.2.2 Object & Episodic Tokens and the Binding of Intrinsic & Extrinsic Information

Based on these results, I will now propose that there are two different kinds of representation underlying the two processes of familiarity and recollection: object tokens and episodic tokens. As this thesis is concerned with the influence of bound object and context features on recognition memory, I further propose that there is a basic difference in the neurocognitive representation of intrinsic object features and extrinsic context features. This distinction is not new; it has been put forth already by Solomon Asch and John Ceraso as early as 1960 (Asch, Ceraso, & Heimer, 1960; Ceraso, 1985, 1990), and a similar distinction can be found in the older literature under the labels of integral vs. separable dimensions (Garner, 1974). Troyer and Craik (2000) defined an intrinsic feature as *"an incidental aspect of the stimulus itself, such as colour, font, or voice of presentation. Extrinsic context is not part of the stimulus itself, but presumably part of the overall encoded event"* (p. 161). In a similar vein, Axel Mecklinger (1998, 2000, 2007) has linked recognition memory for object identity and spatial position to acontextual familiarity and context-based recollection processes, respectively. In a similar vein, using a Remember/Know procedure, Meiser and Sattler (2007, submitted) have recently proposed that familiarity shows only *"residual source memory... [whereas] ...conscious recollection is intrinsically related to the binding of item information and various kinds of context information, including context attributes that are external to the item itself and context attributes from different sensory modalities"* (p. 30 of the submitted manuscript).

Returning to the level of representation within our model, an *object token* can be thought of as a consolidated "object file", a concept introduced by Anne

Treisman (e.g., Treisman, 1992, 2006). An object token represents *intrinsic* information (within-item information belonging to the object, e.g., object colour), thus containing information about structural, accidental, and non-accidental attributes of specific encountered objects. It binds features supplied by fairly automatic data-driven processes when attending to an object, 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. At retrieval, all available information contained in the object token is (again, mainly automatically and involuntarily) reactivated, that is, the object token will typically be activated as a whole. The familiarity signal then results from the match between the object token in memory and the object file in perception (when attending to the test stimulus). We argue that the hippocampus proper is not essential for the binding processes involved in the (re-) construction of this representation, but that instead regions of the posterior neocortex in conjunction with MTL, in particular the perirhinal cortex, serve this purpose (see Figure 8).

Extrinsic or between-item information, on the other hand, is represented by the episodic token. The *episodic token* integrates (intrinsic) object information with multimodal contextual (*extrinsic*) information and thus supplies the basis for recollection, enabling subjects to retrieve the "how", "where" and "when" they encountered an object or person. Note that intrinsic information may be integrated into the episodic token as well; in particular, intrinsic information will be represented in the episodic token if some elaboration takes place at study, for example, if subjects generate predicates such as "that's a funny colour". This way, there can be some redundancy in feature representation (see also Johnson's distinction between perceptual and reflective processes, e.g., Johnson & Chalfonte, 1994). Furthermore, we assume that subjects can exercise a certain amount of control over what they recollect, so feature retrieval is rather deliberate and piecemeal (i.e., not holistic; cf. Trinkler, King, Spiers, & Burgess, 2006; Wilding, Fraser, & Herron, 2005). This also implies that the retrieval of irrelevant context information can be inhibited. 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 type of higher-level binding. In episodic memory, the hippocampus is seen to store patterns supplied by the neocortex, to form a sparse and compact code that is bidirectionally linked to neocortical representations, so that via pattern comple-

tion and separation a partial cue may later reinstate the compact code and thus the neocortical representation (see Figure 7).

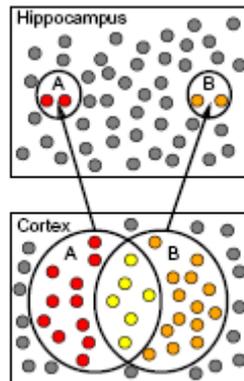


Figure 7: Schematic depiction of the sparse representation in the hippocampus as compared to cortical representation, illustrating pattern separation (less probability of representational overlap) and higher-order binding (units represent larger conjunctions of features); figure adapted from Cer & O'Reilly, 2006.

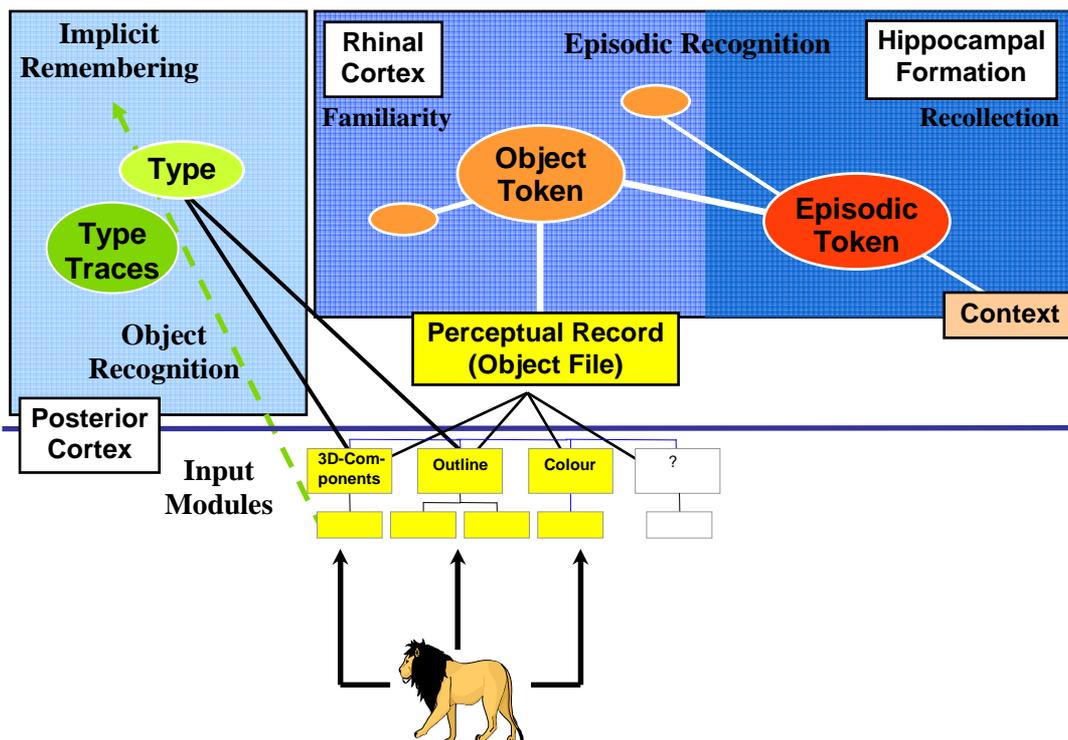


Figure 8: A schematic depiction of the neurocognitive type-token model of object long-term memory developed by Zimmer and colleagues; modified figure adapted from Ecker, Groh-Bordin, & Zimmer (2004).

Thus, only recollection via the episodic token should strongly rely on the hippocampus, whereas adjacent cortical regions should be able to support familiarity via the object token. The model therefore encompasses a neurocognitively plausible hierarchy (cf. Aggleton & Brown, 1999). In summary, we propose three different kinds of memory representation underlying different memory tasks: type-traces, object tokens and episodic tokens (cf. Figure 8). The first contribute to implicit memory, the second to familiarity in explicit recognition, and the third to recollection.

2.2.3 Support for the Token Distinction

A review of evidence supporting our token distinction can be found in Zimmer, Mecklinger, & Lindenberger (2006b). Apart from the cases of human amnesic patients with adult or perinatal onset hippocampal lesions exhibiting a relative sparing of item memory compared to associative memory (Aggleton & Shaw, 1996; Baddeley et al., 2001; Holdstock, 2005; Mayes et al., 2002; Srinivas & Verfaellie, 2000), other findings speak in favour of this conclusion, as well.

Firstly, the animal literature adds to the picture. For instance, Mumby, Gaskin, Glenn, Schramek, and Lehmann (2002) demonstrated in rats 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 in rats, Wan, Aggleton, and Brown (1999) showed that the CA1 field of the hippocampus (and the postrhinal cortex) is selectively 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). Norman and Eacott (2005) reported dissociable effects of perirhinal and postrhinal/fornix lesions in rats, with perirhinal lesions affecting performance in a non-contextual object task and postrhinal/fornix lesions affecting performance in an object-in-context task. Given the inclusion of the fornix in the extended hippocampal system promoted by Aggleton and Brown (1999), these findings are not surprising, although the relationship between hippocampus and postrhinal cortex requires further elucidation. Even in studies in which amnesic patients with relatively confined hippocampal lesions show deficits in episodic object recognition, patients with confirmed additional perirhinal lesions do even worse (Buffalo, Re-

ber, & Squire, 1999). Turning to the encoding side, Ranganath and colleagues (2004) were able to show in a 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, also offer some compelling evidence in favour of two different representation formats underlying these processes, especially when encompassing neuroimaging methods. In an fMRI study, Cansino, Maquet, Dolan, and Rugg (2002) found more right hippocampal activation when subjects correctly retrieved spatial source information as opposed to mere item information. Slotnick, Moo, Segal, and Hart (2003) found more parahippocampal activation when subjects only retrieved item information compared to spatial source information. Again turning to the encoding side, Davachi, Mitchell and Wagner (2003) found encoding activation in the hippocampus and the posterior parahippocampal cortex to predict later source (imagined vs. read) recollection while being uncorrelated with mere item recognition, whereas encoding activation in the perirhinal cortex predicted subsequent item recognition only (see Figure 9). 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 conditions⁴. Assumed prefrontal activation is also a major difference in ERP studies comparing item- and source memory (e.g., Trott et al., 1997).

A dissociation similar to the item- vs. context memory pattern of amnesic patients mentioned above has also been described for the elderly. For example, Cabeza (2006) has linked familiarity and recollection to item vs. relational memory, respectively, although he stresses that both involve associative processing, but to a different degree (see also Mandler, 1980). Accordingly, Yonelinas (2002a) stated that "*familiarity is not expected to support associative memory for two distinct items, unless the two items can be unitized or treated as a single larger item*" (p.447). We thus argue that familiarity memory is only associative as long as the to-be-associated information is part of the specific object (i.e., intrinsic) and its unitised representation (the object token). Similarly, Spencer and Raz (1995) have reported that age-related memory deficits affect "spatiotemporal context" memory

⁴ 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. The role of the PFC will be further discussed in the General Discussion.

more than memory for "perceptual context" (more likely to be encoded *in conjunction with content*) and "content" itself (see also Naveh-Benjamin, 2000, 2006). Likewise, Park and colleagues (Park, Puglisi, & Lutz, 1982; Park, Puglisi, & Sovacool, 1983) found stronger age effects on position- compared to pure item memory.

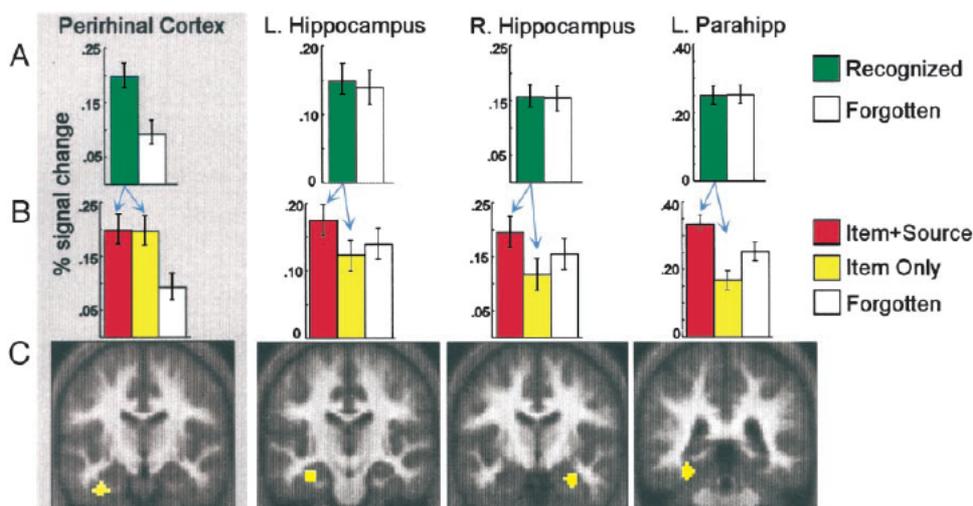


Figure 9. Differential potential of perirhinal cortex activity versus hippocampus and parahippocampal cortex activity to predict later item versus source memory; figure adapted from Davachi et al. (2003).

Concerning processing control, Troyer and Craik (2000; see also Hewitt, 1977, cited in Godden & Baddeley, 1980, and Smith & Vela, 2001) have argued that intrinsic information is automatically or necessarily processed, whereas extrinsic information requires more attentional resources and intentional processing. They argue that incidental (intrinsic) item information, tightly bound to the item, is automatically encoded, whereas richer, multimodal (extrinsic) 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, which suggests intrinsic binding takes place rather automatically. A similar view is promoted by Wilding (2004, Wilding et al., 2005), 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 extrinsic information is more under the control of subjects (Herron & Rugg, 2003).

Accordingly, we argue that *intrinsic* item features are involuntarily activated when an item is retrieved. Evidence for this can be found in the sensory mismatch

effects observed in episodic object recognition, already adumbrated above. As reported in many behavioural studies (Cooper, Biederman, & Hummel, 1992; Jolicoeur, 1987; Zimmer, 1995; Zimmer & Steiner, 2003; for a review, see Engelkamp, Zimmer, & de Vega, 2001), when the size, orientation, or colour of objects is changed from study to test, reaction times in episodic object recognition increase, even if the respective feature is irrelevant for the old/new decision (inclusion task). This is not to say, however, that these effects are always and only based on familiarity. For instance, Yonelinas and Jacoby (1995) found size congruency effects on both familiarity and recollection measures, using process dissociation, independent-Remember/Know and signal detection techniques. Rajaram (1996) even found an influence of size manipulation on "Remember" responses only, however, "Know" responses were not analysed in this study due to the controversial exclusive-Remember/Know procedure used (see also Verfaellie et al., 2003). Thus, note that we do not argue against an influence of perceptual manipulations on recollection; after all, we have stated that the episodic token may comprise *both* item *and* contextual information. Further empirical support for the involuntary activation of intrinsic information can be found in studies on colour memory. Wilton (1989) found better colour recognition for surface vs. background colour even following incidental study. Similarly, Walker and Cuthbert (1998) found incidental memory effects of colour only if colour and shape were unitised, that is, colour was part of the perceptual unit of the item (see also Guillem, Bicu, & Debrulle, 2001; Zimmer & Steiner, submitted). Obviously, information regarding the sensory features of an item is part of its memory representation, and this information is involuntarily accessed in episodic object recognition, even if the features are irrelevant for recognition.

Regarding manipulations of *extrinsic* context, the picture is less clear. Studies on context effects on item memory delimit a quite heterogeneous field with rather diverse definitions of what is considered context. For instance, Smith and Vela (2001) reviewed a number of studies in which experimental context was manipulated. They found that context effects on recognition performance decrease if context processing is suppressed either at study or test. However, Smith and Vela only included studies manipulating incidentally encoded, *global* context in their meta-analysis. The term global context refers to slow-changing contexts such as the room an experiment takes place in. It seems to be widely accepted that the hippocampus proper is important for the integration of global context (but see General Discussion). In order to have a more straightforward test of our hypotheses, in the current experiments we used more object-like, local contexts that were

clearly contextual by definition, but not too abstract, to make sure that contexts were perceptually similar to the objects and not located in attentional periphery. There are only few studies investigating the effects of *local* context manipulations. Murnane, Phelps, and Malmberg (1999), for instance, reported context effects on word recognition, but only in a "rich context" condition (e.g., words written on a blackboard in a classroom scene; as opposed to "simple contexts" such as location or background colour). They argued that the probability of the integration of contextual information is a function of its meaningfulness. The more meaningful a context is, the easier its integration by way of elaboration. Subjects in the experiment of Gooding, Mayes, and Meudell (1997) studied complex arbitrary patterns in the context of unique objects. The authors found strong context effects even in accuracy data. In summary, these results suggest that context influence increases with a decrease of item distinctiveness and with an increase of the richness of context information.

We should stress here that it is not easy to exactly define which features are intrinsic and which are extrinsic. As noted in the introduction, following Reinitz (2003; Reinitz & Hannigan, 2001, 2004), all features that are simultaneously attended to might become a unit in perception and memory. Both behavioural and imaging studies suggest that whole objects are preferably selected by attentional processes in perception, and therefore objects are likely units of memory (Duncan, 1984; Duncan, Martens, & Ward, 1997; Duncan & Nimmo-Smith, 1996; O'Craven et al., 1999). In our terms, focal attention on an object results in the generation of an object token driven by bottom-up processes interacting with top-down processes, and this object token binds intrinsic information as grouped by perceptual mechanisms. The role of attentional processing will be further explored in Experiment 5.

Proceeding to the ERP literature, the ERP method has in recent years been employed in order to assess the plausibility of dual vs. single process accounts of recognition memory. More specifically, source memory paradigms were used in many cases to draw inferences about familiarity and recollection from ERPs. Fortunately for our present concerns, these studies have often involved perceptual manipulations, so given the presumption that ERP effects can be taken as correlates of familiarity and recollection, these manipulations can be reviewed under the current perspective. In these studies, recollection is inferred from the retrieval of a specific piece of source information. This could in fact be any aspect of the studied item or its context, for instance its colour (e.g., Cycowicz et al.,

2001) or its location (e.g., Van Petten, Senkfor, & Newberg, 2000). If a subject recognises an item as old, but fails to correctly assess the specific feature, the response is thought to reflect familiarity without recollection.

In some cases, the items are studied together with a specific feature (e.g., items are presented in different colours or at different screen positions) and are then tested neutrally (e.g., in black or at the centre of the screen). In these studies, there seems to be a tendency for larger ERP old-new effects when source information is additionally retrieved. For instance, Cykowicz et al. (2001) presented coloured line drawings at study which were then tested in black and found that the parietal old-new effect associated with correct source retrieval had a different, more frontally distributed topography compared to incorrect source judgements. Wilding et al. (2005) had subjects study coloured words and at test required them to accept only items – now presented in white – of one study colour while rejecting the other. They found a larger LPC effect for targets than for non-targets in two experiments. One disadvantage of this procedure is that all old test items will be equally familiar, because the feature of interest is always different from study.

To examine familiarity processes more thoroughly, a better suited approach is to change the respective feature only for a subset of old items, and then comparing Same and Different repetitions (i.e., old items presented in the same or different colour/position). A difference in a dependent variable between Same and Different conditions (i.e., a congruency effect) is then interpreted as an index of source memory. Taken together, there is a tendency for larger ERP old-new effects when no item features are changed from study to test. However, evidence is still quite mixed.

Wilding, Doyle, and Rugg (1995) reported a behavioural congruency effect (slower and less accurate responses) in a source memory task manipulating word modality; however, they found no ERP congruency effects. With a procedure quite similar to the one adopted here (manipulating the colour of line drawings), Friedman, Cykowicz, and Bersick (2005) found congruency effects in their behavioural exclusion test data (but not in a pure old/new recognition test). There were no reliable ERP congruency effects, although the authors reported a tendency towards a larger parietal old-new effect (and visual inspection suggests: also a larger mid-frontal effect) for Same presentations. Using a somewhat more perceptual study task, Ranganath and Paller (1999) manipulated the aspect ratio of images and

found congruency effects in both the behavioural and ERP data (which was reported across both an item and a source memory task), although the reported ERP old-new effect had a rather broad and posterior distribution. They concluded that Same items were more perceptually vivid than Different ones.

Van Petten et al. (2000), again comparing an old/new to a source memory test, reported no significant congruency effects when manipulating object position. However, they 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 Fernández and colleagues (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 Fernández study) and later reconstruction (the Van Petten study) of an object- and an episodic token, respectively. Senkfor and Van Petten (1998) found congruency effects in a source memory task when the voice of spoken words was manipulated, but no congruency effects in an item memory task. Again, they interpreted significantly longer reaction times in source- versus item memory tasks and late frontal old-new effects as an indication of two successive processes of item retrieval and source integration. Finally, Schloerscheidt and Rugg (2004) manipulated the picture-word format of stimuli and reported congruency effects in RT and ERP data (in both the FN400 and LPC components; larger for pictures vs. words at test) in an inclusion task.

Thus, given the wealth of behavioural studies reporting such effects, it is somewhat astonishing that there are hitherto relatively few ERP studies (see also references below to Christian Groh-Bordin's work) unequivocally demonstrating RT congruency effects in an item memory task (thus suggesting that these effects are not only due to task demands).

3 Synopsis

Taken together, perceptual study-test manipulations frequently affect behavioural indices of recognition memory, suggesting that perceptual features are included in the representation accessed in such tasks. Yet, these effects do not always occur, and the neural and electrophysiological correlates of this influence remain somewhat unclear. For our purposes, there is one important shortcoming of the reviewed studies with regard to the features they utilise: inferences about recollection and familiarity are made on the basis of whether or not a specific feature is retrieved, or whether or not an altered feature influences recognition. Thereby, intrinsic features of the items (e.g., colour) and extrinsic features of the study context (e.g., study list) are treated as equivalent, without considering the possibility that these features contribute differently to the processes of familiarity and recollection. Our intrinsic/extrinsic distinction could thus have important consequences and could at least partially resolve ambiguities in previous recognition memory and source memory research. For instance, if we assume that familiarity is only influenced by intrinsic information, it becomes clear why some studies using rather extrinsic features have not reported any effects on the ERP component associated with familiarity (e.g., Van Petten et al., 2000). With regard to the two-successive-processes account of Van Petten and Senkfor mentioned above, suggesting feature effects taking place after item assessment, we agree that there are two distinctive processes, but argue that item and feature assessment are only really successive if the to-be-integrated feature is extrinsic (e.g., spatial position) or if the processing of the feature per se takes considerably longer than the identification of the item, as is the case with the voice of spoken words (Senkfor & Van Petten, 1998).

ERP recognition memory studies more explicitly testing the influence of perceptual features include a study by Curran and Cleary (2003), who reported an ERP congruency effect selectively on the LPC when manipulating the orientation of pictures in an exclusion task (following intentional study). In contrast, Groh-Bordin, Zimmer, and Mecklinger (2005), who also manipulated the orientation of picture stimuli, found RT congruency effects accompanied by a selective ERP congruency effect on the FN400 in a pure old/new task with no feature relevance (following incidental study; see Figure 10). Employing a procedure similar to the one here, Groh-Bordin, Zimmer, and Ecker (2006) reported RT congruency effects manipulating the colour of objects in an inclusion task with subsequent fea-

ture decision. Their behavioural findings were accompanied by attenuations of both early and late ERP old-new effects for incongruent items.

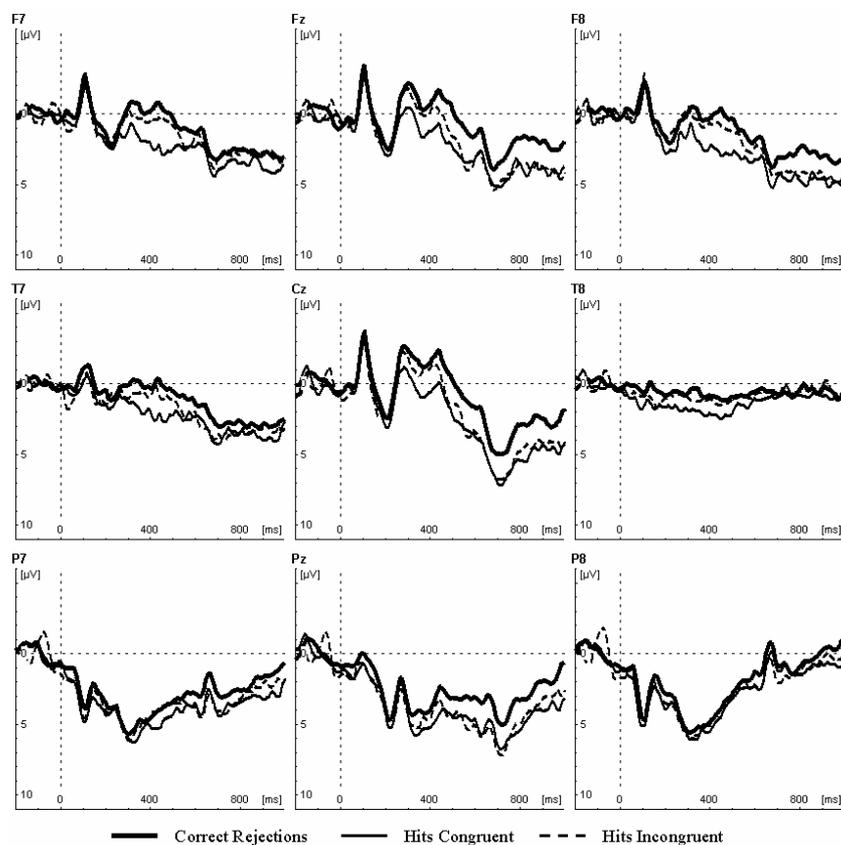


Figure 10. Selective effect of perceptual study-test congruency on the FN400 old-new effect; figure adapted from Groh-Bordin et al. (2005).

One of the few ERP studies investigating local context effects on object recognition was conducted by Tsivilis, Otten, and Rugg (2001). They had subjects study objects embedded in different complex landscape scenes. Contrary to our position, they found context effects on reaction times in an object old/new decision, but no electrophysiological correlate of this behavioural effect, so their results remain somewhat inconclusive (see Experiment 5). In conclusion, it is clear that perceptual manipulations do affect the electrophysiological correlates of recognition memory, although the exact constraints remain somewhat unclear.

In particular and beyond the evaluation of the type-token model, this thesis sought to clarify the issue of context effects on familiarity. In terms of dominant theoretical frameworks, context effects are basically explained by dual-processing (DP) theories in terms of encoding specificity (Tulving & Thomson, 1973). Rein-

stated context leads to higher target accessibility via a slow, controlled recollection or search process. Accordingly, Mandler (1980) claimed that familiarity is "context-free". Single-process or global matching (GM) theories, on the other hand, argue that context affects the assessment of familiarity – if context information is incorporated into the test probe, reinstating the study context will contribute to the assessment of the match-strength (e.g., Gillund & Shiffrin, 1984). Ti-berghien (1986) has suggested that both the familiarity of the context and the item may contribute to the familiarity estimate (see especially Exp. 5). Furthermore, there are claims in the literature that the mid-frontal ERP old-new effect reflects conceptual processing (see especially Voss & Paller, 2006; Yovel & Paller, 2004). These authors also link the FN400 effect to implicit memory (i.e., conceptual priming), but as noted above, even when assuming the effect to reflect explicit familiarity, there is evidence in the literature suggesting a mainly conceptual basis of this process (Curran, 2000; Curran & Cleary, 2003). Given contrary results by Groh-Bordin et al. (2005, 2006), this thesis sought to shed more light on the question of whether or not familiarity is in principle perceptually specific, and how the contradictory findings may have been based on methodological peculiarities of the respective studies.

Basically, given our model, intrinsic and extrinsic information should be differently represented and/or processed in memory, and thus the study-test manipulation of intrinsic and extrinsic (contextual) item features should differently affect the processes of familiarity and recollection. This prediction was tested by analysing both behavioural and electrophysiological (ERP) data in a series of object recognition experiments. In none of the reviewed studies, using behavioural and/or ERP methods, were changes of intrinsic and extrinsic information simultaneously contrasted, holding all other aspects of the study episode constant. This was the aim of Experiment 1.

4 Experiments I

A theory is something nobody believes, except the person who made it. An experiment is something everybody believes, except the person who made it. (Albert Einstein)

4.1 Experiment 1

4.1.1 Design and Hypotheses

Participants studied coloured objects (silhouettes) presented on arbitrarily shaped grey context figures in an intentional study phase. At test, subjects were first required to judge the old/new status of the objects, ignoring their colour and context (object old/new decision). From study to test, we manipulated either the colour of the object (intrinsic feature) or the shape of the background (extrinsic feature). This was a between-subjects manipulation, so there was a Colour and a Context group (i.e., in each group, only one feature was in fact manipulated). For half the repeated items, either the colour or the background was altered from study to test; the other half was repeated identically. Following each "old"-response, items were presented again and subjects were asked to assess whether or not the respective feature had changed (feature decision). Further details follow below.

Concerning the current choice of intrinsic/extrinsic features, we chose local, object-like contexts, because global contexts such as the experimental room are very different from actual objects, and we wanted to make sure that the effects we measure are not due to these basic differences. This implies that our operationalisation of context is perhaps not the most typical, but a quite conservative one with respect to our hypotheses – the image of a tent presented in front of a scrap-of-paper-like background could be perceived (and memorised) as such or simply as a scrap of paper with a tent on it (i.e., one unitised object). Turning to the intrinsic level, colour should be processed as an intrinsic feature, given previous research (see above, and also Zimmer & Steiner, submitted)⁵. We assume that the current

⁵ Line drawings (i.e., only contours are coloured, as opposed to fully coloured silhouettes as used in the present experiments) could be an exception: colour could be perceived as a feature of the medium (e.g., the chalk). This might be the reason Friedman et al. (2005), manipulating the colour of line drawings, did not report a significant congruency effect on the FN400 ERP old-new effect.

choice of features will fit most researchers' definitions, as it incorporates both a spatial and a figure/ground contrast.

Changing an intrinsic feature of the object should involuntarily hamper recognition performance (i.e., reaction times should increase), because the object token will be automatically reactivated in whole when the cue is presented. In contrast, contextual information should rely more on controlled processes, and subjects should thus be able to mask out the irrelevant extrinsic context; hence a changed background should not impair object recognition. Importantly, however, we expected both features to be voluntarily recognisable to a comparable degree, demonstrating that the specific associations of objects with colours and contexts, respectively, had been learnt and were potentially accessible at test (as indexed by feature decision performance). This would constitute hitherto lacking behavioural evidence, taken from a single experiment, supporting the claim of differential processing of intrinsic versus extrinsic features.

As far as object decision ERPs are concerned, we hypothesised that the manipulation of the intrinsic feature should generally affect old-new effects. The rationale behind this claim is that the processes underlying these effects should be sensitive to an exact match of cue and memory representation, thus signalling reoccurrence (Giovanello, Schnyer, & Verfaellie, 2004). In particular, the manipulation of colour should become apparent in a modulation of the frontal old-new effect. However, because of the explicit and associative learning instruction, colour information is potentially also bound into the episodic token by more controlled processes. Hence, the manipulation of colour might also modulate parietal effects. In contrast, the manipulation of context should not affect the FN400 effect; note that this is the central point here, as our model allows for effects of intrinsic features on the LPC, but precludes effects of extrinsic features on the FN400. Finally, the assumption that extrinsic information as part of the episodic token influences recollection suggests the LPC effect should be affected by the contextual manipulation; yet, subjects were instructed to ignore feature manipulations, so to the extent that they followed instructions, the extrinsic manipulation should not affect the LPC.

4.1.2 Methods

4.1.2.1 Material and Procedure

In Experiment 1, an object feature (colour) or the shape of an arbitrary grey background (context) were manipulated between study and test. At study, subjects were presented 80 images of everyday objects, which could appear in one of four different arbitrary colours (red, blue, green, yellow), and on one of four distinct but arbitrary backgrounds (see Figure 11). Every item was presented twice in direct succession to enhance encoding (presentation time was 2 x 1.5 s with a 1 s break, ISI was 2.5 s). In fact, every specific object only existed in two colour versions (Figure 11 thus displays two different objects), and some attention was paid to the assignment of colours, although these were largely arbitrary. Yet, as most objects have some more or less typical colours, we made sure that colours were always equally appropriate across these two versions (e.g., a green and a blue t-shirt), although no formal analysis was carried out. In particular, there were no colour changes that would have implied a change of meaning (e.g., red apple → green apple = “Fuji” → “Granny Smith”). The item set largely consisted of artefacts (77 %). Study 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 either in a different colour or on a different background (i.e., in a new context). This colour-context factor was varied between subjects, that is, in one particular group of subjects only one feature – colour or context, respectively – was manipulated. First and second presentation colours and contexts as well as their transitions were counterbalanced within each subject, that is, seeing a green object was as likely as seeing a yellow one, and the transition from red to blue in an Different study-test case was as likely as a transition from red to green, or any other combination. The same holds true for contexts.

At test, 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). This inclusion task was the focus of interest. We emphasised the need for quick responses in subjects' instructions concerning the old/new decision. The test trial structure was as follows: a fixation cross was presented centrally for 300 ms, followed by a blank screen for 200 ms. The item was presented for 2 s, and subjects were to respond "old" or "new" by pressing a key, with a maximum reaction time of 3 s from stimulus onset. In case of an "old" response, the cue "Colour?" or "Background?" ap-

peared on the screen (after a 1500 ms blank screen), depending on the condition. Participants were then to indicate whether or not the colour or the context of the object, respectively, had changed (feature decision). Features were assessed in order to check if feature information was in principle available. Again, maximum reaction time was 3 s from stimulus onset. The inter trial interval was 2 s from key press or expiration of maximum response time. The Shift keys were used for both the old/new and the feature decision, the assignment of keys to responses was counterbalanced across subjects to avoid undue lateralisation effects in ERPs. Twenty-seven subjects took part in this experiment, but eleven had to be excluded due to bad performance (object recognition at chance level), technical problems, or excessive EOG artefact, leaving sixteen subjects that entered the analysis, eight per group (mean age was 22/21, ranging from 19-29/18-25, in the Colour/Context groups, respectively, 5/6 participants were females).

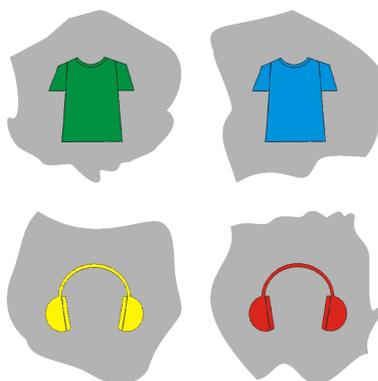


Figure 11. Examples of items used in Experiment 1; modified figure adapted from Ecker et al. (2004).

4.1.2.2 EEG/ERP Recording and Analysis

The EEG was recorded from 63 Ag/AgCl electrodes using an elastic cap (Electro-Cap International Inc., Eaton, OH). Electrodes were arranged according to the extended 10-20 system. Signals were amplified using an AC coupled amplifier (Brain Amp MR, Brain Products, Munich; time constant 10 seconds) and referenced to left mastoid, but later re-referenced offline to linked mastoids. The sampling rate was 250 Hz, and a 50 Hz notch filter was applied online. The impedances of all electrodes were kept below 10 k Ω , and ocular blinks as well as vertical and horizontal eye movements were registered by two electrodes above and below the right eye, and two further electrodes at the outer canthi of both eyes, respectively. EOG artefacts were then corrected offline (Gratton, Coles, & Donchin, 1983). Before averaging, trials containing artefacts (lowest allowed activ-

ity in successive 100 ms intervals \pm 0.5 microvolts, maximum amplitude in the recording epoch \pm 150 microvolts, maximum voltage step between two successive sampling points 50 microvolts, maximum difference between any two sampling points within an epoch 150 microvolts) were excluded (8.7 % of object decision trials). Digital bandpass filtering was applied between 0.1 and 20 Hz. Then, ERPs were calculated by time-locked signal averaging, using the time window from -200 to 1300 ms relative to stimulus onset. Data were baseline-corrected using the 200 ms before stimulus onset, in which none of the compared conditions differed.

Object decision ERPs were calculated for both groups separately. Only trials with a correct old/new response were included into the analysis. There were too few trials available for contrasting object hits with versus without a correct subsequent feature decision. This procedure resulted in the following conditions (mean numbers of trials for Colour group/Context group in parentheses): Same hits (28/27), Different hits (29/27), and correct rejections (59/63). The minimum number of trials for inclusion into a grand average was 16. Statistical analyses were performed by means of analyses of variance (ANOVAs) on mean voltages in several different time windows (details below). Nine regions of interest (ROIs) constituting a three by three matrix were defined. ROIs and respective electrodes were: left-frontal: AF3, F5, F7; mid-frontal: Fz, F1, F2; left-central: C5, CP5, T7; mid-central: Cz, C1, C2; left-posterior: P5, P7, PO7; mid-posterior: Pz, P1, P2; and the respective right counterparts to left-sided regions and electrodes. The resulting three-level factors Anterior-Posterior (AP) and Laterality (Lat) were used in all analyses. Important ERP ANOVAs – indexed by an ϵ in the ERP results section – were additionally performed on nine selected single electrodes, one from each ROI (F/C/P5, F/C/Pz, F/C/P6); results coincided in all cases. The Greenhouse-Geisser correction for nonsphericity was applied (Greenhouse & Geisser, 1959); original degrees of freedom together with respective ϵ -values and corrected p-values are reported in the following. Resulting from our hypotheses, follow-up planned comparisons were calculated. Specific (maximal) p-values are given for these comparisons.

Aspects of EEG/ERP recording pertain to the following experiments as well, unless indicated otherwise in the respective Methods section.

4.1.3 Results and Discussion

4.1.3.1 Behavioural Results and Discussion

As in other experiments (Zimmer & Steiner, 2003), the incongruency of colour produced costs in episodic object recognition, i.e., Colour-Different 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 12). 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 proven 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) Same trials (1271 ms) differed from Colour Different (1373 ms; $df = 24$, $MSE = 12998$, $p = .04$) but not from Context Different trials (1288 ms).

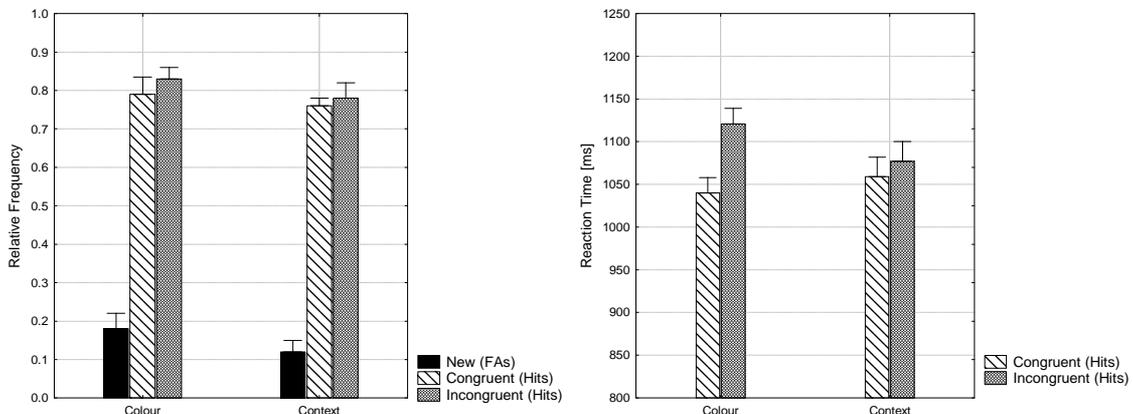


Figure 12: Object (old-new) decision data, Experiment 1. Relative frequencies for all "yes"-responses as a function of item status (left-hand side) and average response times for hits as a function of item status (right-hand side); terms "congruent" and "incongruent" refer to "Same" and "Different" conditions, respectively; FAs refers to false alarms; error bars indicate within subjects standard errors of mean; figure adapted from Ecker et al. (2004).

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 Colour-Same (hits) and Colour-Different (false alarms) trials was highly significant (.59 vs. .17; $F(1,14) = 58.85$, $MSE = .012$, $p < .001$), while there was no difference between Context-Same and Context-Different trials (.57 vs. .52; $F < 1$). The analysis of reaction times for the feature decision yielded no significant results (see Figure 13). 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.

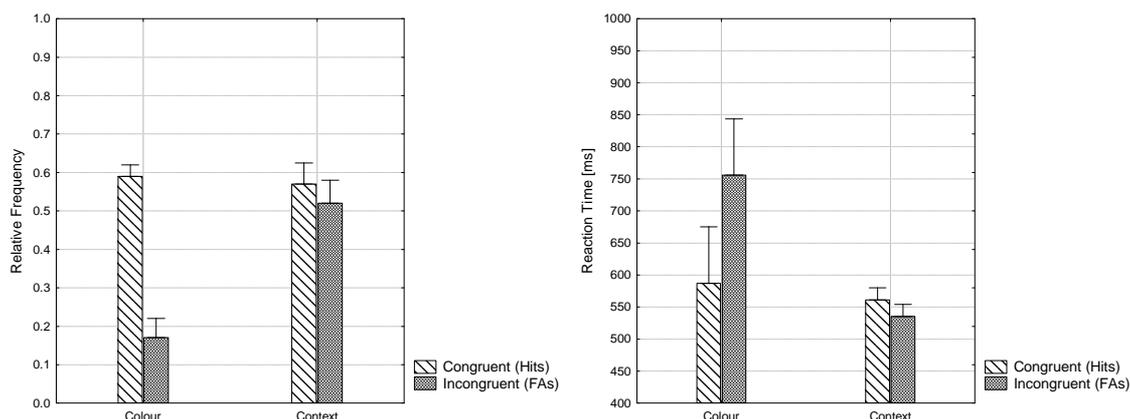


Figure 13: Feature decision data, Experiment 1. Relative frequencies (left-hand side) and average response times (right-hand side) for all "yes"-responses as a function of item status; terms "congruent" and "incongruent" refer to "Same" and "Different" conditions, respectively; FAs refers to false alarms; error bars indicate within subjects standard errors of mean; figure adapted from Ecker et al. (2004).

4.1.3.2 ERP Results and Discussion

Nevertheless shortly turning to the ERP data recorded during the object decision phase, 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, however, no significant circumscribed frontal old-new effect. Yet, 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 14).

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; Groh-Bordin et al., 2005). 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.

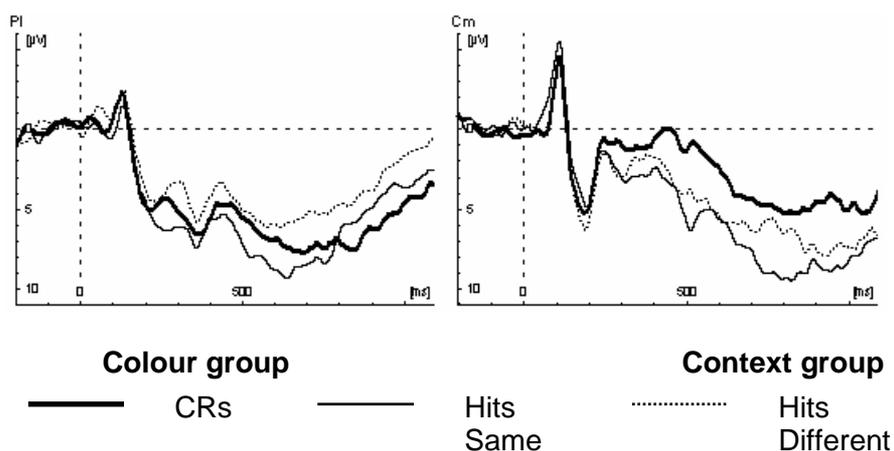


Figure 14: Grand average waveforms from the object (old-new) decision at left parietal ROI for the Colour group (left-hand side) and mid central ROI for the Context group (right-hand side) as a function of item status, Experiment 1; time scaling ranges from -200 to 1100 ms after stimulus onset; positive deflections are displayed downward; modified figure adapted from Ecker et al. (2004).

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 itself⁶ (cf. Rugg, Fletcher, Chua, & Dolan, 1999; Ranganath, Johnson, & D'Esposito, 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.

4.2 Experiment 2

4.2.1 Design, Hypotheses and Methods

The major drawback of Experiment 1 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, 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 15) and we introduced two separate study-

⁶ Note that this effect has nothing to do with the well studied but earlier onsetting familiarity component mentioned above.

test blocks. Subjects were led to believe that the computer randomly selected and assigned one of the two conditions before each test block. Thus, if subjects of the Colour group had judged whether objects' colours had changed in the first test block, they still thought that both conditions were equally probable in the second test block. Thereby, we made sure that subjects did not focus on the feature they had assessed in the first test block during the second study block. Nevertheless, we included a Block factor in behavioural analyses in order to control for possible block effects. 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. Presentation time was 3.5 s, ISI was 2.5 s. At test, we presented each item during the object decision *and again* for the feature decision task (together with the "Colour?" or "Background?" cue) 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).

Analysis was similar to Experiment 1, however, maximum amplitude in the recording epoch was reset to +/- 100 microvolts. 6.9 % of object decision trials were rejected due to artefacts. Only trials with both a correct old/new response and a correct subsequent feature decision (for old items) were included into the analysis. This procedure resulted in the following conditions (mean numbers of trials for Colour group/Context group in parentheses): Same hits (30/29), Different hits (28/26), and correct rejections (69/73).

Thirty-two subjects (16 per group), all students at Saarland University, took part in this experiment (mean age was 23/25, ranging from 19-28/20-36, in the Colour/Context groups, respectively, 10/9 participants were females). The ERP data of three participants, two of the Context and one of the Colour group, had to be excluded due to excessive EEG artefact.

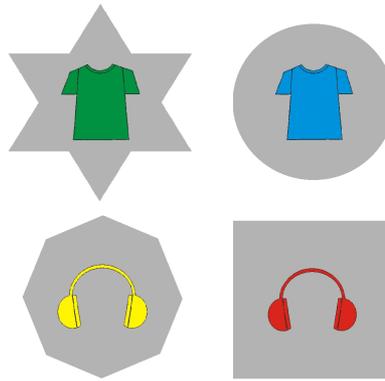


Figure 15. Examples of items used in Experiment 2; figure adapted from Ecker, Zimmer, & Groh-Bordin (in press).

4.2.2 Results and Discussion

4.2.2.1 Behavioural Results and Discussion

a. Object decision.

Accuracy and reaction time data are depicted in Figure 16. The accuracy data show that performances were generally very good⁷. Subjects were able to recognise almost every object that had been part of the study set (see left hand side of Figure 16). Differing from the figure, accuracy analyses were performed on Pr-scores (hit - false alarm rates; cf. Snodgrass & Corwin, 1988), as these are a better indication of true performance levels. Performance in all conditions and blocks was well above chance, all $t(15/31) > 20.48$, $p < .001$. In a $2 \times 2 \times 2$ ANOVA with the factors Block (1 vs. 2), Condition (Same vs. Different), and Group (Colour vs. Context), there was a significant interaction of Condition and Group ($F(1,30) = 11.02$; $MSE = .02$; $p = .002$), indicating worse performance for Colour-Different items (.88) compared to the other conditions (.91-.92). Of course, though, this effect has to be interpreted with caution due to reduced variance caused by near to ceiling performances. Post-hoc contrasts confirmed that Same and Different performance differed in the Colour ($F(1,30) = 15.13$; $p < .001$) but not the Context group ($F < 1$). Although there was a main effect of Block, $F(1,30) = 4.33$; $MSE = .03$; $p < .05$, indicating slightly improved performance in block 2, there were no interactions, all $F < 1.2$. There was a tendency towards a more lib-

⁷ Based on a pre-study (cf. Ecker et al., 2004) in which performances were a lot worse, we introduced dual study-test phases and presented every study item twice. Thus, the high performance level was strived for, also because no effects on accuracy had been predicted.

eral response bias (calculated as $Br = \text{false alarm rate}/(1-Pr)$ ⁸; cf. Snodgrass & Corwin, 1988) in the Colour group (.55 vs. .38), but this was not significant across blocks, $F(1,30) = 3.88, p > .05$.

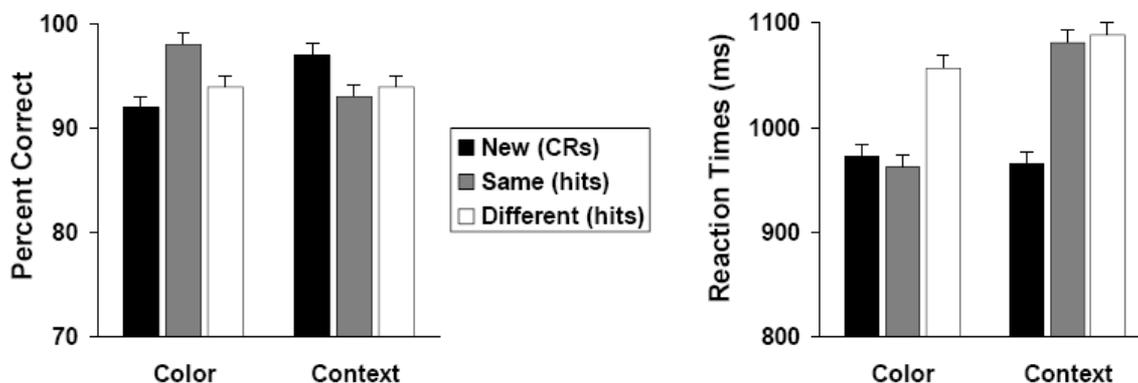


Figure 16. Object (old/new) decision data, Experiment 2. Percent correct (left-hand side) and mean response times in milliseconds (right-hand side) for all correct responses as a function of item status; CRs refers to correct rejections; error bars indicate within subjects standard errors of mean; figure adapted from Ecker et al. (in press).

The according analysis of mean reaction times including correct rejections – a Block by Condition (Same, Different, New) by Group ANOVA – revealed a marginally significant interaction between Condition and Group ($F(2,60) = 2.56; p < .1$), alongside a main effect of Condition ($F(2,60) = 9.84; p < .001$). Post-hoc tests indicated that Different hits differed from both Same hits and correct rejections in the Colour group (both $F > 4.55$, both $p < .05$), whereas in the Context group, correct rejections differed from both kinds of hits (both $F > 7.56$, both $p < .05$).

Restricting this analysis to hits, given the experimental hypotheses, revealed a significant Condition by Group interaction, $F(1,30) = 6.00, MSE = 7293, p < .05$ (see right hand side of Figure 16). This was due to a benefit for identical repetitions in the Colour group, that is, Colour Same objects were recognised faster than Colour Different ones, even though colour was not relevant for the old/new decision (962 ms vs. 1057 ms; $F(1,30) = 19.96, p < .001$). In contrast, context manipulation had no effect on reaction times (1081 ms vs. 1089 ms; $F < 1.01$). Again, there was a main effect of Block, indicating that subjects be-

⁸ In light of ceiling effects, hit- and false alarm rates of 1 and 0, respectively, were adjusted by subtracting or adding $1/(2N)$, in order to allow for the calculation of Br.

came faster with time, but this interacted neither with Condition nor Group, all $F < 1.41$, $p > .24$.

These findings are only relevant, however, if context was indeed integrated in the first place. Therefore, it has to be ruled out that context manipulations might have not affected the object decision simply because subjects had not associated objects with their contexts, as in Experiment 1. This question was addressed by analysing the feature decision data, depicted in Figure 17.

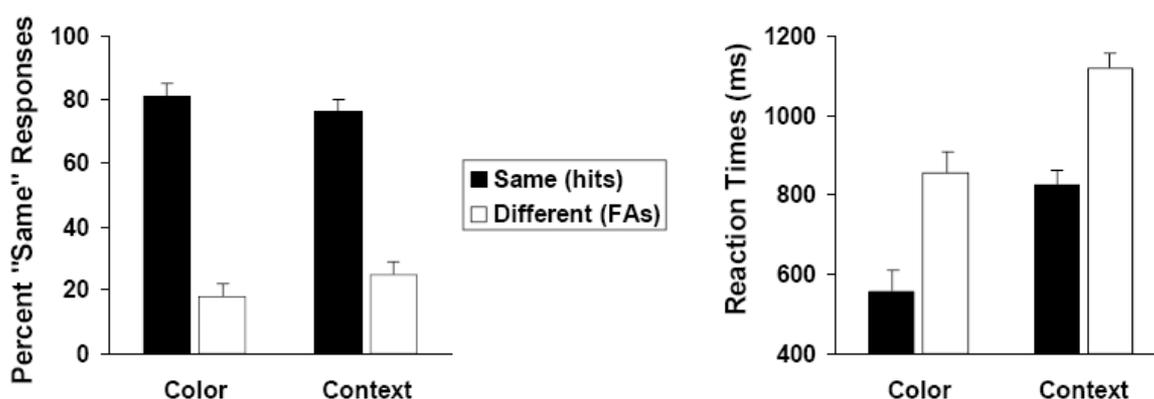


Figure 17. Feature decision data, Experiment 2. Percent "same"-responses (left) and mean response times (right) as a function of item status; FAs refers to false alarms; error bars indicate within subjects standard errors of mean; figure adapted from Ecker et al. (in press).

b. Feature decision.

In order to be able to calculate performance (Pr) scores, we focused analysis on "same" responses in the feature decision, referring to "same" responses to Same items as hits and "same" responses to Different items as false alarms. The difference between hit- and false alarm rates indicates that feature oriented learning did indeed take place. The difference in conditional relative frequencies between Same (hits) and Different trials (false alarms) was significant and, equally important, 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, $F(1,30) = 79.70$, $MSE = .03$, $p < .001$; see left hand side of Figure 17). There was no significant difference in discrimination scores – calculated as the difference between hits (to identical) and false alarms (to changed items) – between groups (Pr-score .64 vs. .52; $t(30) = 1.43$, $p = .16$). This means that the association of object- and feature information was equally successful in both groups. In both

cases, feature information was integrated into a memory representation. There was no difference in group bias (Br-score .50 vs. .51, $t < 1$).

As far as reaction times are concerned, two main effects were apparent: false alarms were slower than hits (averages of 988 vs. 691 ms; $F(1,30) = 58.75$, $p < .001$), and feature decisions in the Context group took longer than in the Colour group (825 vs. 556 ms for hits, 1120 vs. 856 ms for false alarms; $F(1,30) = 8.28$, $p < .01$) (see right hand side of Figure 17).

4.2.2.2 ERP Results and Discussion

a. Object decision.

Stimulus-locked ERPs elicited by old items with both a correct object and feature decision and by correctly rejected new items are shown in Figures 18 and 19, for both groups, respectively. Topographic maps are shown in Figure 20.

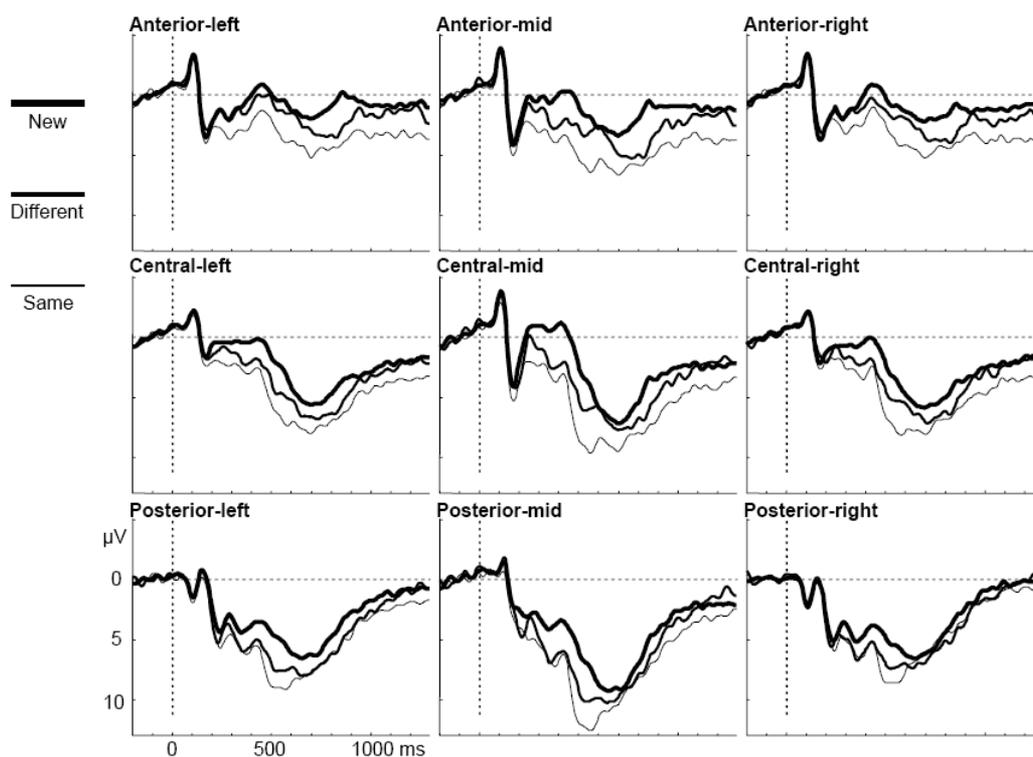


Figure 18. Topographically arranged (ROI) grand average ERP data from the object (old/new) decision, Experiment 2, Colour group; includes all artefact-free trials with both a correct object and subsequent feature judgment; time scaling ranges from -200 to 1300 ms post stimulus onset; positive deflections are displayed downward; figure adapted from Ecker et al. (in press).

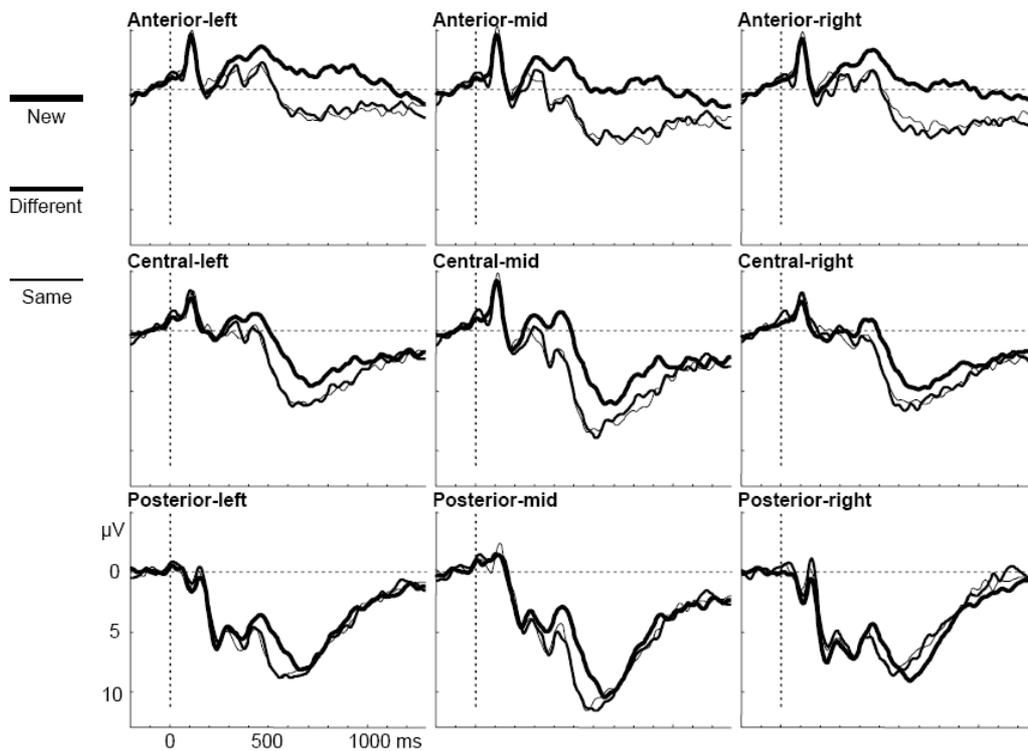


Figure 19. Topographically arranged (ROI) grand average ERP data from the object (old/new) decision, Experiment 2, Context group; includes all artefact-free trials with both a correct object and subsequent feature judgment; time scaling ranges from -200 to 1300 ms post stimulus onset; positive deflections are displayed downward; figure adapted from Ecker et al. (in press).

Old items elicited more positive going waveforms starting at around 250 ms post stimulus onset, especially at frontocentral electrodes. This effect corresponds to the well studied FN400 effect, often associated with familiarity processes, in terms of onset timing and topography (Mecklinger, 2000, 2006). It is apparent in both groups, although it seems to be diminished for Colour-Different items. From about 450 ms onwards, old items elicited more positive going waveforms mainly over centroparietal electrodes. This effect matches well with the LPC effect often associated with recollection (Mecklinger, 2000). Again, both groups show this effect, while it is reduced in Colour-Different trials. In the Context group, this effect also extends to frontal electrode sites, assumingly reflecting activity of an additional frontal cortical source (see below). Third, old item potentials remained more positive until well beyond 1000 ms, especially at frontal and frontopolar electrodes, and in particular in the Context group.

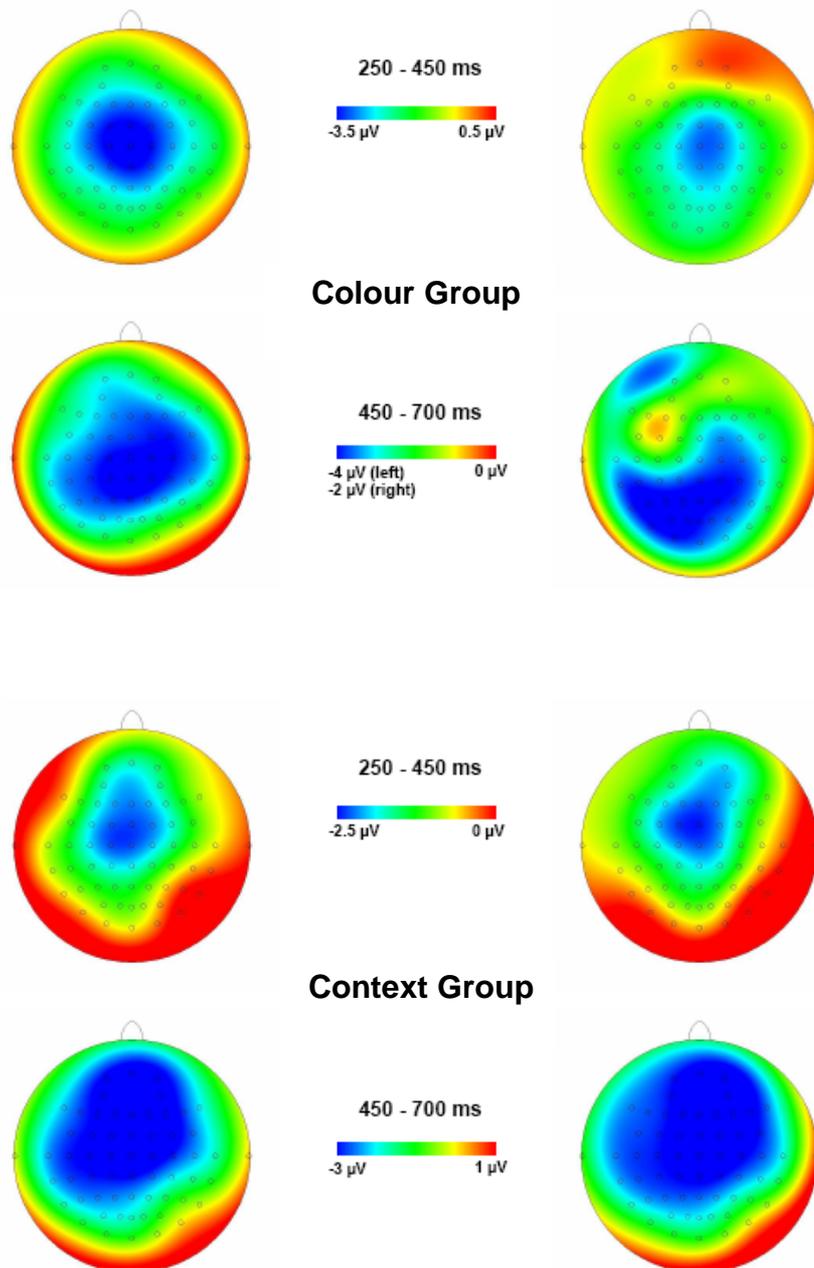


Figure 20. Topographic ERP maps depicting the differences between correct rejections – Same hits (left) and correct rejections – Different hits (right) in the Colour group (top) and Context group (bottom), Experiment 2; modified figure adapted from Ecker et al. (in press).

Analyses were performed in the following manner: based on the literature and on visual inspection of the data, segments were divided into two time windows (250-450 ms, 450-700 ms), corresponding to the old-new effects mentioned above. In these time windows, we then contrasted all conditions by way of repeated measures ANOVAs: New vs. Same, New vs. Different, and Same vs. Different.

Bar graphs displaying early mid-frontal and later posterior old-new effects are shown in Figure 21.

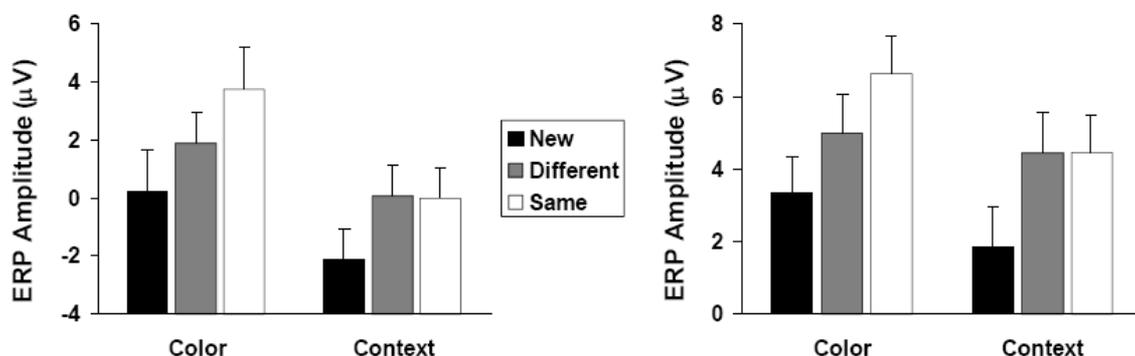


Figure 21. Mean ERP voltages from correctly assessed object (old/new) decision trials (with correct subsequent feature decision; Experiment 2) as a function of condition. Data from the mid-frontal ROI in time window 1 (250-450 ms) are depicted on the left, data from the left-central ROI in time window 2 (450-700 ms) on the right; error bars indicate within subjects standard errors of mean; figure adapted from Ecker et al. (in press).

First, data of *time window 1* (250-450 ms) was analysed across groups to assess familiarity processing. The same analyses were then performed for both groups separately. For ANOVA results, see Table 1. The most important findings are the significant Condition by AP by Group interaction in the New-Different (and Same-Different) analysis and the Condition by AP interaction in the Same-Different analysis of the Colour group. After these coarse analyses, given the significant Condition by Group interactions, planned comparisons were calculated for both groups separately (note that this was also done across groups, with results coinciding except otherwise indicated).

In the Colour group, there was a broad old-new effect for Same repetitions at all ROIs (all $F > 8.99$, all $p < .01$). For Different repetitions, the effect was mainly significant at mid-central and mid-posterior ROIs ($F > 10.27$, $p < .007$), but not at the mid-frontal ROI ($F = 3.02$, $p = .10$; note, however, that this effect was significant in an across group planned comparison: $F = 4.36$, $p < .05$). The theoretically interesting difference between the two Old conditions was significant at the mid-frontal ROI ($F = 4.62$, $p < .05$).

In the Context group, planned comparisons revealed an old-new effect for Same trials at all midline ROIs ($F > 6.86$, $p < .02$). For Different repetitions, the effect was significant at mid-frontal and mid-central sites ($F > 10.67$, $p < .007$). As

indicated by ANOVA, there were no differences between the two Old conditions (note that there were no significant effects in post-hoc contrasts, either).

Conditions	Effects	<i>df</i>	<i>F</i>	ϵ
Across Groups				
New-Same	Condition	1,27	43.91**	
	Condition x Group	1,27	5.26*	
	Condition x AP	2,54	4.75*	.59
	Condition x Lat	2,54	19.13**	.91
	AP x Group	2,54	3.55 ⁺	.57
New-Different	Condition	1,27	8.81**	
	Condition x Lat	2,54	9.38**	.89
	Condition x AP x Group _E	2,54	4.31*	.55
Same-Different	Condition x AP x Group _E	2,54	2.79 ⁺	.67
Colour Group				
New-Same	Condition	1,14	47.34**	
	Condition x Lat	2,28	15.42**	.88
New-Different	Condition	1,14	4.17 ⁺	
	Condition x Lat	2,28	9.40**	.97
Same-Different	Condition x AP _E	2,28	6.30*	.73
Context Group				
New-Same	Condition	1,13	7.96*	
	Condition x AP	2,26	3.09 ⁺	.62
	Condition x Lat	2,26	6.03*	.79
New-Different	Condition	1,13	5.27*	
	Condition x AP	2,26	3.47 ⁺	.56
	Condition x Lat	2,26	3.35 ⁺	.86
Same-Different			all $F < 1$	

Note—AP, Anterior-Posterior; Lat, Laterality. ⁺ $p < .1$; * $p < .05$; ** $p < .01$.

Table 1. AP (3) x Lat (3) x Condition (2) [x Group (2)] ANOVAs, Time window 1, Experiment 2; table adapted from Ecker et al. (in press).

Next, we focused on *time window 2* (450-700 ms), again analysing the data across groups first, then separately for both groups (see Table 2). Again, the most important findings are the significant Condition by AP by Group interaction in the New-Different (and Same-Different) analysis and the Condition by Lat interaction in the Same-Different analysis of the Colour group.

Conditions	Effects	<i>df</i>	<i>F</i>	ϵ
Across Groups				
New-Same	Condition	1,27	39.64**	
	Condition x AP	2,54	4.03*	.59
	Condition x Lat	2,54	9.77**	.95
	Condition x AP x Lat	2,54	3.34*	.75
New-Different	Condition	1,27	14.84**	
	Condition x Lat	2,54	3.52*	.85
	Condition x AP x Lat	4,108	4.73**	.75
	Condition x AP x Group _E	2,54	5.42*	.57
Same-Different	Condition	1,27	4.67*	
	Condition x Lat	2,54	3.23*	.97
	Condition x Group _E	1,27	6.43*	
Colour Group				
New-Same	Condition	1,14	28.68**	
	Condition x Lat	2,28	6.69*	.67
New-Different	Condition	1,14	3.48 ⁺	
Same-Different	Condition	1,14	8.64*	
	Condition x Lat	2,28	4.43*	.92
Context Group				
New-Same	Condition	1,13	13.18**	
	Condition x AP	2,26	5.30*	.62
	Condition x Lat	2,26	4.16*	.78
New-Different	Condition	1,13	13.98**	
	Condition x AP	2,26	6.29*	.57
	Condition x Lat	2,26	2.92 ⁺	.83
	Condition x AP x Lat	4,52	3.87*	.61
Same-Different			all <i>F</i> < 1	

Note—AP, Anterior-Posterior; Lat, Laterality. ⁺*p* < .1; **p* < .05; ***p* < .01.

Table 2. AP (3) x Lat (3) x Condition (2) [x Group (2)] ANOVAs, Time window 2, Experiment 2; table adapted from Ecker et al. (in press).

Focussing on the Colour group, old-new effects for Same repetitions were significant at all ROIs (all $F > 10.94$, all $p < .006^9$). For Different repetitions, effects were reliable primarily at the left-posterior ROI ($F = 16.36$, $p = .001$; left-central, mid- & right-posterior significant at $F > 6.34$, $p < .03$). Same and Different conditions differed significantly at central ROIs, all $F > 9.73$, all $p < .008$, but also at left- and mid-frontal, as well as mid-posterior ROIs, all $F > 5.89$, all $p < .03$. The difference at the left-posterior ROI was marginally significant ($F = 3.38$, $p = .09$). In the Context group, old-new effects for both Old conditions occurred at all ROIs except the right-posterior one (all $F > 5.32$, all $p < .04$). There were no differences between the two Old conditions.

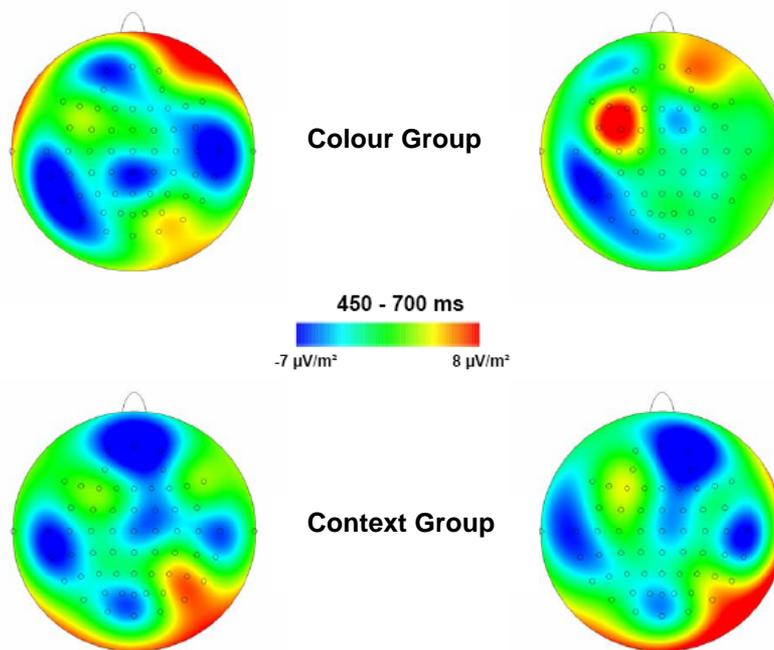


Figure 22. Topographic CSD maps depicting the differences between correct rejections – Same hits (left) and correct rejections – Different hits (right) in the Colour group (top) and Context group (bottom) of Experiment 2.

The assumption that the rather unusual anterior topography of old-new effects in this time window in the Context group was due to an additional frontal cortical generator was further investigated with current source density (CSD) analy-

⁹ Note that, although significant ROIs are the same as in the respective analysis of Time window 1, the effects in the two time windows still differ topographically, reflecting the more widespread and posterior distribution of the later effect: a $2 \times 3 \times 3$ ANOVA with the factors Time window (1 and 2), AP, and Laterality, including only Same difference waves of the Colour group, revealed a significant 3-way interaction, $F(4,56) = 4.96$, $\epsilon = .68$, $p < .01$, which was confirmed in an analysis on vector-scaled data (McCarthy & Wood, 1985; see also Urbach & Kutas, 2002), $F(4,56) = 3.58$, $\epsilon = .74$, $p < .05$.

sis. CSD analysis is more sensitive to high spatial frequency local cortical potentials than it is to potentials of low spatial frequency due to volume conduction from distant sources (Gevins et al., 1994; Picton, Lins, & Scherg, 1995). Thus, CSD maps are assumed to show mainly cortical activity, allowing for the separation of multiple cortical sources of broad raw potential distributions. Analysis confirmed the assumption that the frontal part of the effect is generated by a separate cortical source (see Figure 22; the across group CSD analysis revealed a significant AP by Group interaction, $F(2,54) = 4.58$, $\epsilon = .56$, $p < .05$).

Looking at the relationship between behavioural performance and electrophysiological measures in the Colour group, we found the interesting result that the congruency effects on reaction times on the one hand and on the early mid-frontal ERP component on the other correlated, $r = .45$, $p < .05_{\text{one-sided}}$. That is, the stronger the increase in response times for Colour Different compared to Same items, the larger the reduction of the FN400 old-new effect at the mid-frontal ROI. The respective correlation with the later posterior effect was not significant (irrespective of the ROI used for analysis, left-posterior, left-central, or mid-central), the correlation being highest for the left-posterior ROI: $r = .38$, $p > .05_{\text{one-sided}}$.

Taken together, subjects of the Context group showed no effects of the study-test manipulation, although context information was available (as indicated by feature decision performance). Presumably, whereas the relevant intrinsic information is supplied rather effortlessly in the Colour group, there is a higher need for controlled retrieval processes when extrinsic information has to be integrated (i.e., in the Context group). To further clarify this matter, we additionally analysed data from frontopolar electrodes (shown in Figure 23) in an additional late time window (800-1200 ms), based on visual inspection and prior studies reporting late frontal activity when there was need for source reintegration (e.g., Schloerscheidt & Rugg, 2004; Van Petten et al., 2000; Wilding & Rugg, 1996).

In this late time window, for both the analysis of New vs. Same and New vs. Different, the Condition by Lat by Group interaction was marginally significant, $F(2,54) = 3.66/3.23$, $\epsilon = .65/.82$, $p = .054/.058$. The comparison of the two Old conditions yielded no effects ($F < 1.2$). Post-hoc contrasts showed that in the Colour group, there were old-new effects at the left frontopolar electrode for both Old conditions, $F > 6.41$, $p < .02$. In the Context group, however, there were significant old-new effects at all frontopolar electrodes for both Old conditions (Same: effects

between $F = 5.04, p = .03$ and $F = 12.84, p = .001$; Different: effects between $F = 7.83, p = .01$ and $F = 13.09, p = .001$).

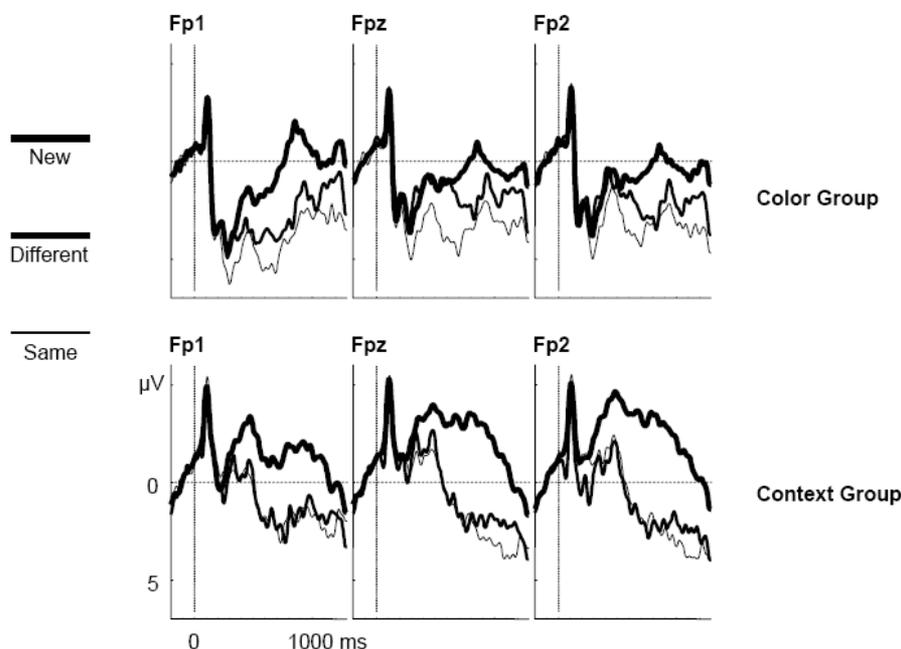


Figure 23. ERPs from frontopolar electrodes, Experiment 2; includes all artefact-free trials with both a correct object and subsequent feature judgement; time scaling ranges from -200 to 1300 ms post stimulus onset; positive deflections are displayed downward; figure adapted from Ecker et al. (in press).

Subjects of the context group showed no effects of congruency whatsoever, although context information was available. Perhaps subjects of the colour group began to process feature information quite early in light of the upcoming feature decision – that is, already during the object decision phase of the trial – simply because the relevant intrinsic information was supplied rather effortlessly. Subjects of the context group, however, might have postponed their decision until items were actually re-presented for the feature decision. This would indicate a higher need for controlled retrieval processes when extrinsic information has to be integrated. To further clarify this matter, we also looked at the ERPs recorded during the feature decision phase.

b. Feature decision.

Hence, we first calculated stimulus-locked ERPs in order to compare Same and Different trials; only trials featuring a correct response were included. The feature decision ERPs are depicted in Figures 24 and 25.

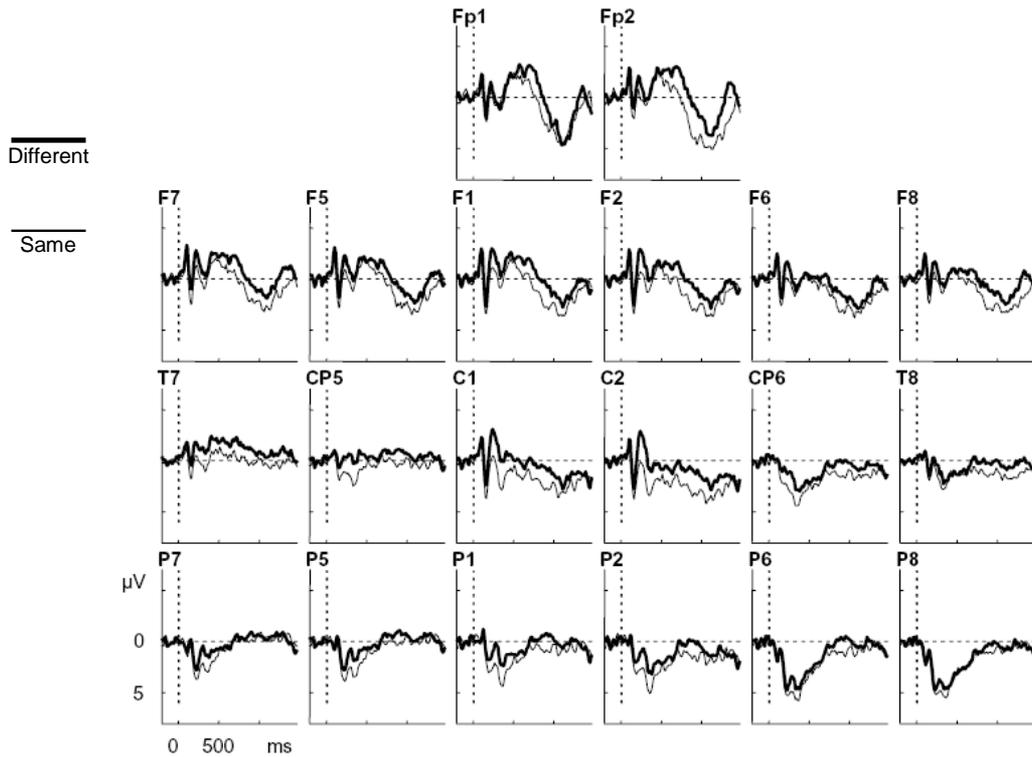


Figure 24. ERP data from the feature decision, Colour group, Experiment 2. Grand average waveforms at selected electrodes; time scaling ranges from -200 to 1500 ms post stimulus onset; positive deflections are displayed downward.

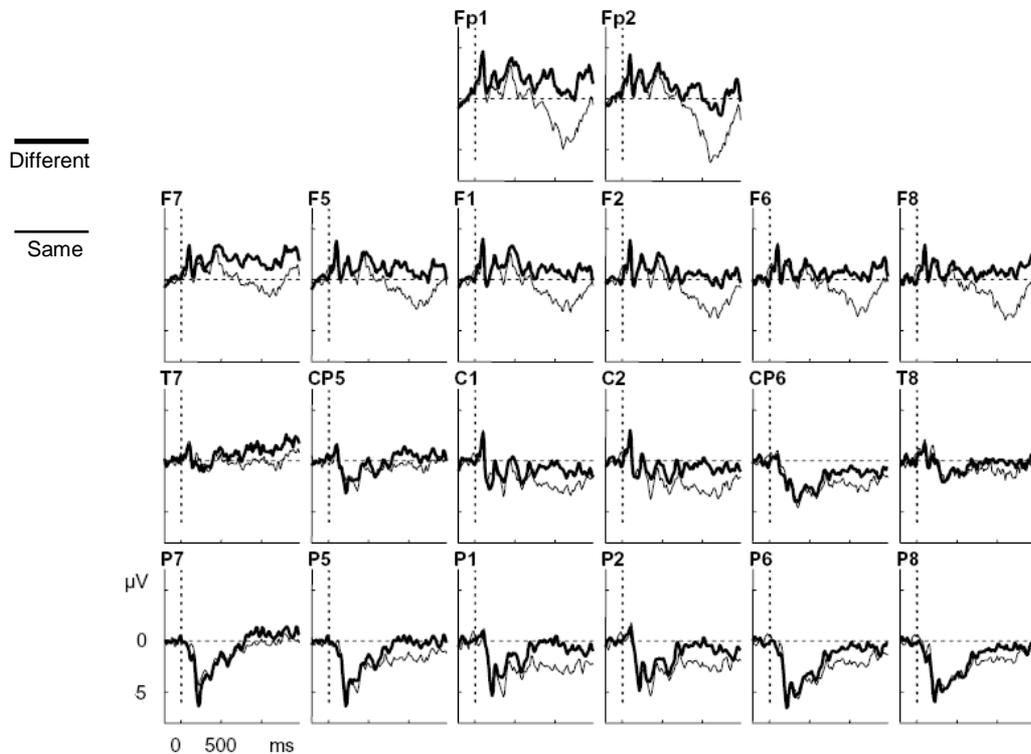


Figure 25. ERP data from the feature decision, Context group, Experiment 2. Grand average waveforms at selected electrodes; time scaling ranges from -200 to 1500 ms post stimulus onset; positive deflections are displayed downward.

Following the line of argumentation presented in the previous section, we expected differences to occur only in the context group. We had no specific hypotheses with regard to timing and topography, although we thought frontal effects might best match the assumed controlled processes mentioned above. In the colour group, the waveforms differ slightly, starting from about 200 ms post cue presentation, mainly at frontocentral electrodes. In the context group, waveforms start to differ from about 450 ms onwards, especially at frontal and frontopolar electrode sites, peaking at about 1100 ms. Based on visual inspection, four time segments (200-450 ms, 450-750 ms, 750-1050 ms, and 1050-1350 ms) were analysed separately in 3 x 2 x 2 x 2 (AP by Laterality by Condition by Group) ANOVAs.

There was an AP by Laterality by Condition interaction in time window 1, $F(4,116) = 2.94$, $\epsilon = .67$, $p = .044$. In time windows 2 and 3, all effects including the factors Condition or Group remained nonsignificant. There was a main effect of Condition in time window 4, $F(1,29) = 4.59$, $p < .05$, accompanied by a significant interaction of AP and Condition, $F(2,58) = 3.91$, $\epsilon > .63$, $p < .05$. No group effects emerged in any of these analyses. Yet, in follow-up comparisons, the only significant contrast was found in time window 4 of the context group: congruent and incongruent trials differed at right frontal electrodes $F(1,29) = 10.17$, $p < .0055$. Since, however, the effect is largest at frontopolar electrodes, we subsequently analysed frontopolar effects in the late time window. The 3 x 2 x 2 (Laterality by Condition by Group) ANOVA yielded a significant Condition by Group interaction $F(1,29) = 4.20$, $p < .05$, besides a main effect of Condition, $F(1,29) = 7.08$, $p < .05$. Planned comparisons revealed that, in the colour group, congruent and incongruent trials did not differ at any of the frontopolar electrodes, all $F < 1.1$. In the context group, on the other hand, all three contrasts were significant, all $F > 8.53$, all $p < .0167$ ¹⁰.

Experiment 2 was successful in demonstrating that intrinsic manipulations affect both behavioural as well as ERP data as expected. Moreover, contextual manipulations did not affect the mid-frontal old-new effect, exactly as predicted by our model. However, there is another possible interpretation of the data: for in-

¹⁰ One could argue that it would have been justified to include all available trials into the analysis of feature decision ERPs, in order to examine more general, response-independent processes. Inclusion of the relatively few incorrect trials, however, did not alter the results, except for an additional main effect of Condition together with a significant AP by Condition interaction in time window 3.

stance, one could assume that context has no influence on the FN400 effect only because context retrieval is more effortful than colour retrieval. Perhaps during object processing subjects do perform an unneeded task if it is easy to do, but not if it is effortful. Rather, the effortful task is postponed to the moment it is really needed (feature decision ERPs of Experiment 2 point in this direction). This would mean the lack of context effects on the familiarity component may only be a matter of different strategies: if context was directly and immediately task relevant and therefore the effort of retrieval was not needless, participants would access this information early and context would then also influence the early familiarity component. In contrast, we argue that the two features are retrieved by different processes. Colour features are provided by object tokens and context features by episodic tokens, and this difference cannot be overcome by strategic decisions. If the familiarity signal results from access to object token and context information is not provided by this unit, we still predict that the familiarity component is not influenced by a changed context, even if it is directly relevant, and even if it can be retrieved.

4.3 Experiment 3

4.3.1 Design, Hypotheses and Methods

Thus, in Experiment 3, we again manipulated context, but now we used an exclusion instead of an inclusion task, thereby putting context information into the focus of attention and making it directly task relevant. If in this case, the FN400 familiarity effect would still be unaffected by contextual manipulation, this would be strong evidence for our notion that contextual features are not bound in the object token. In contrast, we expected an influence of the contextual manipulation on the LPC effect. As Context-Different objects now were to be rejected, context had to be processed in order to solve the task (we knew from the feature decision of Experiment 2 that this information is available), and the mismatch of context information should thus influence the LPC recollection effect. Thus, a differential influence of the contextual manipulation on the FN400 (no modulation) and LPC old/new effects (modulation) was expected in the exclusion task of Experiment 3.

Sixteen subjects, all students at Saarland University, took part in this experiment (mean age was 22, ranging from 18-29, 10 participants were females). They were paid for participation.

Apart from instructions (and thus, of course, no more additional feature decision), all further details concerning design, procedure, and analysis were exactly the same as in the Context condition of Experiment 2, with the following minor exceptions: instead of an “Electro-Cap”, a 63-channel “Easycap” (Easycap GmbH, Herrsching-Breitbrunn, Germany) was used, after hardware had been exchanged in the whole laboratory. Related to this, ROIs were changed, as the most lateral electrodes (columns 7 & 8) in this experiment (and others) showed virtually no old-new effects. Thus, lateral ROIs were now made up of the following electrodes: F3, F5, AF3 (anterior); C3, C5, CP5 (central); and P3, P5, CP3 (posterior); and their right-sided counterparts, respectively. Following artefact rejection (elimination of 4 % of trials), ERPs were calculated to correct responses to Same (mean number of trials: 32), Different (25), and new items (76), the only difference being that Different items now had to be rejected.

4.3.2 Results and Discussion

4.3.2.1 Behavioural Results and Discussion

Accuracy and reaction time data are shown in Figure 26. Subjects were almost perfect in rejecting new items (rate .98 correct), and both rates of hits to Same items and correct rejections of Different items were reliably above chance (both $t(15) > 6.18$; $p < .001$). ANOVA including a Block factor revealed only a main effect of Condition ($F(2,30) = 103.85$; $MSE = .01$; $p < .001$), and follow up contrasts signalled reliable differences between all three conditions (all $F(1,15) > 43.97$; $p < .001$), that is, there were more correct rejections of new items than there were hits (rate .83), and there were more hits than correct rejections of Different items (rate .65). Additionally, Pr scores were calculated on the basis of false alarms to Different items (rate .31; neglecting almost perfect rejection of new items). Mean Pr was .52, which differed significantly from chance performance ($t(15) = 16.28$; $p < .01$).

Reaction time analysis was performed in the same way. ANOVA including a Block factor revealed only a main effect of Condition ($F(2,30) = 84.10$; $MSE = 17130$; $p < .001$). Post-hoc contrasts showed that all three conditions differed from each other (all $F > 13.72$; $p < .01$), that is, correct rejections of new items were fastest (684 ms), followed by hits (981 ms) and correct rejections of Different items (1102 ms). For sake of completeness, the mean latency of false

alarms to Different items was 1110 ms. Thus, RT data mirrored the accuracy findings.

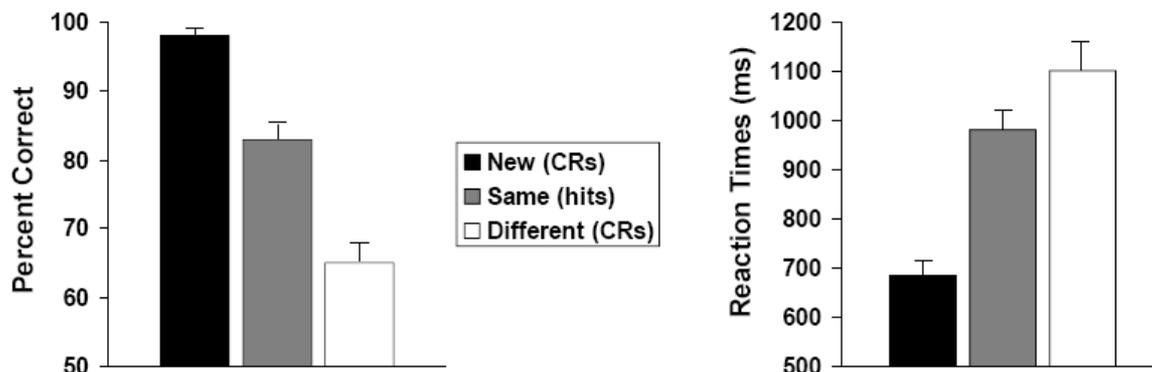


Figure 26. Recognition data, Experiment 3. Percent correct (left-hand side) and mean response times in milliseconds (right-hand side) for all correct responses as a function of item status; CRs refers to correct rejections; error bars indicate within subjects standard errors of mean; figure adapted from Ecker et al. (in press).

The quick and reliable correct rejections of new items likely indicate that responses relied significantly on object familiarity (or novelty). Slower and less accurate responses to items requiring contextual integration are completely inline with expectations, in particular as subjects responded slowest and most imprecisely when they had to resolve conflict between the signalling of high object familiarity and the need to reject an item due to a mismatch of context in recollective retrieval.

4.3.2.2 ERP Results and Discussion

Stimulus-locked ERPs elicited by items correctly responded to are shown in Figure 27. Topographic maps are shown in Figure 28.

Visual inspection suggests that old items elicited more positive going waveforms starting at around 300 ms post stimulus onset, especially at frontal sites. Later in time, the effect remains largest at frontal sites while extending more strongly to left and mid posterior sites, as well. From about 500 ms, correct responses to Same and Different items differ, especially at left posterior sites. Statistical analyses were again carried out by way of repeated measures ANOVAs in selected time windows. After visual inspection, these were set to the standard values of 300-500 ms and 500-800 ms.

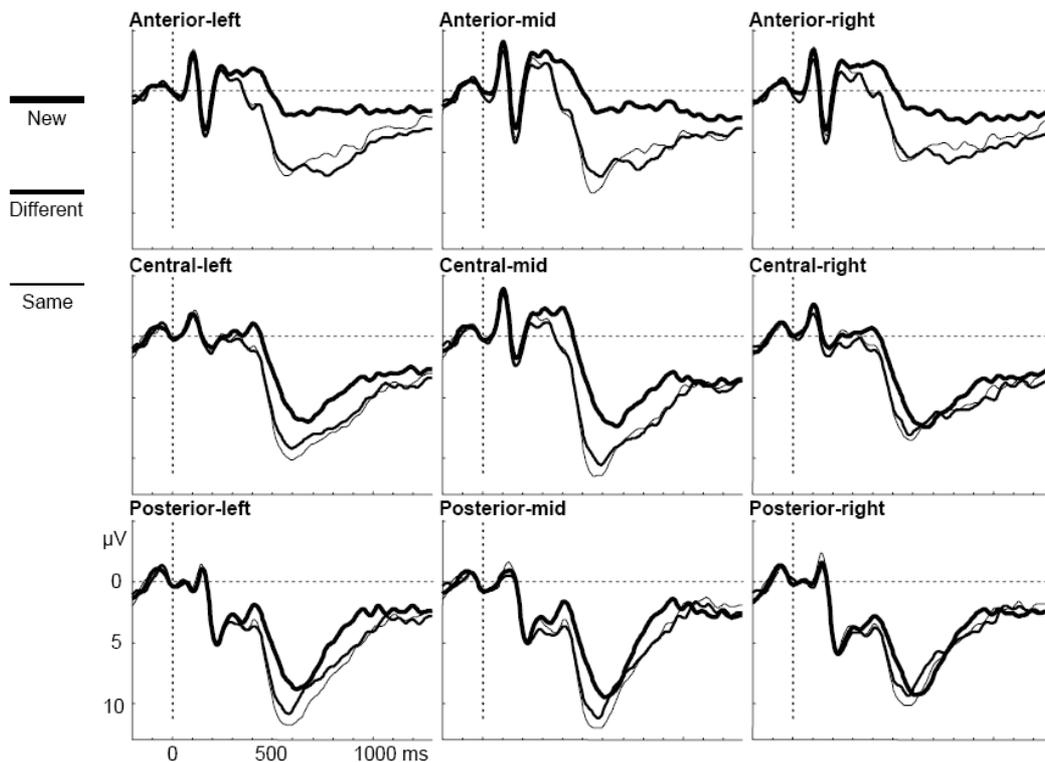


Figure 27. Topographically arranged (ROI) grand average ERP data from Experiment 3; includes all artefact-free trials with correct responses; time scaling ranges from -200 to 1300 ms post stimulus onset; positive deflections are displayed downward; figure adapted from Ecker et al. (in press).

First, we analysed data from time window 1 in order to assess familiarity processing. Table 3 shows ANOVA results. Most importantly, while overall old-new effects were reliable, there were no effects in the comparison of the two old conditions. Planned comparisons showed that the old-new effect for Same hits, although largest at the mid frontal ROI, was significant at all ROIs (all $F > 5.06$, $p < .04$). Likewise, for Different items, the old-new effect was reliable at all ROIs (all $F > 9.17$, $p < .01$) except the right posterior one. Despite the nonsignificant ANOVA comparing the two Old conditions, planned comparisons were calculated, which substantiated the null effect (all $F < 1$).

The ANOVA results for time window 2 are displayed in Table 4. Again, old-new analyses yielded reliable results, the most noteworthy finding being, however, the AP by Condition interaction in the comparison of the two Old conditions¹¹.

¹¹ Note that in the additional single-electrode analysis, the Condition x Lat and the Condition x AP x Lat interaction were also significant.

In planned comparisons, the old-new effect for Same hits was significant at all ROIs (all $F > 6.73$, $p < .02$) except the right central and right posterior ones (all $F < 1.92$, $p > .1$). The old-new effect for correct rejections of New vs. Different items was significant at all ROIs (all $F > 5.55$, $p < .03$) excluding right central, right posterior and mid posterior regions (all $F < 2.19$, $p > .1$). Planned comparison of Same hits and Different CRs revealed a significant difference at the theoretically most relevant left posterior ROI ($F = 4.73$, $p < .05$).

Conditions	Effects	<i>df</i>	<i>F</i>	ϵ
Across Groups				
New-Same	Condition	1,15	17.56**	
	Condition x AP	2,30	8.29**	.69
	Condition x Lat	2,30	14.58**	.95
	Condition x AP x Lat	4,60	3.29*	.69
New-Different	Condition	1,15	16.64**	
	Condition x AP	2,30	7.63**	.66
	Condition x Lat	2,30	13.53**	.82
Same-Different			all $F < 1.1$	

Note—AP, Anterior-Posterior; Lat, Laterality. + $p < .1$; * $p < .05$; ** $p < .01$.

Table 3. AP (3) x Lat (3) x Condition (2) ANOVA, Time window 1, Experiment 3; table adapted from Ecker et al. (in press).

Conditions	Effects	<i>df</i>	<i>F</i>	ϵ
Across Groups				
New-Same	Condition	1,15	16.00**	
	Condition x AP	2,30	11.33**	.65
	Condition x Lat	2,30	20.71**	.83
	Condition x AP x Lat	4,60	3.59*	.45
New-Different	Condition	1,15	11.93**	
	Condition x AP	2,30	39.39**	.60
	Condition x Lat	2,30	15.87**	.92
	Condition x AP x Lat	4,60	2.39 ⁺	.59
Same-Different	Condition x AP _E	2,30	5.65*	.92

Note—AP, Anterior-Posterior; Lat, Laterality. + $p < .1$; * $p < .05$; ** $p < .01$.

Table 4. AP (3) x Lat (3) x Condition (2) ANOVA, Time window 2, Experiment 3; table adapted from Ecker et al. (in press).

The broad and rather anterior distribution of the old-new effects in time window 2 were again examined in CSD analysis, which again suggested that temporally overlapping activity of two spatially distinct cortical sources contribute to the broad scalp effect, a left-lateralised posterior part and an additional strong frontal component (see Figure 29).

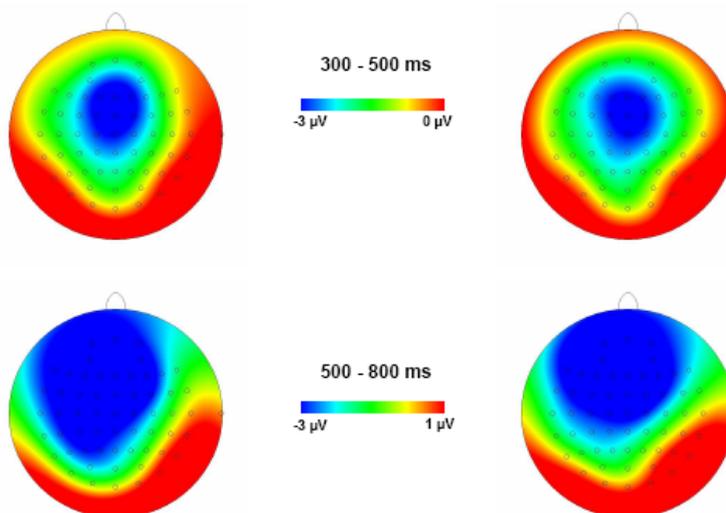


Figure 28. Topographic ERP maps depicting the differences between correct rejections of New items – Same hits (left) and correct rejections of New items – correct rejections of Different items (right) in Experiment 3; figure adapted from Ecker et al. (in press).

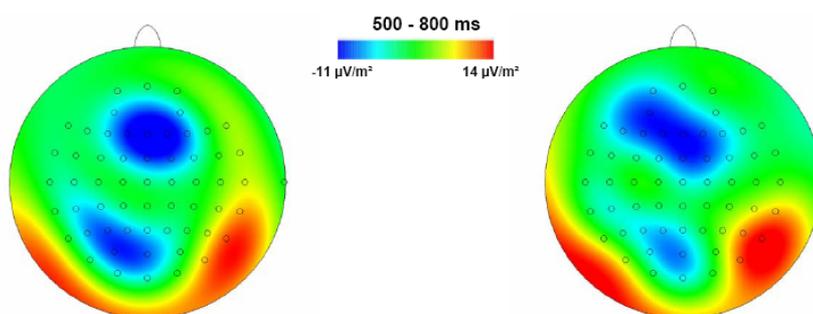


Figure 29. Topographic CSD maps depicting the differences between correct rejections of new items – Same hits (left) and correct rejections of new items – correct rejections of Different items (right) in Experiment 3.

Taken together, there was a frontally focused FN400 old-new effect of equal magnitude for both Old conditions in time window 1, even though context was directly task relevant. This effect was independent of study-test congruency.

In time window 2, while the broad old-new effects were reliable for both Old conditions, Same items elicited a significantly larger left posterior LPC effect than Different items. Thus, as expected, a contextual manipulation impacted on the LPC effect associated with recollection if context was made relevant for the immediate decision. The fact that even under this prerequisite, the FN400 effect associated with familiarity was not affected by contextual factors is in line with our predictions. This pattern corroborates the model assumptions concerning the representation of intrinsic and extrinsic features and the time course of their processing.

5 Interim Discussion

5.1 Summary

The aim of the first series of experiments was to test whether intrinsic and extrinsic features are differently processed in episodic recognition memory. We therefore manipulated an intrinsic (colour; Experiments 1 and 2) and an extrinsic (context, Experiments 1, 2, and 3) feature in three recognition experiments.

In Experiments 1 and 2, we adopted a sequential test procedure, with an old/new object recognition test (inclusion task) followed by a feature recognition (source memory) test. In this inclusion task, we expected the manipulation of the intrinsic feature to slow down object recognition, but expected no such effect for the extrinsic feature. We predicted that both kinds of features themselves, however, could be voluntarily recognised to a similar degree.

In line with predictions, Experiment 1 demonstrated that the manipulation of an intrinsic feature such as colour indirectly affects behavioural indices of episodic object recognition, even though the feature is irrelevant for the decision. Moreover, the extrinsic manipulation did not influence recognition performance, just as predicted. This pattern was shown in both a within and a between subjects design, suggesting it to be a genuine effect and no artefact of group differences (e.g., in strategy). However, the flaw of Experiment 1 was that direct associative recognition of object-context pairings did not reliably differ from chance. Thus, the possibility that context did not indirectly impact on object recognition merely because it was not mnemonically represented in association with the object could not be ruled out.

Therefore, some changes in stimulus material and design were implemented in Experiment 2. These changes were successful, and the behavioural results of Experiment 2 confirmed our hypotheses, in line with the behavioural literature. Results imply that the study-test manipulation of an irrelevant intrinsic feature affects object recognition accuracy and reaction times, whereas the manipulation of an extrinsic feature does not affect object recognition performance in an inclusion task. Equivalent performance in associative feature recognition across groups demonstrates that this holds true even though both kinds of information had been learnt and associated with object information to a comparable

degree¹². This pattern indicates that it is not a quantitative difference in memory strength underlying the object decision effects, but a more fundamental difference in processing and representation. This makes the retrieval of contextual information a more deliberate process as compared to the retrieval of intrinsic information, which is supplied rather automatically. Likewise, reaction times in the Same Colour condition were fastest, suggesting that participants may have had no additional memory work to do on these trials. The reaction times in the feature decision (i.e., faster responses in the Colour group) point in the same direction.

Furthermore, we hypothesised that both kinds of manipulations would modulate ERP old-new effects in a distinctive manner. In particular, in Experiments 1 and 2, a manipulation of the intrinsic but not the extrinsic feature was thought to impact on the frontal old-new effect associated with familiarity. An influence of a colour mismatch on the parietal recollection effect was considered possible due to the automatic supply of intrinsic information. On the other hand, if context influences old-new effects at all, it should be the LPC that is affected, as extrinsic information is only bound in the episodic token. However, an influence of context on the parietal effect was nevertheless not expected in Experiments 1 and 2 due to inclusion instructions and the model assumption that extrinsic feature retrieval is a controlled and effortful process. Experiment 3 was thus designed to test the assumption that context would impact on recollection as soon as it was made task-relevant (in an exclusion task). Hence, a context effect on the parietal component was predicted, whereas, importantly, an influence on the early mid-frontal effect was still precluded.

ERP results of Experiment 1 were quite equivocal. Apart from a power problem due to a too little number of subjects per group condition, the reasons for the non-occurrence of the mid-frontal FN400 old-new effect are unclear. Yet, the overall pattern of results did have some interesting features. There were reliable congruency effects in both conditions; these occurred quite early (from about 200-800 ms) in the Colour condition and only quite late (from about 700-900 ms). This is in line with predictions from the model that intrinsic colour information is memory-effective at early stages of processing and is thus supplied rather effortlessly.

12 Our notion of activation of objects and their intrinsic features „in whole“ may lead the reader to assume that colour recognition should be close to perfect, whenever an object itself is recognized as old. However, this is only an ideal way of thinking: for instance, colour could not have been encoded in the first place, information decays, or there might be access problems. After all, even the information in object tokens consists of different pieces of information bound together, and binding is always prone to failure. Of course, there will also be some old objects that are only guessed old, so the feature decision can only be guessed, too.

The duration of the effect indicates that more intentional retrieval processes are also affected. In contrast, context initially does not affect memory processing. This is not surprising given the behavioural effects, however, the presence of late congruency effect may again point to the involvement of at least two consecutive processes (cf. Van Petten et al., 2000), initial object familiarity appraisal – uninfluenced by context – and intentional contextual integration. However, due to the lack of behavioural support for this claim, this remains speculative.

Resembling the behavioural data, ERP results of Experiment 2 and 3 were in line with predictions. The intrinsic manipulation (Experiment 2) modulated both frontal and parietal ERP old-new effects, but there was no effect of the extrinsic manipulation on object recognition ERPs, as long as the feature was not made directly task relevant, in the exclusion task of Experiment 3. In this case, context affected the LPC recollection effect as expected, but the FN400 familiarity effect remained uninfluenced by context and can thus be considered acontextual independent of task relevance (but see Tsivilis et al., 2001, and Ecker, Zimmer, Groh-Bordin, & Mecklinger, 2007, or Experiment 5, respectively). Apparently, the representation subjects address in order to make an old/new decision via familiarity (the object token) includes intrinsic information, but it does not comprise contextual information – even if this information is voluntarily accessible and/or task relevant.

5.2 Effects of the Intrinsic Feature Manipulation

Focussing mainly on Experiment 2 for reasons given above, the manipulation of object colour affected episodic object recognition as expected. Although colours were arbitrary and the task was an inclusion task, subjects were faster and more accurate when items were identically repeated. This replicates previous behavioural results. The effect of this perceptual manipulation on the parietal ERP old-new effect in the Colour group is also in accordance with previous research (Curran, 2000; Curran & Cleary, 2003; Ranganath & Paller, 1999) and comprehensible in light of the integrative, intentional study. Intentional integration seems to be an important factor; for instance, Groh-Bordin et al. (2005) found no congruency effect on the LPC following incidental study, in accordance with the notion of Moscovitch (1992): what is consciously and intentionally bound will be consciously reactivated when subjects are in the respective retrieval mode. Also, associative study instructions will occasionally lead subjects to generate verbal predicates concerning the feature (e.g., “that’s a funny colour”), which can then potentially be

recollected. At test, the automatically arising familiarity signal indicates a mismatch at an early stage of processing. This mismatch signal makes a re-check likely – the system may know that “something is wrong”, but may not yet know exactly what. This is where conscious recollection comes into play (cf. the distinction between “matching” and “retrieval”, Humphreys et al., 1989). In light of the upcoming feature decision, this may have led to a subset of feature decisions being made or prepared during the old/new decision part of the trial, and the reason there is an effect on the LPC only in the Colour group lies in the automaticity of processing (i.e., colour information is involuntarily supplied by the system, context information is not). Thus, intrinsic features may affect recollection, but extrinsic features should not affect familiarity (which is why our hypotheses have allowed for an effect of colour change on the LPC-, but have precluded an effect of context change on the FN400 effect).

The correlation between the effect of study-test congruency on reaction times and the FN400 effect indicates that the acceleration of reactions to Colour-Same objects was based on a stronger familiarity signal, underscoring the role of familiarity as a trigger for further (recollective) processing. This also implies that at the data level, familiarity and recollection might not be fully independent – they might be independent processes per se, but nevertheless operating on representations stemming from the same study episode, and thus showing some dependence on the effect side. In a similar vein, Humphreys et al. (2003) regarded estimates of familiarity and recollection as dependent, because they rely on the same stored memories. In those states in which pure familiarity is thought to occur (exclusion errors and “know” responses), there is a higher likelihood of recollection to occur in a subsequent test as after those states without familiarity or recollection (inclusion errors, “new” responses). This view is in accordance with more neurophysiological models of episodic memory (Aggleton & Brown, 1999) and also the notion of Yonelinas and Jacoby (1995) that the truth about the relationship between familiarity and recollection may fall “*somewhere between [...] independence and [...] redundancy*” (p.641). By a similar token, although I assume the two processes to be independent in principle, familiarity without recollection may be more common than recollection without familiarity.

The effect of the intrinsic manipulation on the early mid-frontal effect speaks against a view of familiarity as a purely semantic matching process. Given that slight non-semantic manipulations have been found to affect only the parietal but not the early mid-frontal old-new effect (Curran, 2000; Curran & Cleary, 2003),

a semantic matching account of familiarity seems straightforward at first. Our results indicate, however, that perceptual manipulations can indeed affect familiarity and the FN400 effect, depending on characteristics of the task, for example the stimulus material used (Groh-Bordin et al., 2005; see also Curran & Dien, 2003; Curran et al., 2002; Friedman et al., 2005). We thus agree with the recent notion of Curran, Tepe, and Piatt (2006) that familiarity can be sensitive to both perceptual and conceptual dimensions of similarity. Compatibly and as mentioned before, Srinivas and Verfaellie (2000) reported that picture recognition performance of amnesic patients with intact familiarity-based recognition was sensitive to manipulations of perceptual attributes such as orientation (likewise manipulated in Curran & Cleary, 2003), and argued convincingly that these effects were neither based on recollection nor priming. In a similar vein, Diana, Peterson, and Reder (2004) reported evidence for a perceptual impact on familiarity, leading to spurious recognition of new words in often repeated (vs. seldom repeated) unusual fonts.

The results of the intrinsic manipulation are also broadly in accordance with a finding reported by Kelley, Jacoby, and Hollingshead (1989), who had subjects alternately identify briefly presented words in an indirect memory test and judge their source (read/heard/new) on a trial-by-trial basis. They reported a dependence between these measures (i.e., identified words mostly attracted a "read" response) along with an old-new recognition advantage for same modality repetitions. Although we do not generally agree to their notion of perceptual fluency as the basis of familiarity (cf. Gabrieli et al., 1995; Srinivas & Verfaellie, 2000; Wagner et al., 1998), we do agree that the latter effect may well be grounded in familiarity; after all, beyond the conceptual match there is an additional perceptual match in the same modality condition. In contrast to some other studies finding no effect of modality manipulation on recognition memory (Hayman & Rickards, 1995; Roediger & Blaxton, 1987), the trial-by-trial structure of the Kelley et al. design probably fostered perceptual processing, thus the effect of the perceptual manipulation on familiarity (see also Jacoby & Dallas, 1981; Kirsner, 1974). As far as the contingency between perceptual identification and modality judgement (identified words attracting a "read" judgement) is concerned, however, we regard meta-cognitive strategy use a more likely interpretation and see no need to refer to familiarity in this regard.

Overall, seemingly changes of sensory features sometimes do and sometimes do not influence familiarity-based recognition. Familiarity is an ineffective

mechanism to detect slight semantic or sensory stimulus variations (Holdstock et al., 2002; Mayes et al., 2002). Thus, the change of the familiarity signal, and hence impairment, will be small or even absent, if the magnitude of mismatch caused by changed perceptual features is minor compared to the magnitude of matching information. However, if the mismatch is substantial and memory access relies on a considerable degree of perceptual processing, familiarity is not purely semantic, but also perceptually specific.

Also, note that the effect of a purely perceptual manipulation speaks against the view of the FN400 effect as an index of conceptual priming mediated by reading or subvocal naming of stimuli, as proposed by Ken Paller (Yovel & Paller, 2004; Voss & Paller, 2006). 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. There is no persuasive reason to believe, however, that purely perceptual manipulations such as a change in arbitrary colour or orientation affect the conceptual interpretation of an object (remember that no colour-specific objects such as apples – where green could lead to the association “Granny Smith” and red to “Fuji” – were used). Furthermore, in our laboratory we have found FN400 effects even with meaningless stimuli (blob-like non-objects), for which there was no pre-existing conceptual knowledge that could mediate conceptual priming (Groh-Bordin et al., 2006; see also Curran et al., 2002). Finally, the correlation between the effect of study-test congruency on reaction times and the FN400 effect indicates that the acceleration of reactions to Colour-Old/same objects was based on a stronger familiarity signal.

5.3 Effects of the Extrinsic Feature Manipulation

Consistent with our expectations, context did not influence episodic object recognition in the inclusion task of Experiment 2. We have pointed out that the reintegration of specific contextual detail in the process of recollection is somewhat controlled and piecemeal. Because context information was not directly relevant for the object old/new decision (inclusion task), subjects were seemingly able to ignore the potentially available (but not automatically supplied) contextual information. Thus, the context manipulation did not even affect reaction times or the ERP recollection component. The higher demand for controlled retrieval and post-retrieval processing in the context condition is assumingly reflected in the late broad frontal and frontopolar effects (cf. Van Petten et al., 2000; Wilding & Rugg,

1996). The question of whether these specifically reflect processes of retrieval inhibition, response monitoring, or actual contextual reintegration effort, remains speculative and awaits further research.

Yet, when the contextual information was made crucial for subjects' decision in the exclusion task of Experiment 3, contextual manipulation affected the LPC effect associated with recollection, just as our model would predict. Importantly, there was still no effect on the FN400 component in Experiment 3, corroborating our hypotheses that only intrinsic item information affects the early process of familiarity and contextual integration occurs at a later stage of processing, from about 500 ms onwards. This interpretation is supported by the behavioural data of Experiment 3, as well: correct rejections of New items were made very fast, probably relying mainly on object familiarity, whereas responses requiring context integration were slower, especially when context integration led to a conflicting signal – in the case of familiar items to be rejected due to an altered context (i.e., correct rejections of Different items, with lowest accuracy and highest reaction times).

Most ERP studies investigating the effects of contextual manipulations did not focus on local context. For instance, Curran and Friedman (2003, 2004) manipulated a combination of local and global contextual features. They found a larger late (right-) frontal/frontopolar old-new effect for a rather reconstructive (recollection-like) context test compared to a more familiarity-like judgement of temporal distance, but no influence on the mid-frontal FN400 effect. This is broadly consistent with our findings of pronounced frontopolar activation in the Context group compared to the Colour group, and no modulation of the FN400 effect as long as only extrinsic, contextual (be it local or global) features are manipulated.

One of the few ERP studies examining the effects of local contextual manipulations on ERP old-new effects (Tsvilis et al., 2001), reported an FN400 effect that was sensitive to the unspecific combination of object- and context repetition, while identically repeated and recombined object-context pairs did not elicit different waveforms. Assumingly, the rich and unique landscape scenes used were distinct and salient enough to become "more than context" and achieve the status of familiar objects themselves (thus generating an additional familiarity signal via an object token laid down at encoding (see Experiment 5, and also Murnane et al., 1999). Yet, as in the present study, Tsvilis et al. found no *specific* influence of a context manipulation on the ERPs; thus, the assessment of the old/new status

of an object can be performed without influence of its context (but see Curran, Tepe, & Piatt, 2006). Experiment 2 shows that this holds true even if contextual information is potentially available (as demonstrated by subjects' feature recognition performance) and about to become relevant (in the feature decision immediately following each old/new decision). The current data is also compatible with the novelty account of the mid-frontal effect proposed by Tsivilis et al., assuming that an old object with a "new" colour is "newer" than an identically repeated object. Since we did not introduce any new contexts at test, however, our results offer no further evidence concerning this account. In contrast to Tsivilis et al., we found no adverse influence of a context manipulation on object decision reaction times (i.e., a difference between Same and Different context conditions). As mentioned before, Tsivilis et al. reported no electrophysiological correlate of their behavioural result, so its basis is unknown. Furthermore, in a second, behavioural experiment they reported, this effect was no longer reliable. They discussed associative priming as a possible foundation of this effect. Anyhow, in light of our results and the missing electrophysiological correlate it seems highly unlikely that it is – if reliable – associated with episodic memory processing. Perhaps the nature of the highly associative study task and the semantically rich contexts used by Tsivilis et al. fostered associative priming. Further research must therefore clarify these matters.

Taken together, our data support the model assumptions that in general both intrinsic and extrinsic information may modulate recollection, depending on task characteristics, but that only intrinsic features (information bound in a unitised representation) affect familiarity memory, whereas contextual information does not.

6 Experiments II

6.1 Experiment 4

6.1.1 *Design, Hypotheses and Methods*

The aim of Experiment 4 was to corroborate previous findings of perceptual specificity for intrinsic information only, and to extend these to test situations with direct feature relevance. Another aim was to contrast the manipulation of intrinsic and extrinsic feature manipulations while keeping perceptual conditions as similar as possible. In Experiments 1 and 2, the intrinsic feature was colour and the extrinsic feature was shape. Manipulating shape as an intrinsic feature would mean to distort the object itself; thus, we decided to design an experiment in which colour was manipulated both as an intrinsic and an extrinsic feature, holding all other factors constant. Therefore, objects were either presented as coloured silhouettes or as black line drawings encased by a coloured frame (Intrinsic vs. Extrinsic conditions; see Figure 30); colour was manipulated between study and test for a subset of old items (Same v Different repetitions; see below for details).

Subjects studied 144 line drawings of everyday objects on the white background of a computer screen with a presentation rate of 2500 ms. Half the objects were presented as fully coloured silhouettes (with black outlines; Intrinsic condition); for the other half, the black line drawings were encased with a coloured rectangular frame (Extrinsic condition). The frame contained the same number of colour pixels as the fully coloured version of the respective line drawing, so physically, the amount of colour information was identical (see Figure 30 for details). There were six different colours: green, red, magenta, turquoise, dark blue, and yellow; every specific object existed in two colour versions. Instructions were to memorise the object and its colour. At test, subjects were presented with all old items intermixed with 72 new items (half Intrinsic, half Extrinsic). The colour of half the old items was changed between study and test (Different condition), the other half was presented identically (i.e., no colour change; Same condition). First and second presentation colours as well as their transitions were counterbalanced within each subject. That is, seeing a green object was as likely as seeing a yellow one, and the transition from red to blue in a Different study-test case was as likely as a transition from red to green, or any other combination. Most objects had no specific prototypical colour; yet, to preclude an influence of pre-existing seman-

tic knowledge, both colour versions of a specific object were designed to match in terms of semantic appropriateness, although no formal testing was carried out (e.g., a chilli pepper may have existed in red and green, or in turquoise and dark blue). Subjects made a three-fold decision (same/different/new) using three keys of a standard keyboard; there were four different combinations of keys used and this was counterbalanced across subjects to avoid undue EEG lateralisation effects. Keys were A, X, 2, and 6 (of the number block); for each combination, Same and Different conditions were assigned to two keys on the same side of the keyboard (i.e., 2 and 6 or A and X), while the new condition was assigned to the other side (e.g., X or 2).

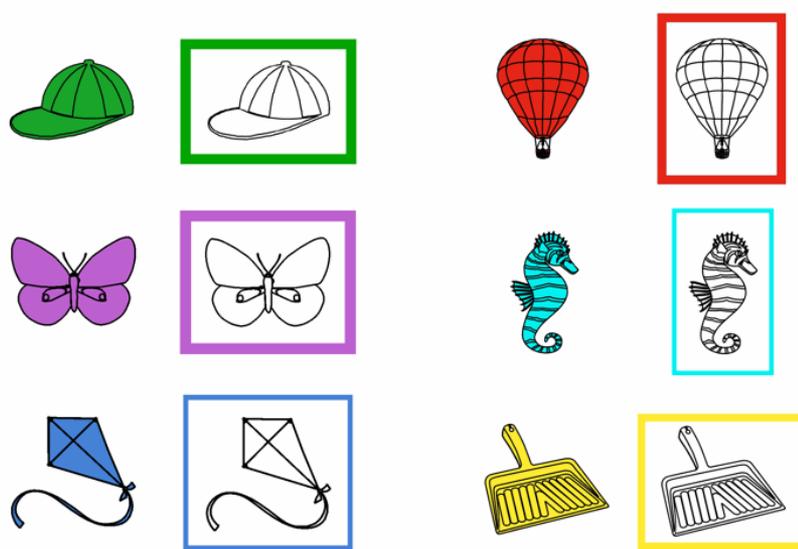


Figure 30. Sample items used in Experiment 4; figure adapted from Ecker, Zimmer, & Groh-Bordin (under revision).

The two types of items (intrinsic, extrinsic) were presented block-wise, and there were four study-test blocks. The Intrinsic-Extrinsic sequence of conditions was counterbalanced across subjects. That is, one group of subjects was given two Intrinsic study-test blocks and then proceeded to the two Extrinsic study-test blocks, or vice versa (there were only sequences of the AABB type). Every item was presented twice during study to enhance performance. The actual experiment was preceded by a practice phase, in which subjects first internalised key assignments and then practiced the task with three items (of the intrinsic/extrinsic style as according to their starting condition) not used in the experiment proper. After completion of the first two blocks, there was another practice phase with three items of the intrinsic/extrinsic style not yet encountered by the specific sub-

ject. Thirty-two right-handed subjects took part in this experiment and were paid for their effort. Subjects were non-psychology students at Saarland University (mean age 23.9, range 20-39, 17 subjects were female).

Hypotheses were that in the Intrinsic case, a colour manipulation should affect performance (i.e., RT) and the FN400 ERP old-new effect associated with familiarity. Because colour information was relevant for subjects' decision, we expected an effect on the LPC effect associated with recollection, as well. In the Extrinsic case, we predicted that the manipulation should not affect the FN400 effect, but should only influence the LPC effect and behavioural performance.

Again, an Easycap was utilised to record the EEG. 5.2 % of trials were rejected due to artefacts. Analysis was based on trials with correct responses, resulting in the following mean trial numbers per condition: Intrinsic-New/Same/Different (33/29/27), Extrinsic-New/Same/Different (32/28/26). The minimum number of trials per condition included in a grand average was 16. Following suggestions by Dien and Santuzzi (2005), statistical analyses were performed by means of repeated measures MANOVAs on mean voltages in several different time windows (details below). Nine ROIs constituting a three by three matrix were defined. ROIs and respective electrodes were: left-frontal: AF3, F3, F5; mid-frontal: FCz, F1, F2; left-central: C3, C5, CP5; mid-central: CPz, C1, C2; left-posterior: P3, P5, PO3; mid-posterior: POz, P1, P2; and the respective right counterparts to left-sided regions and electrodes. The resulting three-level factors Anterior-Posterior (AP) and Laterality (Lat) were again used in all analyses. Analyses were followed up by planned comparisons, applying Holm's sequential Bonferroni correction of alpha levels where applicable (Holm, 1979).

6.1.2 Results and Discussion

6.1.2.1 Behavioural Results and Discussion

Accuracy data are depicted in Figure 31. Differing from the figure, analysis was based on corrected recognition scores (Pr-score = hit rate – false alarm rate; Snodgrass and Corwin, 1988), as these offer a better estimate of true performance level. Pr-scores were .73 for Intrinsic/Same, .67 for Intrinsic/Different, .70 for Extrinsic/Same, and .65 for Extrinsic/Different conditions, respectively. Performance was well above chance in all conditions, all $t(31) > 15.24$, $MSE < .05$, $p < .001$. In a 2 x 2 ANOVA with the factors Congruency (Same vs. Different) and In-

trinsic/Extrinsic, there was a main effect of Congruency, $F(1,31) = 14.77$, $p < .001$, indicating better performance for Same repetitions. Performances did not differ reliably between the Intrinsic and Extrinsic conditions, and there was no interaction, both $F(1,31) < 1$.

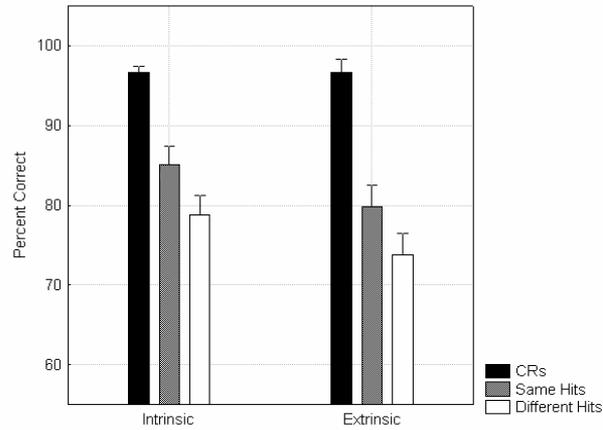


Figure 31. Recognition memory performance in the Intrinsic and Extrinsic conditions, Experiment 4. CRs denotes correct rejections of new items. Vertical bars denote standard errors of the mean; figure adapted from Ecker et al. (under revision).

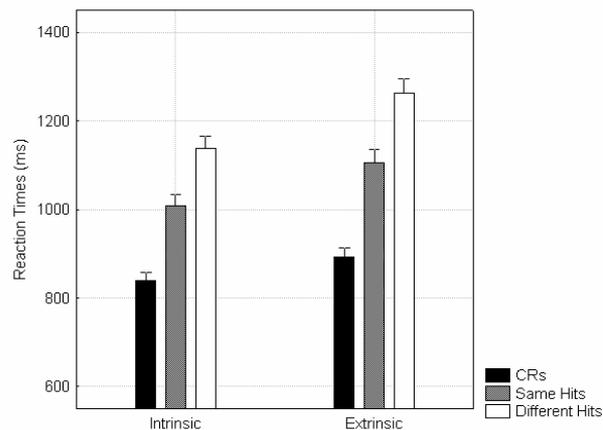


Figure 32. Mean response times in the Intrinsic and Extrinsic conditions, Experiment 4. CRs denotes correct rejections of new items. Vertical bars denote standard errors of the mean; figure adapted from Ecker et al. (under revision).

Reaction time data are depicted in Figure 32. New items were rejected rather quickly, response times were 839 ms in the Intrinsic and 892 ms in the Extrinsic case, the latter being significantly slower, $F(1,31) = 11.01$, $p < .01$. Given the experimental hypotheses, further analysis of reaction times was restricted to hits. Mean hit RTs were 1008 ms for Intrinsic/Same, 1138 ms for Intrinsic/Different, 1105 ms for Extrinsic/Same, and 1263 ms for Extrinsic/Different

conditions, respectively. Thus, in the analysis of RT data (analogue to accuracy data analysis), there were main effects of Congruency, $F(1,31) = 70.82, p < .001$, and Intrinsic/Extrinsic, $F(1,31) = 43.60, p < .001$, but no interaction, $F(1,31) = 2.28, p > .1$. Post-hoc testing (Tukey HSD) revealed that all conditions differed significantly from all other relevant conditions, all $p < .01$ (i.e., Intrinsic/Different and Extrinsic/Same did not differ significantly, $p > .05$).

6.1.2.2 ERP Results and Discussion

Grand average ROI waveforms are depicted in Figures 33 and 34. In both Intrinsic and Extrinsic conditions, waveforms elicited by new and old items differ from about 300 ms onwards, especially at frontal sites. In the Intrinsic condition, this old-new effect is more pronounced for Same vs. Different repetitions.

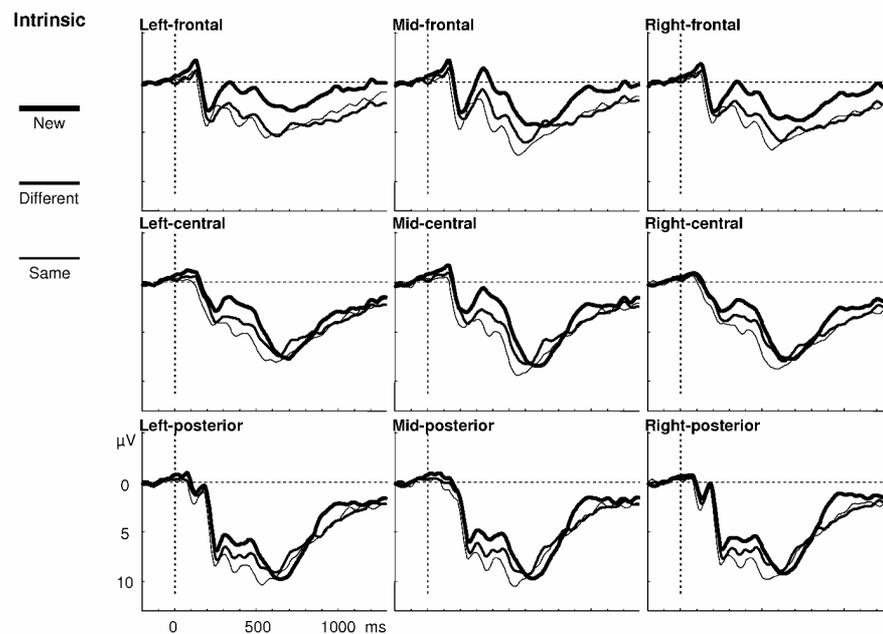


Figure 33. Topographically arranged (ROI) grand average ERP data from the Intrinsic condition, Experiment 4. Time scaling ranges from -200 to 1300 ms post stimulus onset; positive deflections are displayed downward; figure adapted from Ecker et al. (under revision).

In Time window 1 (300-500 ms), an AP by Lat by Intrinsic/Extrinsic by Condition analysis yielded a significant four-way interaction, $F(8,24) = 2.58, p < .05$. Comparing Intrinsic and Extrinsic conditions, the interesting interaction contrast between Same and Different amplitudes at the mid-frontal ROI was significant, $F(1,31) = 5.10, p < .05$. That is, mid-frontal Same and Different waveforms dif-

ferred only in the Intrinsic condition in the first Time window. Table 5 shows the planned comparisons in both conditions.

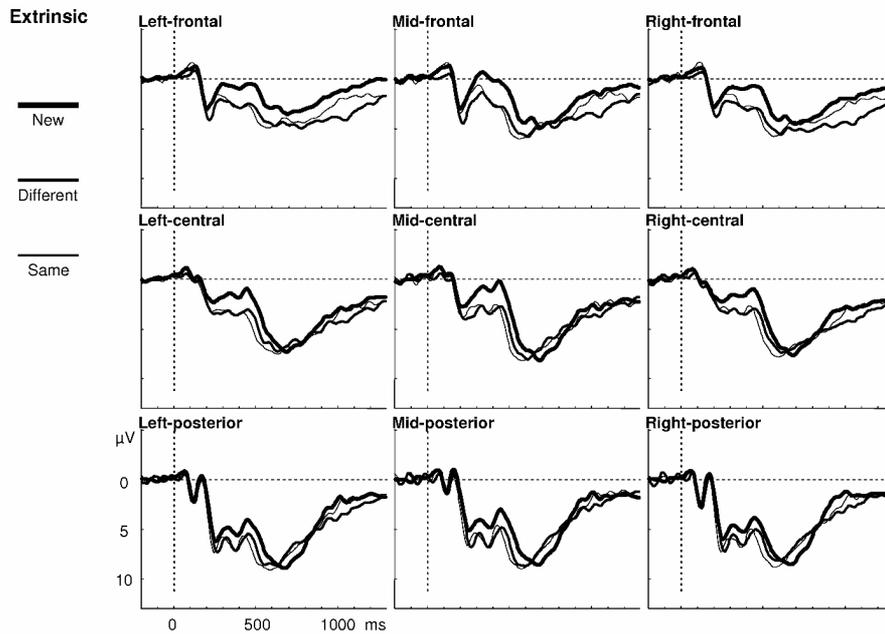


Figure 34. Topographically arranged (ROI) grand average ERP data from the Extrinsic condition, Experiment 4. Time scaling ranges from -200 to 1300 ms post stimulus onset; positive deflections are displayed downward; figure adapted from Ecker et al. (under revision).

Contrast	<i>df</i>	<i>F</i>	<i>p</i>
Intrinsic condition			
New – Same	1,31	49.37	< .0001
New – Different	1,31	19.46	.0001
Same – Different	1,31	11.68	.0018
Extrinsic condition			
New – Same	1,31	29.48	< .0001
New – Different	1,31	34.66	< .0001
Same – Different	1,31	< 1	

Table 5. Planned comparisons concerning Intrinsic and Extrinsic conditions at the mid-frontal ROI in time window 1, Experiment 4; table adapted from Ecker et al. (under revision).

In Time window 2 (500-700 ms), an AP by Lat by Intrinsic/Extrinsic by Condition analysis yielded only an AP by Condition interaction, $F(4,28) = 8.35$,

$p < .001$, due to the fact that there were basically no old-new effects whatsoever at posterior sites.

To investigate this rather puzzling finding, we looked at the ERPs of single subjects and discovered that virtually every single subject exhibited an LPC old-new effect at posterior sites around 500-800 ms, only that many effects were reversed in polarity (i.e., waveforms elicited by new items were more positive). Therefore, the described null effect seemed to be an averaging effect. We thus decided to establish a new Group factor in order to compare ERPs of subjects with a standard LPC effect with those showing an inverse effect. For that purpose, Intrinsic and Extrinsic conditions were collapsed, and so were Same and Different repetitions. Subjects were then grouped according to the resulting plain old-new effects at the left-posterior ROI between 500-700 ms. Exactly half the subjects showed a standard old-new effect, that is, waveforms elicited by old as compared to new items were on average more positive (range was .3 to 6.3 microvolts). The other half of subjects demonstrated an inversed LPC old-new effect, with waveforms elicited by old items more negative (effect range was -.2 to -5.9 microvolts). This Group factor (Standard vs. Inverse) was incorporated into the following analyses.

Grand average ERPs of the two groups are depicted in Figures 35 to 38. In the Intrinsic/Standard case, Same repetitions show a posterior old-new effect between 500 and 700 ms. As in previous research from our laboratory (Ecker et al., in press, 2007), the effect does not, however, have a posterior focus. In the Extrinsic/Standard condition, the effect also extends from 500 to 700 ms and beyond; again, it is larger for Same repetitions. Finally, in both Intrinsic and Extrinsic Inverse cases, there is a positive component in the waveform elicited by new items mainly between 600 and 800 ms (inverse LPC effect). Peak latency analysis revealed that correct rejection waveforms peaked later in the Inverse as compared to the Standard group (690 vs. 629 ms; $F(1,30) = 5.55$, $p < .05$). Importantly, however, the grouping does not affect the FN400 effect pattern described above. In both groups, the FN400 old-new effect is larger for Same vs. Different test cases in the Intrinsic but not the Extrinsic condition.

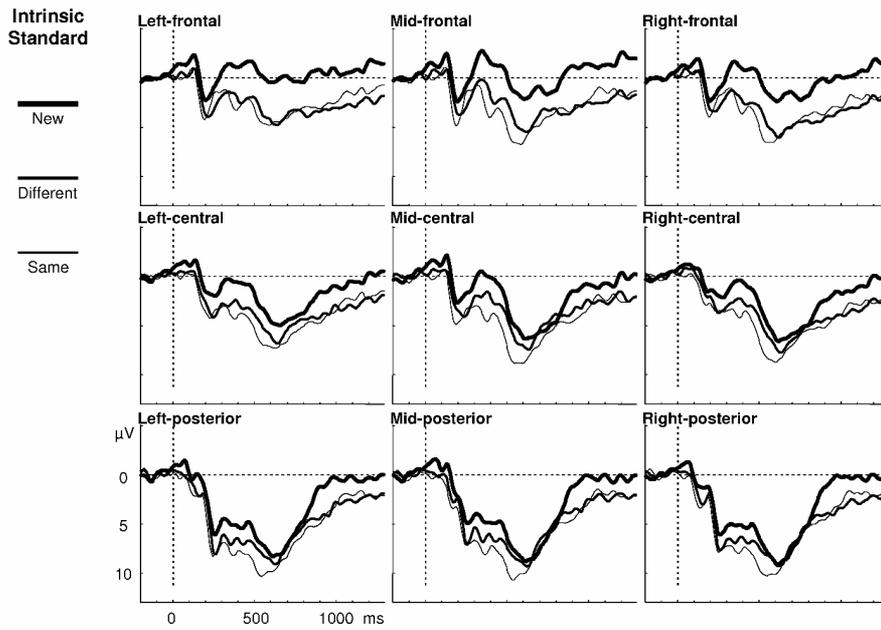


Figure 35. Topographically arranged (ROI) grand average ERP data from the Intrinsic condition, Standard group, Experiment 4.

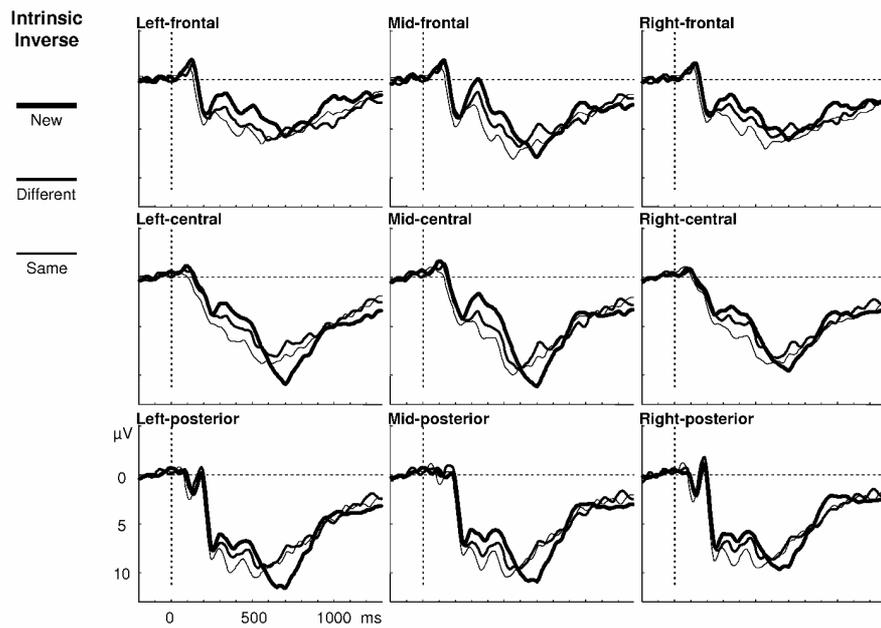


Figure 36. Topographically arranged (ROI) grand average ERP data from the Intrinsic condition, Inverse group, Experiment 4.

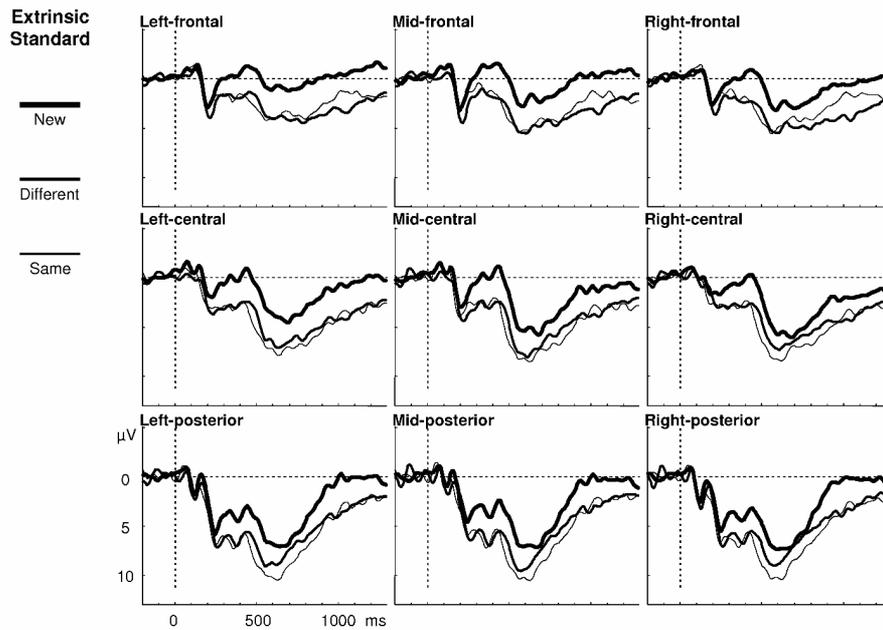


Figure 37. Topographically arranged (ROI) grand average ERP data from the Extrinsic condition, Standard group, Experiment 4.

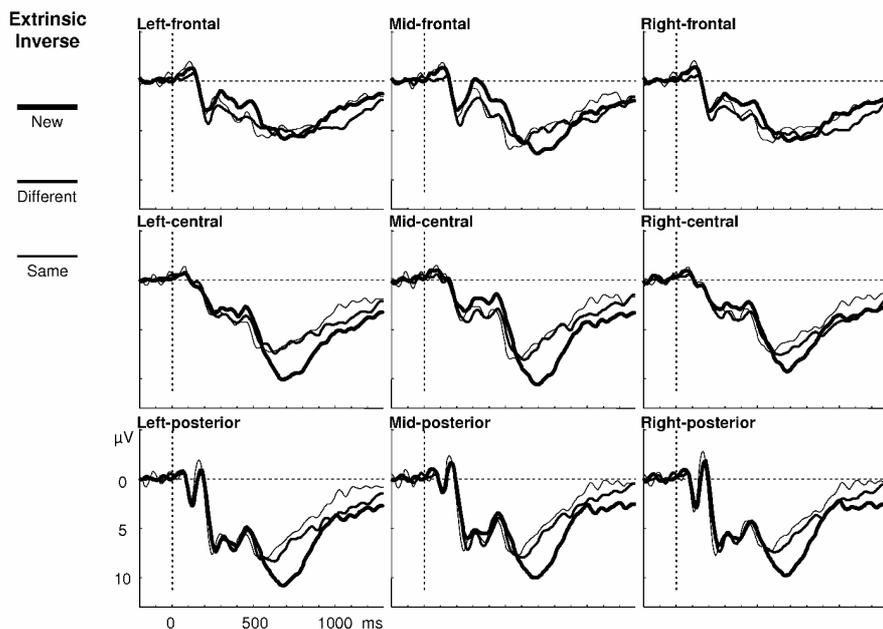


Figure 38. Topographically arranged (ROI) grand average ERP data from the Extrinsic condition, Inverse group, Experiment 4.

In Time window 1 (300-500 ms), an AP by Lat by Intrinsic/Extrinsic by Condition by Group analysis was performed. The AP by Lat by Intrinsic/Extrinsic by Condition interaction was of course still significant, $F(8,23) = 2.61$, $p < .05$, but not modulated by Group ($F(8,23) = 1.03$). Although the overall Group by Condition

interaction was also significant ($F(2,29) = 5.67, p < .05$), there were no further effects involving both Condition and Group (all $F < 1.88, p > .1$). All planned comparisons complied with hypotheses, a very minor exception being the New – Different old-new effect in the Intrinsic-Inverse condition, which just failed to reach significance. In sum, however, the grouping by LPC shape had no influence at all on the FN400 effect pattern (see planned comparisons in Table 6).

Contrast	<i>df</i>	<i>F</i>	<i>p</i>
Intrinsic condition – Standard group			
New – Same	1,30	43.08	< .0001
New – Different	1,30	21.25	< .0001
Same – Different	1,30	5.92	.0211
Extrinsic condition – Standard group			
New – Same	1,30	28.88	< .0001
New – Different	1,30	37.67	< .0001
Same – Different	1,30	< 1	
Intrinsic condition – Inverted group			
New – Same	1,30	14.52	.0006
New – Different	1,30	3.59	.0680
Same – Different	1,30	5.39	.0272
Extrinsic condition – Inverted group			
New – Same	1,30	6.96	.0131
New – Different	1,30	7.76	.0091
Same – Different	1,30	< 1	

Table 6. Planned comparisons concerning Intrinsic and Extrinsic conditions in the Standard and Inverse groups at the mid-frontal ROI in time window 1, Experiment 4.

Concerning the LPC effect, following the peak latency analysis mentioned above, time windows were set to 500-700 ms in the Standard and 600-800 ms in the Inverse case. In an AP by Lat by Intrinsic/Extrinsic by Condition by Group analysis, there was an AP by Lat by Condition by Group interaction, $F(8,23) = 2.76, p < .05$, which was not modulated by Intrinsic/Extrinsic, $F(8,23) = 1.86, p > .1$. In the Intrinsic case, the LPC effect seemed to be larger for Same vs. Different repetitions in the Standard group, while there was no differ-

ence in the Inverse group, so the respective interaction contrast of Congruency (Same vs. Different) and Group (Standard vs. Inverse) was not significant ($F < 1$). In the Extrinsic case, however, the LPC effect was larger for Same vs. Different repetitions in both the Standard and the Inverse case. That is, the old-new effect was accentuated in the Same condition in both groups, even though this implies that the Same waveform was the most negative in one and the most positive in the other group. Thus, the interaction contrast of Congruency and Group was significant ($F(1,30) = 4.77, p < .05$). Single planned comparisons are listed in Table 7. Although old-new effects seemed to be somewhat larger in the Extrinsic condition, a comparison of unsigned differences was nonsignificant, $F(1,30) = 2.08, p = .16$.

Contrast	<i>df</i>	<i>F</i>	<i>p</i>
Intrinsic condition – Standard group			
New – Same	1,30	4.41	.0442
New – Different	1,30	1.04	> .1
Same – Different	1,30	1.07	> .1
Extrinsic condition – Standard group			
New – Same	1,30	22.56	< .0001
New – Different	1,30	10.77	.0026
Same – Different	1,30	4.21	.0491
Intrinsic condition – Inverted group			
New – Same	1,30	7.49	.0103
New – Different	1,30	9.67	.0041
Same – Different	1,30	< 1	
Extrinsic condition – Inverted group			
New – Same	1,30	19.06	.0001
New – Different	1,30	15.16	.0005
Same – Different	1,30	1.08	> .1

Table 7. Planned comparisons concerning Intrinsic and Extrinsic conditions in the Standard and Inverse groups at the left-posterior ROI in time window 2, Experiment 4.

In a next step, we considered possible other differences between the two groups. As far as demographic characteristics are concerned, mean age in the

Standard group was 22.4 years (range 20 - 27), mean age in the Inverse group was 25.3 years (20 – 39). The difference was marginally significant, $t(30) = 1.82$, $p = .08$. Yet, there were only two outliers over the age of 30 (37 and 39), and these two subjects of the Inverse group were ranked 13th and 16th in the size of the inverse effect, that is, they were not the main contributors. Thus, age cannot be the crucial factor. In the Standard group, 8 participants were female, there were 9 females in the Inverse group, this difference was not significant, $t(30) < 1$.

Performance-wise, including the factor Group into accuracy analysis yielded no significant effects involving the Group factor, there was only a slight tendency for a larger effect of Congruency in the Standard group, $F(1,30) = 2.35$, $p = .14$. Mean performance was slightly better in the Standard group (Pr score .73 vs. .65), but this difference was not significant, $F(1,30) = 1.28$, $p > .1$, and neither did performance levels in the individual subconditions (Intrinsic/Extrinsic-Same/Different) differ according to Group status, all $t(30) < 1.3$, all $p > .1$. The performance difference was based on hits, not false alarms, as false alarm rates did not differ across groups (.08/.10 in the Standard and .10/.14 in the Inverse group, both $t(30) < 1$), suggesting that there were no bias differences. This was confirmed in an analysis of Br-scores (false alarm rate / 1-Pr; Snodgrass & Corwin, 1988). An Intrinsic/Extrinsic by Congruency (Same vs. Different) by Group ANOVA yielded no effects involving the Group factor (all $F < 1$), and individual t-tests were also nonsignificant (all $t(30) < 1.05$).

In terms of reaction times, the Group factor had a significant influence on the congruency effect, that is, the difference between correct Same and Different responses was larger in the Standard group compared to the Inverse group (181 ms vs. 107 ms). Overall hit reaction times (1140 vs. 1116 ms) did not differ across groups, $F < 1$, and neither did correct rejection RTs differ (863 ms vs. 868 ms, $F < 1$). In an Intrinsic/Extrinsic by Group analysis on correct rejection RTs, there was a marginally significant interaction, indicating a larger RT difference between Intrinsic and Extrinsic conditions in the Standard group, $F(1,30) = 3.59$, $p = .07$.

In terms of reaction times, the Group factor had a significant influence on the congruency effect reported above, that is, the difference between correct Same and Different responses was larger in the Standard group compared to the Inverse group (181 ms vs. 107 ms; $F(1,30) = 5.43$, $p < .05$; see Figure 39). Overall hit reaction times (1140 vs. 1116 ms) did not differ across groups, $F < 1$, and neither did correct rejection RTs differ (863 ms vs. 868 ms, $F < 1$). In an Intrinsic/Extrinsic by Group analysis on correct rejection RTs, there was a marginally significant interaction, indicating a larger RT difference between Intrinsic and Extrinsic conditions in the Standard group, $F(1,30) = 3.59$, $p = .07$.

sic/Extrinsic by Group analysis on correct rejection RTs, there was a marginally significant interaction, indicating a larger RT difference between Intrinsic and Extrinsic conditions in the Standard group, $F(1,30) = 3.59, p = .07$ (see Figure 39).

Finally, "Sequence of Condition" (Intrinsic/Extrinsic vs. Extrinsic/Intrinsic) and "Response Key Assignment" (old left vs. old right) factors were controlled, which did not moderate the described LPC group effects (all $F(1,28) < 1.07, p > .1$).

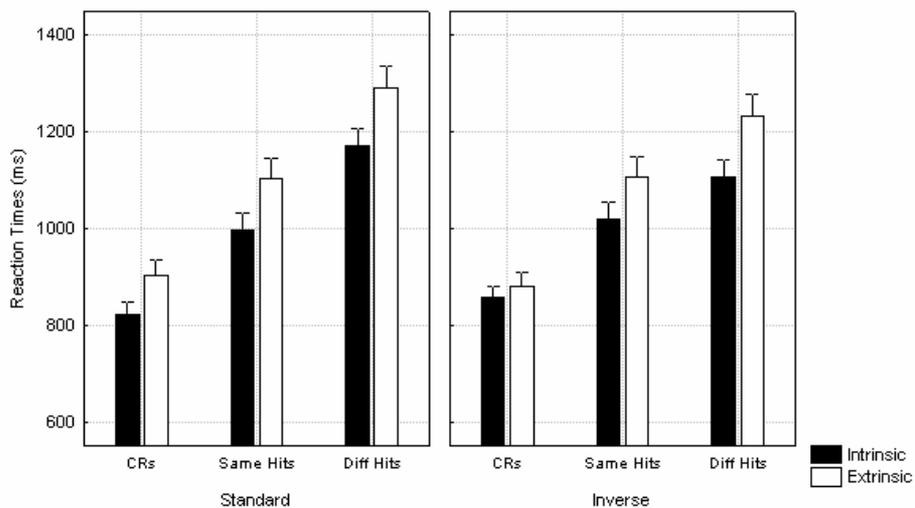


Figure 39. Mean response times in the Intrinsic and Extrinsic conditions, for Standard and Inverse groups, Experiment 4. CRs denotes correct rejections, Diff refers to the Different condition. Vertical bars denote standard errors of the mean.

Taken together, there was no obvious and straightforward indication how the two groups may differ beyond their ERPs. Yet, the Standard group had slightly better performance and in particular showed larger congruency effects. Even in correct rejection RTs, the Inverse group showed less evidence for a processing of the sensory colour information. This suggests that there was very likely a strategy difference between the two groups. The Standard group seems to have relied more on sensory processing, showing larger effects of the perceptual manipulation in their behavioural data, and even incorporating colour information into their processing of new objects (as indicated by higher response times in the correct rejection of extrinsic vs. intrinsic novel items). To further investigate this idea, we looked at performance in a different way, making a two-fold decision out of the three-fold-decision, so to speak, and pooling Same and Different hits. This way, a Same item drawing a Different response would no longer be considered a miss,

but a hit (the item was recognised as old), thus allowing for a purer estimation of item memory devoid of colour "source" information. In this case, the performance difference between groups was even smaller (Pr-score .86 vs. .82, $F(1,30) < 1$), suggesting a potential true difference in source but not item memory.

6.1.3 Discussion

The aim of the experiment was to investigate whether the manipulation of a perceptual feature would impact on recognition memory performance, and in particular whether it would impact differentially on ERP measures of familiarity and recollection, depending on its intrinsic versus extrinsic status. Therefore, we designed an experiment manipulating the same feature – colour – in an intrinsic and an extrinsic condition, holding constant all other factors, even including the number of colour pixels in the two conditions.

As expected, performance in both Intrinsic and Extrinsic conditions was worse when colour was changed from study to test. Given the task-relevance of the feature at both study and test, this is best explained by the partial mismatch between perceptual and mnemonic representations. In the Different condition, there was thus a conflict between matching item information calling for an "old" response and mismatching colour information. New items, on the other hand, could be rejected based on item information alone and were therefore fastest. Interestingly, overall hit responses were slower in the Extrinsic condition, suggesting that the integration of extrinsic colour information is slower and likely less automatic than intrinsic integration.

Turning to ERPs, the results concerning the FN400 old-new effect associated with familiarity were clear-cut. Changing an intrinsic object feature from study to test diminished the FN400 old-new effect, whereas the extrinsic manipulation had no effect whatsoever. Notably, even the grouping of subjects into two groups according to the shape of their later LPC old-new effect (Standard vs. Inverse, see below) did not alter this effect pattern. Thus, presumably, intrinsic colour is part of the representation used to assess object familiarity, whereas extrinsic colour is not. This offers an explanation for the behavioural result pattern, that is, extrinsic feature integration is slower because it cannot be based on familiarity processing. In other words, because subjects' decision needed to take colour into account, reactions were quicker in the Intrinsic case because subjects could use the early familiarity signal as a first indication of Same/Different status. Given the quite high

latencies, subjects apparently did not base their decisions on the rather equivocal familiarity signal alone. Yet, the familiarity signal may have influenced further recollective processing, thus accelerating responses in the Intrinsic condition.

We had recently reported a similar FN400 pattern in an inclusion task, for which the intrinsic colour information was thus not relevant for the decision, in contrast to the present case (Ecker et al., in press; Experiment 2). Therefore, it can now be concluded that familiarity can be perceptually specific, and that this effect does not depend on task relevance of the feature at test. The data from our laboratory (see also Groh-Bordin et al., 2005, 2006) seems to indicate that, given item processing is not purely conceptual due to, e.g., task demands, perceptual features are included in the representation subserving familiarity memory as long as they are integral to the object. The present experiment shows that it is truly the Intrinsic/Extrinsic factor determining whether or not feature manipulations will impact on familiarity, as all other factors were held constant; most importantly, the same feature was manipulated in both conditions. There are also reported null effects of perceptual manipulations on familiarity ERP effects (Curran, 2000; Curran & Cleary, 2003). Yet, these studies had implemented only rather small changes (e.g., adding a plural –s to a word) that were perhaps therefore not picked up by the rather coarse familiarity estimate (Holdstock et al., 2002; Mayes et al., 2002). Furthermore, because in the present case colouring was arbitrary and did not affect semantic appropriateness, the present results contradict an alternative conceptual priming account of the early mid-frontal old-new effect (Yovel and Paller, 2004; Voss and Paller, 2006; see also Groh-Bordin et al., 2006, and Curran et al., 2002).

As far as recollection is concerned, hypotheses were that the feature manipulation should impact on the LPC effect in both conditions. Overall effects tended to be larger in the Extrinsic condition, although this was not a significant difference. In the Extrinsic condition, while both Same and Different conditions yielded significant old-new effects (in both Standard and Inverse groups), there was a reliable difference between the two old conditions in the Standard group (and a respective trend in the Inverse group resulting in a significant interaction contrast). This is evidence for feature integration in recollective processing. In the Intrinsic condition, on the other hand, only the Same old-new effect was reliable in the Standard group at all, which is indirect evidence for the impact of feature processing, but there was no difference in the Inverse group between Same and Different. One can thus conclude that the influence of the feature manipulation was

pronounced in the Extrinsic condition. This suggests there was a higher need for feature processing and integration in the Extrinsic condition as compared to the Intrinsic condition, in which feature binding already impacted on familiarity signal calculation, as expected.

The unexpected occurrence of inverse LPC effects in a subgroup of participants poses some further questions. Post-hoc analysis suggests that there were no straightforward demographic characteristics such as age or sex that could explain the difference. Notably, a somewhat similar pattern of a reversed LPC effect was reported by Nessler, Friedman, and Bersick (2004). They argued that in a paradigm requiring subjects to discriminate between old items, semantically similar lures, and new items (a false memory paradigm), new items at test can be rejected on the basis of semantic information alone. As a result, subjects may use a strategy focussing on the detection of categorical novelty, a strategy not well suited for standard old-new tasks. Nessler et al. reported similar mid-frontal old-new effects in both standard and false memory tasks, but a marked difference concerning the later LPC effect. Namely, there was a standard LPC effect in the standard task, but an inverse effect – due to a positivity for new items (somewhat akin of the novelty P3 as reviewed by Friedman, Cycowicz, & Gaeta, 2001) – in the false memory task. The present design was much like the "false memory paradigm" implemented by Nessler et al. inasmuch as there were lures (Different items) that were semantically similar (or rather, identical) to old (Same) items, whereas new items could be identified as such on the basis of conceptual information alone. In the present experiment's behavioural data, it became evident that effects of the feature manipulation were more pronounced in the group showing a standard LPC effect, in line with the ERP data. Also, this is in keeping with the assumption that subjects for which perceptual information had less effect were those to adopt a strategy focussing on novel categorical information. Thus, a difference in processing strategy indeed seems to offer the most plausible interpretation. Presumably, subjects of the Standard group focused more on the integration of old items and the comparison of Same and Different items, whereas subjects of the Inverse group focussed more on the processing of new items, perhaps in the sense of a "recall to reject" or rather an "exhaustive search" strategy (Rotello & Heit, 1999, 2000; note that their conception of "recall-to-reject" only applies to similar lures, whereas "exhaustive search" refers to recollection-based rejection of similar *and* dissimilar new items; also see Jones, 2005; Lampinen, Odegard & Neuschatz, 2004; Yonelinas et al., 2005). Further research manipulating task strategy via instructions (i.e., comparing ERP effects following instruc-

tions to either focus on novelty or employ recollection, holding all other aspects constant), should aim to clarify this.

In an exploratory source analysis applying standardised low resolution brain electromagnetic tomography (sLORETA; Pascual-Marqui, 2002), the waveforms corresponding to the correct rejection of new items were investigated. Analysis was focused on "new" trials because this was where the striking LPC difference between subgroups arose¹³. sLORETA analysis revealed that in the Standard group, main activation at 616 ms – the time point with the waveform's maximum amplitude – was likely to arise from the left middle frontal gyrus (Brodmann area 11). There was also some activity visible at other left frontal areas and the left temporal lobe and uncus (BA 21, 38), as well as bilateral occipital activity (BA 18 and 19). In contrast, activity in the Inverse group (at 692 ms) was more right lateralised. There was major activity again at bilateral occipital cortex, largest at cuneus (BA 19), and also bilateral temporal activation, greatest at the right inferior and middle temporal gyrus (BA 20 and 21).

A very recent 4T fMRI study (Daselaar, Fleck, & Cabeza, 2006) has associated occipital activity with both familiarity and recollection, although it is suggested that this brain region is not a crucial contributor to these processes per se. Interestingly, they have reported lateral temporal activity to be associated with novelty processing bilaterally. Henson, Rugg, Shallice, Josephs, and Dolan (1999) reported bilateral middle temporal gyrus activation to be associated with "new" judgements. Likewise, Henson, Hornberger, and Rugg (2005) reported pronounced left middle frontal gyrus activation for hits (among many others) and left medial temporal lobe activation for correct rejections. Although this is an extremely selective review and one needs to be aware of the very low spatial resolution of the sLORETA method, the resulting pattern corroborates the notion of strategic processing differences and is also at least consistent with the functional imaging literature. Presumably, subjects of the Standard group used frontally controlled integration processes more strongly, perhaps also relying on verbal predicates generated at study, whereas the Inverse group focused more on the rejection of new items; whether or not one should call this recollection is an open issue, touching the question of whether or not recognition memory can be neatly explained by one or two distinctive processes or should rather be seen as the dy-

¹³ It is granted that this is not the standard approach to source analysis, as usually one would report statistical comparison of sources for some given contrast. Typically, precise statistical images are shown, hardly ever raw images; thus, this analysis served rather exploratory and illustrative purposes.

dynamic interaction of parallel and hierarchical subprocesses flexibly adapted to task demands (see General Discussion).

6.2 Experiment 5

In the experiments reported so far, we were able to show that familiarity and the associated FN400 effect are sensitive to study-test manipulations of intrinsic item features (e.g., the colour of an object), but insensitive to contextual manipulations. That is, the FN400 old-new effect was diminished if the colour of objects was changed from study to test, but it was not affected by a change of contextual features, even though this specific context information was available to subjects in a direct memory test and/or influenced performance. In contrast, recollection and the associated LPC effect were affected by both item and contextual study-test changes. I arrived at the interim conclusion that familiarity is an acontextual process matching conceptual and perceptual features of specified test stimuli and object memory representations.

Yet, as noted before, Tsivilis et al. (2001) did report a contextual influence on the FN400 effect. They had subjects study object images on highly salient landscape (context) scenes, and manipulated the old/new status of objects, contexts, and their specific combinations, resulting in five test conditions: old objects presented on the SAME background as at study (i.e., identical repetition), old objects presented on an old context, but REARRANGED with respect to study, old objects presented on new backgrounds (OLD/NEW), and new objects presented on either old (NEW/OLD) or new (NEW/NEW) backgrounds. Instructions were to judge the old/new status of objects, irrespective of context (inclusion task). They reported an FN400 effect only for SAME and REARRANGED repetitions, but not for OLD/NEW items. At first glance, this finding speaks against the view that familiarity is an acontextual process. Interestingly, however, SAME and REARRANGED conditions did not differ in their ERP effects¹⁴, suggesting that the FN400 signal was not based on activation of an integrated representation of item and context. Tsivilis et al. concluded that the FN400 effect indexes some process "downstream" of familiarity and/or rather reflected novelty processing.

¹⁴ Note that there was a difference in reaction times, i.e., RT was lower for SAME vs. REARRANGED.

An alternative interpretation of the lacking effect for OLD/NEW items stems from a careful examination of the processes leading up to a familiarity judgement. Most recognition memory studies use single, stand-alone items, whereas in reality the visual environment at any given time usually consists of scenes of many different overlapping objects and backgrounds. Thus, attention and perception processes first need to establish stable and bound representations of what is to be assessed. This implies that there is a "race" of features and objects for representation and (conscious) perception. Usually, this race will be won by the object that is either most salient for any given reason (e.g., size, colour, brightness, occlusion, figure-ground phenomena may all play a role for attentional capture and the speed of initial processing, independent of task-relevance; cf. Brockdorff & Lamberts, 2000; Hickey, McDonald, & Theeuwes, 2006; Lamberts, 1998) or it will be won by the object that has a certain attentional top-down advantage (biased competition; cf. Beck & Kastner, 2005, for a report of a neural mechanism concerning this matter). Then, the familiarity signal results from a comparison of object representations in perception (object file; cf. Treisman, 2006) and episodic memory (object token; cf. Ecker et al., 2004). Assuming that this signal is an encapsulated signal of the object and its intrinsic features, context information should not have any influence (Cabeza, 2006; Ecker et al., in press; Yonelinas, Kroll, Dobbins, & Soltani, 1999). The Tsivilis et al. (2001) data seemingly stand in contrast to this notion; what might have happened at least in a subset of their trials is that memory was initially not cued with the actual target object, but the highly salient context. That is, if the context stimulus won the competition for representation due to its advantage in salience and was thus perceived first, it initially affected familiarity processing before an attention shift put the actual target into focus, allowing subjects to perform the task at a high level of accuracy. In other words, an alternative interpretation of the FN400 data pattern is that contexts in the Tsivilis et al. study were so salient that they achieved object status themselves, hence becoming "more than context" and eliciting an own electrophysiological familiarity signal. It seems likely that at test, attention was automatically drawn to these large and highly salient landscapes, so the cognitive system was not able to treat them as contextual noise irrelevant for the decision. Therefore, the effect pattern may not represent a direct influence of context on target familiarity, but rather an independent familiarity signal of the context (or rather, a lack of such a signal in the case of a new context stimulus).

The aim of Experiment 5 was to test this idea by adopting the Tsivilis et al. (2001) design and manipulating the potential of the contexts to automatically cap-

ture attention. This was done by implementing a two-group design: one group followed the Tsivilis et al. procedure, whereas we introduced a cueing technique in the other group, following spotlight/zoom lens conceptions of visual attention (Cave & Kosslyn, 1989; Paul & Schyns, 2003; Posner, Snyder, & Davidson, 1980; Yantis & Jonides, 1990). This was stipulated by a recent fMRI study analysing neural activity in multiple visual areas as a function of the size of an attended region, defined by a spatial cue (Müller, Bartelt, Donner, Villringer, & Brandt, 2003). After cueing, a target stimulus (a specific shape-colour conjunction) had to be identified within the region. Neural activity preceding the objects correlated with the size of the region, as did performance. While the extent of activated retinotopic visual cortex increased with the size of the attended region, the level of activity at any given subregion decreased, consistent with physiological predictions of the zoom lens model. Largest effects were found for early visual areas (bear in mind that this was pre-target activity, i.e., before biased competition), presumably fostering efficient feature binding and object identification. Details concerning the current cueing technique are reported below.

6.2.1 Design, Hypotheses and Methods

The design followed the one by Tsivilis et al. (2001) in many aspects. Throughout the experiment, object images of varying size¹⁵ (max. expansion 90 – 160 pixels) were presented superimposed on rectangular background images (300 x 400 pixels). The object images depicted both natural and man-made items, including animals, food items, and tools. The background images depicted landscapes with the limitation that no buildings, animals, or people appeared. Landscapes were always presented centrally, on a 17" flat screen monitor. The experiment took place in a sound- and electromagnetically shielded cabin, subjects sat about 80 cm from the screen. Objects took up a visual angle of approximately 2 – 4 degrees; the angle for landscapes was approximately 9 x 7 degrees.

Altogether, 180 object images and 105 landscapes were used. For every participant, one of seven sets of 15 contexts each was randomly selected for the

¹⁵ Note that the only reason for different sizing of objects was the application of the cueing technique – if all objects were virtually the same size, cues would not be very helpful. There were no study-test size manipulations.

study phase. Subjects studied 120 objects, each presented on one of the four quadrants of the 15 different landscape images (i.e., every selected context appeared 8 times in the study phase). Subjects' task was to mentally place the object anywhere within the landscape scene, and to think of a reason or narrative why they placed it there. Additionally, and departing from the original Tsvilis et al. (2001) study, instructions were given to memorise the material. Presentation rate was self-paced; however, every item was presented at least 3000 ms. The ISI was 500 ms, in which a fixation cross was presented centrally. A practice phase with four items not appearing in the actual experiment preceded the study phase; during practice, subjects spoke out loud the narrative, which was controlled by the experimenter. Between the practice and study phase, subjects were presented with all fifteen contexts to appear in the study phase for the purpose of familiarisation; each background was shown for 2000 ms, with an ISI of 500 ms.

Preceding the actual test phase, another practice phase with five trials – one from each test condition, using the material of the first practice phase plus new items also not included in the experiment proper – was carried out. At test, all objects were presented centrally on the background image. There were five test conditions: 30 old objects appeared on the background they had already appeared on during study (SAME), 30 old objects were presented on an old but different background (REARRANGED), and 60 old objects were presented on new backgrounds (OLD/NEW). Additionally, 30 new objects appeared on old (NEW/OLD) and new (NEW/NEW) backgrounds, respectively (see Figure 40). All old contexts appeared twice per pertinent condition (i.e., SAME, REARRANGED, and NEW/OLD). The task was an inclusion task, that is, subjects were to classify all repeated objects as old, irrespective of context or context changes. Throughout the experiment, there were pauses after every 60 items for subjects to relax their eyes; there was one filler item at the beginning of each test block of 60 trials.

There were two groups of subjects. For the NoCue group, the trial course was as follows: after a fixation cross (1500 ms), the test item was presented for 1000 ms and subjects were to respond as quickly as possible with a maximum response time of 2000 ms. The test item disappeared with the response (or after presentation time had elapsed), and a central x appeared for another 1000 ms. For the Cue group, the procedure was the same, except that the fixation cross was only presented for 500 ms, and instead a cue was presented for 1000 ms, immediately preceding the test item. The cue was a grey rectangle with a red frame, exactly encasing the following target object. Subjects of the Cue group

were told that the cue would help them focus their attention on the object and ignore the irrelevant context. The cueing technique thus served to counteract early bias effects of salience on representational competition by strengthening bottom-up and top-down attention focusing (cf. Cave & Kosslyn, 1989). Predictions were that the Tsvilis et al. FN400 effect pattern could be replicated in the NoCue group, whereas for the Cue group, equivalent FN400 old-new effects were predicted for the three conditions featuring old objects (SAME-REARRANGED-OLD/NEW).



Figure 40. Items and test conditions of Experiment 5; figure adapted from Ecker et al. (2007).

After the experiment proper, there was another test designed to directly tap source memory, that is, whether or not subjects had associated the objects with the specific contexts. This was a two-alternative forced-choice associative recognition test: every old test object was presented together with two landscape scenes beneath it. One of the contexts was the same as in the study phase, the other was also an old context (i.e., one of the 15 that had appeared in the study phase), but one that had not been presented with the specific object before – neither in the study phase, nor in the REARRANGED condition of the test phase. Subjects were to indicate on which context the specific object had been presented at study.

Thirty-two students of Saarland University – sixteen per group – took part in this study and were paid for their participation. Mean age, age range, and number of females was 26, 20-32, and 10 for the NoCue group, and 24, 20-27, and 9 for

the Cue group. One participant of the NoCue group had to be excluded from analysis due to excessive EEG artefact.

In EEG artefact rejection, values were set as follows: the maximum allowed amplitude in the segment was +/- 100 microvolts, the maximum voltage step between two successive sampling points was 40 microvolts, and the maximum difference between any two sampling points within an epoch was 100 microvolts). Trials violating these boundaries were discarded from analysis (5.6 % of trials). Analyses were again based on mean voltage amplitudes in specific ROIs (see below for details); only trials with correct old/new responses were included in analyses. Repeated measures ANOVAs corrected for non-sphericity using the Huynh-Feldt procedure were followed up by planned comparisons, applying Holm's sequential Bonferroni correction of alpha levels (Holm, 1979).

6.2.2 Results

6.2.2.1 Behavioural Results

a. Old-new recognition.

Accuracy and reaction time data are depicted in Figures 41 and 42. Repeated measures ANOVA on hit rates across groups indicated no interaction between Condition (SAME, REARRANGED, OLD/NEW) and Group ($F < 1$) and no significant main effect of Group, $F(1,29) = 2.02$, $p > .1$. In the NoCue group, the main effect of test condition was significant, $F(2,28) = 3.34$, $p < .05$; post-hoc testing (Tukey HSD) revealed a significant difference between SAME and OLD/NEW conditions, $p < .04$. In the Cue group, there was also a significant main effect of test condition, $F(2,30) = 4.49$, $p < .02$. The SAME condition differed significantly from OLD/NEW, $p < .02$. Concerning the two NEW conditions, there was no significant across group interaction or main effect of group, $F < 1$. Performance rate (NEW/NEW vs. NEW/OLD) did not differ in either group (both $F < 1.16$, $p > .2$).

Hit reaction time analysis yielded a marginally significant Group main effect, $F(1,29) = 2.83$, $p = .10$, indicating somewhat longer RTs in the Cue group (789 vs. 746 ms); there was no significant Condition by Group interaction, $F(2,58) = 2.00$, $p > .1$. Yet, there was a significant main effect of condition in the NoCue group, $F(2,28) = 5.04$, $p < .02$, whereas there was no such effect in the Cue group, $F < 1$. Post-hoc testing indicated that both SAME and REARRANGED RTs differed from the OLD/NEW condition in the NoCue group, $p < .02 / .05$). Regard-

ing RTs in the NEW conditions, there was no group main effect or interaction in the across group analysis ($F < 1$). RTs differed in neither the NoCue ($F < 1$) nor the Cue group ($F(1,15) = 2.97, p > .1$).

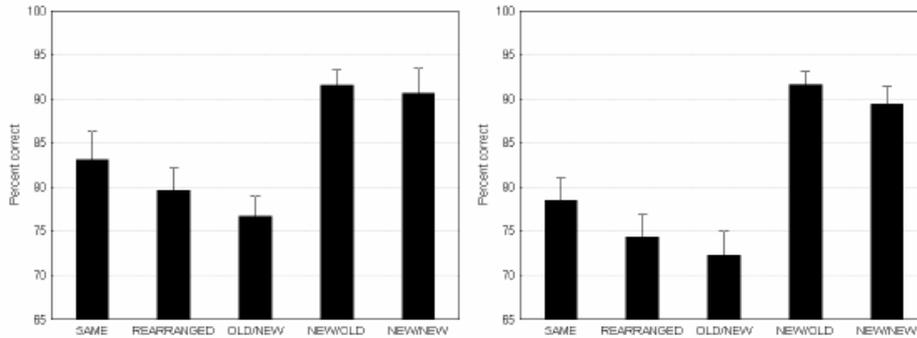


Figure 41. Old/new recognition performance in the NoCue (left) and Cue (right) groups, Experiment 5; vertical bars denote standard errors of the mean; figure adapted from Ecker et al. (2007).

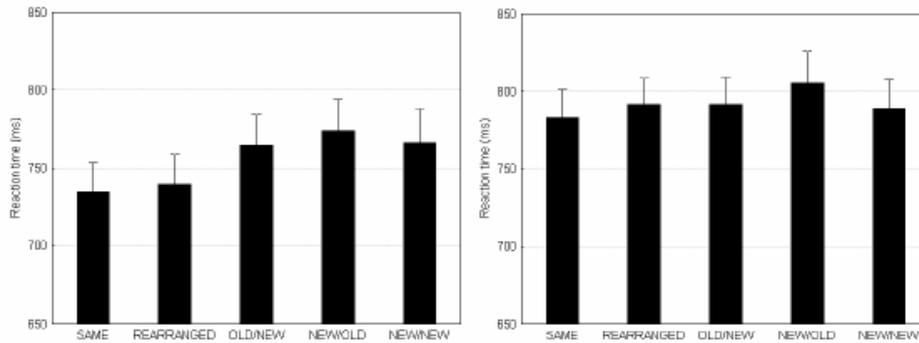


Figure 42. Reaction times in the NoCue (left) and Cue (right) groups, Experiment 5; vertical bars denote standard errors of the mean; figure adapted from Ecker et al. (2007).

b. Forced-choice associative recognition.

In the associative context recognition test at the end of the experiment, the mean rate of correct context-to-object assignment was .87 ($MSE .02$) and .86 ($MSE .02$) in the NoCue and Cue groups, respectively. Performances were consistently above chance in both groups, with $t(14) = 20.41, p < .001$ and $t(15) = 27.68, p < .001$, respectively. There was no group difference in performance level, $t < 1$, and no difference between mean reaction times (2635 vs. 2353 ms), $t < 1$.

6.2.2.2 ERP Results

Overall, the expected old-new effects (see Introduction) were observed (see Figures 43 and 44).

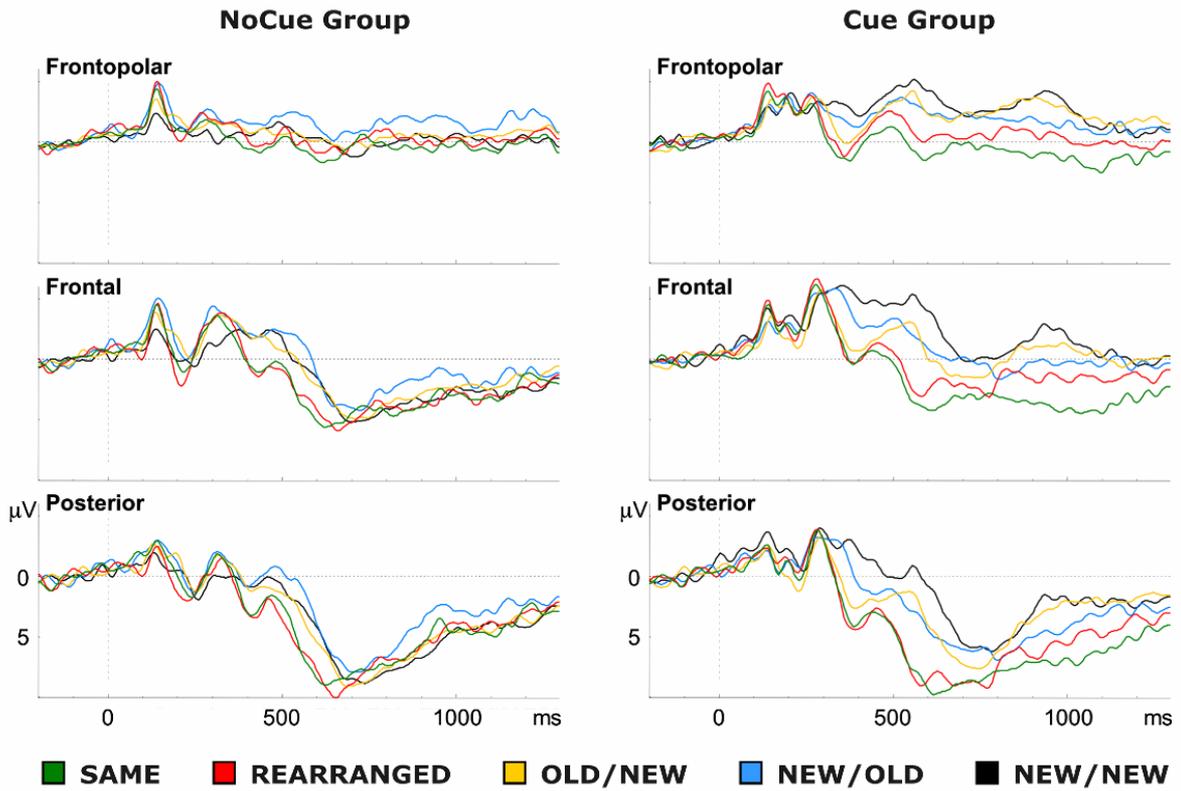


Figure 43. Stimulus-locked grand average ERPs at central ROIs, Experiment 5; figure adapted from Ecker et al. (2007).

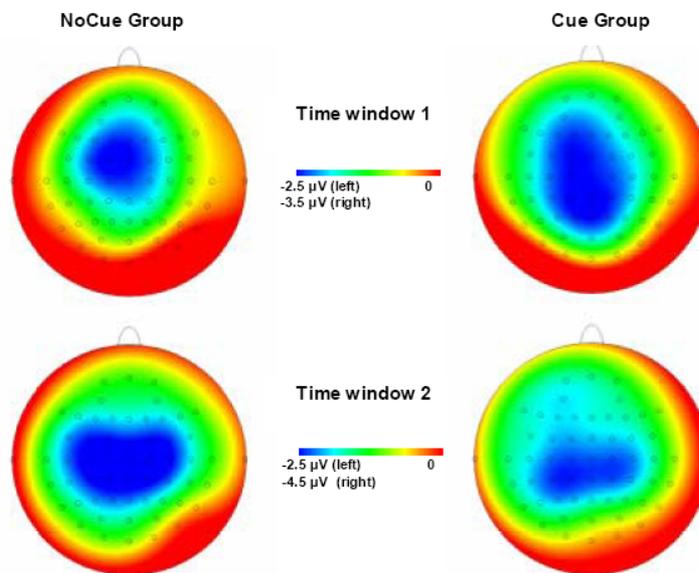


Figure 44. Topographic maps depicting the differences in the NoCue group (left) between SAME & REARRANGED vs. OLD/NEW, NEW/OLD, & NEW/NEW conditions in time windows 1 (top) and 2 (bottom), and the differences in the Cue group (right) between SAME, REARRANGED, & OLD/NEW vs. NEW/OLD & NEW/NEW in time window 1 (top), and SAME & REARRANGED vs. OLD/NEW, NEW/OLD, & NEW/NEW in time window 2 (bottom), Experiment 5; figure adapted from Ecker et al. (2007).

In the NoCue group, ERPs of SAME and REARRANGED conditions differ from the other conditions around 400 ms, mainly at frontocentral recording sites (the FN400 effect). A more centro-posterior effect with a similar pattern arises somewhat later, between 500 and 700 ms (the LPC effect). In the Cue group, SAME, REARRANGED, and OLD/NEW conditions elicit a more positive waveform than NEW/NEW (and NEW/OLD) early on. The effect has a somewhat unusual topography, spreading along the midline from frontal to posterior electrodes. At later points in time, SAME and REARRANGED differ from NEW/NEW (with OLD/NEW and NEW/OLD in-between), again with a centro-posterior maximum.

As effects were generally largest along the midline, ERP analyses were carried out on central ROIs only. ROIs were set a priori, but modified following visual inspection. Similar to the Tsivilis et al. (2001) study, three ROIs were utilised: frontopolar (Fpz, Fp1, Fp2), frontal (Fz, FC1, FC2), and posterior (Pz, CP1, CP2).

Concerning the standard old-new effects, looking at peak latencies at respective ROIs, it became obvious that the FN400 peaked somewhat earlier in the Cue group as compared to the NoCue group (388 vs. 428 ms), whereas the LPC peaked later in the Cue group (639 vs. 612 ms). This interaction was significant in an across group ANOVA, $F(1,29) = 4.55$, $p < .05$. Based on this interaction and visual inspection of the data, time window 1 was set to 300-450 ms in the Cue group and 350-500 ms in the NoCue group. Time window 2 was set to 550-750 ms and 500-700 in the Cue and NoCue groups, respectively.

To avoid type I error due to post-hoc electrode selection, we first analysed both early and late effects using data from all 56 head electrodes. For this purpose, we contrasted the two conditions most likely to show memory-related effects – SAME and NEW/NEW – in group-wise Condition by Electrode analyses. In both groups and time windows was the Condition by Electrode interaction significant (NoCue group: $F(55,770) = 4.06 / 2.17$, $\epsilon = .17 / .12$, $p < .05$; Cue Group: $F(55,825) = 6.74 / 7.54$, $\epsilon = .16 / .23$, $p < .01$).

In an analysis across time windows, the Time window by Electrode by Condition interaction was also significant in the Cue group, $F(55,825) = 3.05$, $\epsilon = .15$, $p < .01$, but the interaction failed to reach significance in the NoCue group, $F(55,770) = 1.55$, $\epsilon = .07$, $p > .05$). Despite this lack of support for distinct effects across time windows in the NoCue group, these results demonstrate the presence

of reliable memory-related effects in both time windows and justify the more focused ROI analyses, which were followed up by detailed planned comparison inspection of effects.

Firstly, in an across group analysis of *time window 1* including data from all five conditions, there were significant Condition by ROI ($F(8,232) = 3.08, \epsilon = .79, p < .01$) and Condition by Group ($F(4,116) = 3.13, \epsilon = .92, p = .02$) interactions. Focusing on the frontal ROI, there was still a marginally significant Condition by Group interaction, $F(4,116) = 2.45, \epsilon = 1.00, p = .050$, with the OLD/NEW condition showing the most obvious difference between groups, in line with the main prediction (see Figure 45).

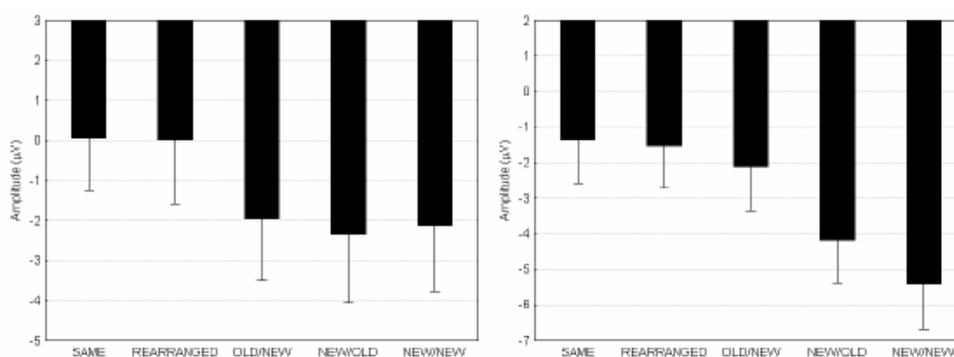


Figure 45. Mean voltage amplitudes in the NoCue (left) and Cue (right) groups at the frontal ROI in time window 1, Experiment 5; vertical bars denote standard errors of the mean; figure adapted from Ecker et al. (2007).

In the *NoCue group*, besides a main effect of Condition, $F(4,56) = 6.26, \epsilon = 1.00, p < .01$, there was a significant ROI by Condition interaction, $F(8,112) = 2.42, \epsilon = .78, p < .05$. As predicted, contrasts at the mid-frontal ROI indicated that both SAME and REARRANGED differed from NEW/NEW, NEW/OLD, and OLD/NEW conditions (see Table 8). There were no differences within these two clusters of conditions (all $F < 1.41$, all $p > .25$). This pattern exactly replicates the Tsivilis et al. (2001) data.

In the *Cue group*, there was a main effect of Condition, $F(4,60) = 17.38, \epsilon = .81, p < .01$, and a reliable ROI by Condition interaction, $F(8,120) = 2.26, \epsilon = .91, p < .05$. In line with the major hypothesis, planned comparisons revealed that all "old object" conditions (SAME, REARRANGED, OLD/NEW) differed from NEW/OLD and NEW/NEW conditions at the frontal ROI (see Table 8). There were

no significant differences within these two clusters of conditions, all $F < 3.61$, all $p > .05$).

In an across group analysis of *time window 2*, Condition interacted with Group ($F(4,116) = 3.32$, $\varepsilon = .96$, $p = .01$) and ROI ($F(8,232) = 5.42$, $\varepsilon = .71$, $p < .001$). Focusing on the posterior ROI, the condition by Group interaction was still significant, $F(4,116) = 2.83$, $\varepsilon = .92$, $p < .05$).

Contrast	<i>df</i>	<i>F</i>	<i>p</i>
NoCue Group			
SAME – NEW/NEW	1,14	9.84	.0073
SAME – NEW/OLD	1,14	9.35	.0085
SAME – OLD/NEW	1,14	6.90	.0199
REARRANGED – NEW/NEW	1,14	13.39	.0026
REARRANGED – NEW/OLD	1,14	12.27	.0035
REARRANGED – OLD/NEW	1,14	7.50	.0160
Cue Group			
SAME – NEW/NEW	1,15	32.27	< .0001
SAME – NEW/OLD	1,15	18.26	.0007
REARRANGED – NEW/NEW	1,15	21.25	.0003
REARRANGED – NEW/OLD	1,15	9.74	.0070
OLD/NEW – NEW/NEW	1,15	28.29	.0001
OLD/NEW – NEW/OLD	1,15	33.58	< .0001

Table 8. Planned comparisons at the frontal ROI in time window 1, Experiment 5; table adapted from Ecker et al. (2007).

In the *NoCue group*, besides the main effect of Condition, $F(4,56) = 6.32$, $\varepsilon = 1.00$, $p < .01$, the interaction of Condition and ROI was reliable, $F(8,112) = 3.12$, $\varepsilon = .92$, $p < .01$. Follow-up contrasts indicated that at posterior sites in time window 2, the effects were equivalent to the effects at frontal sites in time window 1. SAME and REARRANGED differed from OLD/NEW, NEW/OLD, and NEW/NEW (see Table 9). There were no significant differences within these two clusters (all $F < 1.46$, $p > .2$).

Analysis of the *Cue group* data yielded a significant interaction of ROI and Condition, $F(8,120) = 2.97$, $\epsilon = .55$, $p = .02$), besides a main effect of Condition, $F(4,60) = 18.82$, $\epsilon = .94$, $p < .001$). Planned comparisons at the posterior ROI indicated that SAME and REARRANGED differed from the remaining conditions, while NEW/NEW also differed from NEW/OLD and OLD/NEW (see Table 9). Remaining contrasts were nonsignificant ($F < 1$).

Contrast	<i>df</i>	<i>F</i>	<i>p</i>
NoCue Group			
SAME – NEW/NEW	1,14	6.67	.0217
SAME – NEW/OLD	1,14	26.16	.0002
SAME – OLD/NEW	1,14	11.54	.0043
REARRANGED – NEW/NEW	1,14	8.59	.0110
REARRANGED – NEW/OLD	1,14	26.02	.0002
REARRANGED – OLD/NEW	1,14	7.39	.0166
Cue Group			
SAME – NEW/NEW	1,15	31.70	< .0001
SAME – NEW/OLD	1,15	30.03	.0001
SAME – OLD/NEW	1,15	20.25	.0004
REARRANGED – NEW/NEW	1,15	25.23	.0002
REARRANGED – NEW/OLD	1,15	16.54	.0010
REARRANGED – OLD/NEW	1,15	13.00	.0026
NEW/NEW – NEW/OLD	1,15	7.02	.0182
NEW/NEW – OLD/NEW	1,15	9.82	.0068

Table 9. Planned comparisons at the posterior ROI in time window 2; table adapted from Ecker et al. (2007).

Two other potentially interesting effects arose in mainly one of the two groups, apparently: an early frontopolar effect observed especially in the NoCue group, and a late frontal effect in the Cue group. These were analysed as follows.

In the NoCue group, the NEW/NEW condition elicits a less negative waveform than other conditions at frontopolar sites from about 100 ms onwards. This has some resemblance to the Tsivilis et al. (2001) data, although polarity was re-

versed with respect to their 2001 study. Looking at the Cue group, there is a slight tendency for SAME and REARRANGED waveforms to be more negative in a similar time range. Looking at the topography of the effects, it became clear that effects were even more apparent at right parieto-occipital recording sites up to about 300ms (see Figure 46). Figure 47 displays the difference between conditions NEW/NEW and REARRANGED, where the effects were largest overall. Thus, analyses of early effects were focused on frontopolar and right parieto-occipital ROIs; the latter was composed of electrodes O2, PO4, and PO8. Time window 0a and 0b were set to 120-180 ms and 220-300 ms, respectively (only parieto-occipital effects were examined in the latter).

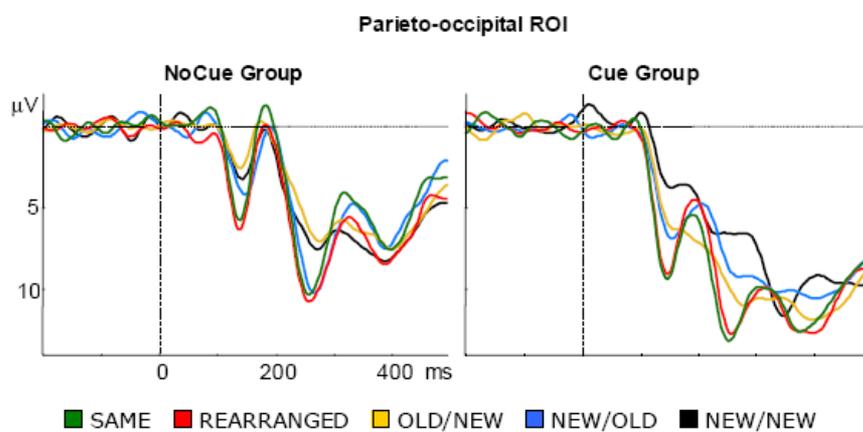


Figure 46. Stimulus-locked grand average ERPs at right parieto-occipital ROI, Experiment 5; figure adapted from Ecker et al. (2007).

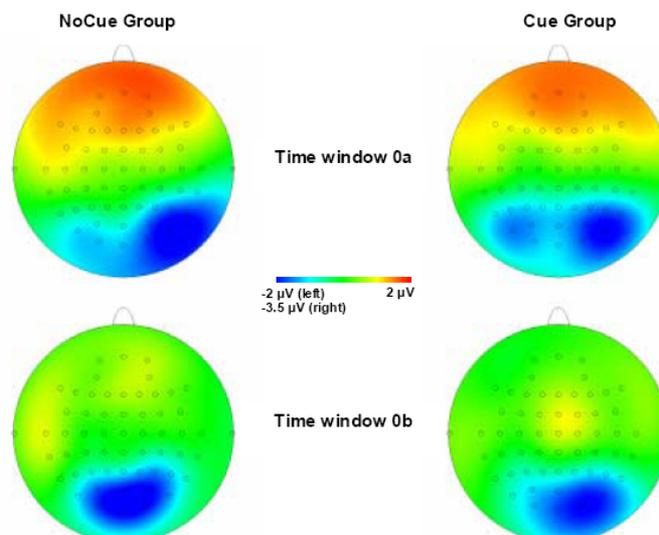


Figure 47. Topographic maps depicting the difference between NEW/NEW and REARRANGED conditions in the NoCue (left) and the Cue group (right) in time windows 0a (top) and 0b (bottom), Experiment 5; figure adapted from Ecker et al. (2007).

In *time window 0a*, a Group by Condition (all five conditions) by ROI (frontopolar vs. parieto-occipital) ANOVA was carried out. Condition interacted significantly with both ROI and Group, $F_s(4,116) > 3.10$, $\epsilon > .64$, $p < .05$. For significant contrasts see Table 10. A comparison between OLD/NEW and NEW/OLD conditions – the vital comparison for the test of different initial attentional foci – yielded a marginally significant Condition by Group interaction, $F(1,29) = 3.81$, $p = .06$, at the frontopolar ROI.

Contrast	<i>df</i>	<i>F</i>	<i>p</i>
NoCue Group; frontopolar ROI			
NEW/NEW – NEW/OLD	1,14	13.83	.0023
OLD/NEW – NEW/OLD	1,14	18.51	.0007
Cue Group; frontopolar ROI			
NEW/NEW – REARRANGED	1,15	9.27	.0082
OLD/NEW – REARRANGED	1,15	13.21	.0024
Cue Group; parieto-occipital ROI			
NEW/NEW – SAME	1,15	18.18	.0007
NEW/NEW – REARRANGED	1,15	11.47	.0041
NEW/NEW – OLD/NEW	1,15	13.03	.0026

Table 10. Planned comparisons in time window 0a, Experiment 5.

At the parieto- occipital ROI of the NoCue group, no contrasts were significant in time window 0a following Bonferroni correction ($F(1,14) < 6.30$, $p > .02$).

In a further step, we analysed newly merged superordinate conditions according to the old/new status of objects and/or contexts. First, we contrasted conditions with an "old context" vs. "new context" (SAME, REARRANGED, NEW/OLD vs. OLD/NEW, NEW/NEW) in the NoCue group. The ROI by Condition interaction was significant, $F(1,14) = 7.64$, $\epsilon = 1.00$, $p < .05$, indicating a more negative course for old vs. new context conditions at the frontopolar ROI ($F(1,14) = 6.39$, $p = .02$) and a complementary pattern at the parieto-occipital ROI ($F(1,14) = 4.67$, $p < .05$). In the Cue group, contrasting conditions featuring "something new" (NEW/NEW, NEW/OLD, OLD/NEW) vs. "nothing new" (SAME, REARRANGED) yielded a significant ROI by Condition interaction ($F(1,15) = 14.26$, $\epsilon = 1.00$, $p <$

.01); there was a more negative course for "nothing new" vs. "something new" conditions at the frontopolar ROI ($F(1,15) = 6.79, p < .02$) and a significant complementary effect at the parieto-occipital ROI ($F(1,15) = 12.14, p < .01$). Accordingly, both the comparison of new vs. old context- and new vs. old object conditions also yielded significant effects at the parieto-occipital ROI ($F_s(1,15) > 7.22, p < .0169$).

In *time window 0b*, a Group by Condition (all five conditions) ANOVA was carried out for parieto-occipital ROI data. Condition interacted significantly with Group, $F(4,116) = 4.65, \epsilon = .88, p < .01$ (for contrasts see Table 11). A comparison between OLD/NEW and NEW/OLD conditions yielded a significant Condition by Group interaction, $F(1,29) = 7.85, p < .01$.

Contrast	<i>df</i>	<i>F</i>	<i>p</i>
NoCue Group			
NEW/NEW – REARRANGED	1,14	7.68	.0150
OLD/NEW – REARRANGED	1,14	14.42	.0020
OLD/NEW – SAME	1,14	11.42	.0045
OLD/NEW – NEW/OLD	1,14	8.26	.0123
Cue Group			
NEW/NEW – SAME	1,15	25.76	.0001
NEW/NEW – REARRANGED	1,15	21.37	.0003
NEW/NEW – OLD/NEW	1,15	12.63	.0029
NEW/OLD – SAME	1,15	9.42	.0078
NEW/OLD – REARRANGED	1,15	8.74	.0098
OLD/NEW – SAME	1,15	8.20	.0118

Table 11. Planned comparisons at the parieto-occipital ROI in time window 0b, Experiment 5.

Newly merged "old context" vs. "new context" conditions differed significantly at the parieto-occipital ROI of the NoCue group, $F(1,14) = 10.26, p < .01$. Likewise, "old object" vs. "new object" conditions differed significantly at the parieto-occipital ROI of the Cue group, $F(1,15) = 11.31, p < .01$. The contrast of conditions including "something new" vs. "nothing new" yielded was also reliable in the Cue group, $F(1,15) = 21.22, p < .001$.

Finally, a last effect we examined was a late fanning effect mainly visible at frontal electrodes in the Cue group, maximal between 900-1100 ms, that is, after subjects' response (Time window 3). *Time window 3* analysis across groups showed that there was no significant ROI by Condition (by Group) interaction ($F_s < 1$) despite a significant Condition by Group interaction, $F(4,116) = 5.43$, $\epsilon = 1.00$, $p < .001$. Thus, contrasts were calculated where the effect was largest, at the frontal ROI of the *Cue group* (see Table 12).

Contrast	<i>df</i>	<i>F</i>	<i>p</i>
Cue Group			
SAME – NEW/NEW	1,15	26.49	.0001
SAME – NEW/OLD	1,15	33.03	< .0001
SAME – OLD/NEW	1,15	20.80	.0004
REARRANGED – NEW/NEW	1,15	9.80	.0069

Table 12. Planned comparisons at the frontal ROI in time window 3, Experiment 5.

6.2.3 Discussion

Summarizing the main results of Experiment 5, all three old object conditions elicited equivalent FN400 effects in the Cue group, whereas in the NoCue group, only SAME and REARRANGED conditions showed reliable effects. The central finding was thus that the FN400 old-new effect associated with familiarity was present in the OLD/NEW condition of the Cue group, but not the NoCue group. The LPC effect was largest in both groups in SAME and REARRANGED conditions, in line with behavioural context effects indexing better performance in the SAME vs. OLD/NEW condition across groups. Early frontopolar and parieto-occipital effects differentiated old vs. new context conditions in the NoCue group, whereas they were novelty-sensitive in a broader sense in the Cue group.

Experiment 5 sought to integrate some discrepant findings which have fuelled the debate on the extent of contextual influences on familiarity (Bogacz, Brown, & Giraud-Carrier, 2001; Cabeza, 2006; Ecker et al., in press; Meeter, Myers, & Gluck, 2005; Tsivilis et al., 2001; Wan et al., 1999; Yonelinas et al., 1999). Our results suggest that the ERP signature of familiarity processing – the FN400 old-new effect – can be influenced by contextual manipulations, thereby replicating a finding of Tsivilis et al. Adding to the existing literature, however, we

were successful in demonstrating that this context effect is mediated by salience and can therefore be eliminated if subjects' attention at test is focused on the to-be-recognised item. In other words, the most likely explanation of the FN400 effects reported in this study (NoCue group) and by Tsivilis et al. is that highly salient backgrounds are perceived and memorised more like objects, and that two old "objects" together elicit a strong familiarity signal – or alternatively, that a novelty signal is produced as soon as one of the stimulus components is new¹⁶. If, however, the background's potential to capture attention is counteracted by giving subjects a cue (Cue group), the background is treated by the system as truly contextual – at least in a substantial subset of cases – and the familiarity signal is therefore not affected. The zooming in and out of attention is very likely also captured in the ERPs: the unusual midline topography of the FN400 effect in the Cue group could be due to the influence of combined bottom-up and top-down attentional processes mediated by anterior-posterior networks (Hahn, Ross, & Stein, 2006; Praamstra, Boutsen, & Humphreys, 2005).

The fact that the familiarity signal occurred earlier in the Cue group as compared to the NoCue group is an indication that the cueing technique we employed did in fact work, although the tendency of a positive-going drift for NEW/OLD items suggests that it did not work in each and every case. Given the above line of reasoning, the seemingly contradictory finding of prolonged reaction times in the Cue group also becomes understandable: although the system supplies a trustworthy familiarity signal quite early, subjects prefer not to rely on a cognitively impenetrable signal and thus strive to integrate contextual information into their decision process as well. Although statistically, counterbalancing precluded any direct inference from background- to object old/new status, context may well have served as an affirmative retrieval cue in cases of object status uncertainty. That is, although behavioural performance does indeed show context effects even in the Cue group (and thus there is no differential behavioural effect concerning the OLD/NEW condition across groups), ERP data suggest these are not based on familiarity. The fact that SAME and REARRANGED waveforms in the Cue group become more positive than OLD/NEW waveforms after about 500 ms may indicate this type of voluntary context check, an alternative explanation being that

16 Strictly speaking, the additive familiarity assumption would predict a graded FN400 effect in the NoCue condition (NEW/NEW < NEW/OLD = OLD/NEW < SAME = REARRANGED). Further research must thus clarify whether the lack of such an effect in both the present and the Tsivilis et al. (2001) data is due to a lack of sensitivity of the ERP measure, or due to a novelty signal elicited by a new stimulus component overriding familiarity. Thus, present results do not unequivocally support the association of the FN400 ERP component with "pure" familiarity.

backgrounds are so salient that they simply cannot be masked out permanently. The late effects in the Cue group, however, also point to controlled post retrieval checks following contextual integration processes. Methodologically, this pattern of results (i.e., somewhat dissociating behavioural and ERP-FN400 effects) speaks in favour of a dynamic and interactive account of processes leading up to response, which in our view highlights the potential of ERPs to supply a fine-grained online measure of processing, whereas standard behavioural measures mainly reflect an "end-product" of processing.

It should be noted that there are other findings in the literature that can be seen under the current perspective. Jacoby and Hay (1998), for instance, manipulated the paired associate of words as "context" and reported evidence in line with Tiberghien's (1986) note that both the familiarity of the context and the item may contribute to the familiarity estimate. They reported context effects on both familiarity and recollection estimates, depending on the time available for responding, and a similar finding was reported by McKenzie and Tiberghien (2004), using a response signal technique.

With respect to the LPC effect, Experiment 5 alone does not serve to further clarify its characteristics. The Time window by Electrode by Condition interaction in the Cue group speaks in favour of two distinctive processes – an initial assessment of object familiarity followed up by a more controlled and integrative recollection process indexed by the LPC effect. However, a decision strength account (Finnigan, Humphreys, Dennis, & Geffen, 2002; see also Dunn, 2004) cannot be excluded based on our data: firstly, the two old-new effects do not differ distinctively in their topographies. Although many studies reporting left-lateralised LPC effects have employed verbal materials, the effect was left-lateralised in the original Tsivilis et al. (2001) study, as well. Data from Experiments 2 and 3 (see also Groh-Bordin et al., 2006), however, has indicated that the LPC effect need not show a lateralised distribution under all circumstances, potentially co-dependending on the utilised site of reference. Secondly, the equivalent modulation of early and late old-new effects in the NoCue group offers no further support for the assumption of two distinct memory processes. Yet, based on the literature, the most likely interpretation of the LPC effect is in terms of recollection processes (Mecklinger, 2000; Rugg, Schloerscheidt, & Mark, 1998). The fact that in both groups, SAME and REARRANGED conditions elicited more positive-going waveforms compared to OLD/NEW is in line with the behavioural context effects and the idea that recollection draws on a mnemonic representation that includes con-

textual information (see Introduction). Tsivilis et al. had reported an LPC effect for OLD/NEW repetitions as well; in contrast to their behavioural data, however, OLD/NEW responses in the present NoCue condition were selectively decelerated. This data pattern may imply that the partial mismatch of featural information and accompanying response uncertainty processes precluded the finding of a reliable LPC effect in the OLD/NEW condition of the NoCue group. Also note that Experiment 5 differed from the Tsivilis et al. study in terms of study instructions, which were intentional and integrative in the present study. This too may have had a selective influence on recollective processing via stronger integration of context into the mnemonic representation.

The implications of the early frontopolar/parieto-occipital effects remain somewhat unclear, especially as the frontopolar effects reported here are reversed in polarity compared to the effect reported by Tsivilis et al. (2001; see also Curran & Dien, 2003, Speer & Curran, submitted). In an fMRI study, Tsivilis, Otten, and Rugg (2003) reported extrastriate cortex regions as likely sources of their frontopolar ERP effects reported earlier, which is highly compatible with our finding of an early bipolar ERP effect (120-180 ms) followed by a parieto-occipital effect (220-300 ms). Besides priming and figure-ground separation processes, a possible interpretation of these effects already adumbrated by Tsivilis et al. is based on the idea that novelty processing takes place in the system very early, from 100 ms onwards¹⁷. Due to our cueing technique, context may have been in the focus of attention first in the NoCue group – due to its salience (see also Bar, 2004) –, whereas initial attention tended to be focused on the object in the Cue group. Accordingly, in the NoCue group, there were significant differences between old vs. new context conditions in both early time windows and both ROIs tested. In contrast, effects in the Cue group seem to suggest that initial processing was focused more on the object, although context was still influential; therefore, early effects in the Cue group rather followed an all-old vs. something-new distinction. Likewise, the across group interactions of NEW/OLD and OLD/NEW conditions at both ROIs further corroborate this interpretation. The ERP literature on attentional capture (which is proposed to be reflected in the modulation of a parieto-occipital N2pc component; cf. Luck & Hillyard, 1994; Hickey et al., 2006; Jolicoeur, Sessa, Dell'Acqua, & Robitaille, 2006) is in line with this interpretation of the parieto-occipital effects, and the present results are also in accordance with

¹⁷ Note that a recent fMRI study has yielded some evidence for an independent contribution of novelty assessment to recognition memory (Daselaar et al., 2006).

other reports of memory-related modulations of very early visual processing (Busch, Groh-Bordin, Zimmer, & Herrmann, submitted; Herrmann, Munk, & Engel, 2004; Kimura, Katayama, & Murohashi, 2006). The fact that P1 differences (time window 0a at right parieto-occipital ROI) were obviously greater in the Cue group is in accordance with top-down modulation of attentional and mnemonic processing, usually reflected in event-related synchronisation in the alpha-band (Klimesch, Sauseng, & Hanslmayr, 2007). Yet, given the polarity differences across the more memory-related studies, further research must clarify the dynamic interactions of top-down and bottom-up attentional mechanisms (cf. also Crottaz-Herbette & Menon, 2006) with novelty detection at very early stages of processing. Indeed, the cognitive system may assess familiarity/novelty not in a single step, but by an attentionally modulated, iterative approach (Humphreys et al., 1989; Tsivilis et al., 2001; also see General Discussion).

7 General Discussion

The outcome of any serious research can only be to make two questions grow where only one grew before. (Thorstein Veblen)

7.1 Summary

The data presented in this thesis (see also peer-reviewed publications Ecker et al., in press, under review, 2007; Groh-Bordin et al., 2006) thus broadly corroborate key assumptions of the type-token model. Beyond that, the findings have theoretical implications for current views of recognition memory, in particular concerning feature binding and representation, context effects, and control.

The data presented in this thesis offer compelling evidence for *perceptual specificity in familiarity memory*, as indexed by differential effects on the FN400 ERP old-new effect associated with familiarity. Consistently across studies 2 to 4, the manipulation of intrinsic perceptual features reduced the familiarity signal, speaking strongly for *intrinsic binding capabilities of familiarity* processing. Extrinsic features across studies did not impact on familiarity, but – depending on task demands – on recollection, as indexed by the LPC ERP old-new effect. This pattern of findings suggests *different representational formats* for the storage of intrinsic object and more highly integrated object-in-context information. These formats have been termed object token and episodic token, respectively, within the neurocognitive model of human object memory, the type-token model, developed by Hubert Zimmer and colleagues (cf. Chapter 2; Ecker et al., 2004; Engelkamp & Zimmer, 2006).

Furthermore, results suggest that subjects can exert considerably more *control* over the piecemeal integration of contextual detail at retrieval, as evident in the comparison of Experiments 2 and 3, making it a more flexible mechanism – seemingly only what is needed to solve a task is reliably reintegrated. On the other hand, the reactivation of intrinsic information is faster and more *automatic*¹⁸, as supported by specificity effects in an inclusion task (Experiment 2). It should be noted that this does not imply that responses based on familiarity will necessarily

¹⁸ Regarding the notion of automaticity, the fact that ERP familiarity effects are not always present in implicit memory studies (Groh-Bordin et al., 2005) is most likely explained in terms of retrieval mode (see below), although this notion requires further experimental investigation.

be faster than those based on recollection, because subjects will typically not rely on an unspecific feeling and prefer to gain confidence from recollection (cf. Experiment 5; Dewhurst, Holmes, Brandt, & Dean, 2006).

The presented data further suggest that *contextual influences on familiarity* are mediated by the characteristics of the context and should be viewed from a dynamic processing perspective. Arbitrary contexts low in salience do not impact on object familiarity despite being retrievable (Experiments 1-3, 4), whereas highly salient contexts can affect the familiarity signal (Experiment 5). I have suggested that the latter is not a direct contextual influence on object familiarity, but an additional independent familiarity effect of the context stimulus. If the attentional impact of salient contexts is experimentally controlled – as in Experiment 5 – this influence is diminished. In other words, if context is treated as context by the system, the familiarity signal is not prone to contextual influences. However, claiming familiarity to be acontextual in principle would be too simple.

7.2 Familiarity is Perceptually Specific. Is it also Associative?

7.2.1 Associative Familiarity

Speers and Curran (submitted; see also Curran, Tepe, & Piatt, 2006) have demonstrated that familiarity can be associative even when using non-object stimuli carrying no conceptual meaning (two fractals presented side by side). While this underpins claims of perceptual specificity, it seemingly runs counter to claims of familiarity being only sensitive to intrinsic associations (e.g., object-colour). The fractals were presented repeatedly; thus, the unitisation of the two perceptually quite similar stimuli may have been fostered. Speaking against this argument is the fact that there were irrelevant changes in left-right position assignment during acquisition. Yet, in contrast to the experiments reported in the present thesis, associations were unique; that is, while contexts or background features in the present experiments were paired with at least two different objects during both study and test phases, fractal pairings were unique in Speer and Curran's study (the behavioural literature suggests that uniqueness enhances context effects, cf. Murnane & Phelps, 1994). Assuming that contexts are not specific to items, the approach taken here may be the more appealing one in terms of ecological validity, because in the real world, you would typically see many different objects in the same context. However, paired-associate learning (which is basically the paradigm used by Speer & Curran) should depend mainly on recollection according to

our model. Yet, neuropsychological research has indicated that repeated presentation may lead to associative learning even in amnesics (Baddeley et al., 2001; see also Musen & Squire, 1993), although this remains a highly debated topic in itself. Emrah Düzel and colleagues (Düzel, Habib, Guderian, & Heinze, 2004; Düzel et al., 2003) have reported that differential brain networks show *associative novelty* and *associative familiarity* responses, respectively, with some overlap in frontopolar and extrastriate cortex. Most interestingly for present purposes, MTLC showed repetition enhancement for repeated *arrays* of familiar items, whereas the anterior hippocampus showed higher activations for new configurations of familiar stimuli (in contrast to in vivo results of Xiang & Brown, 1998, and the Meeter et al., 2005 model, see below). Although these studies also point to the associative nature of familiarity, again subjects learnt over five repetitions, thence fostering unitisation.

Mayes and colleagues (2001, 2002) have reported that hippocampally lesioned adult patient Y.R. shows intact word-pair associative learning in two-alternative forced-choice recognition memory after only one exposure (while being impaired at cued recall) as long as the to-be-associated information is of the same kind (e.g., word pairs), suggesting that the hippocampus proper may only be vital for bindings across different types of information. A similar finding was reported by Van Petten, Luka, Rubin, and Ryan (2002), namely an apparently larger FN400 effect for identically repeated word pairs compared to recombined word pairs (the effect was not, however, formally tested as it was outside the major focus of the paper). Yet, the encoding task of subjects involved combining the mental images of the two words of each study pair, thereby potentially generating a unitised representation. Nevertheless, seemingly items of the same type may be easier to unitise or integrate and this binding may thus differ fundamentally from across domain bindings (see also Yonelinas, 2002a; Yonelinas et al., 1999). Adding strongly to this case, recent reports concerning patient Y.R. (Mayes et al., 2004) have focused on different types of associative memory performance requiring differential levels of binding. It was found that Y.R. was able to perform standard yes/no as well as forced-choice recognition tasks at normal level when these tasks were concerned with either pure item memory, intrinsic bindings, or associations of items of the same kind. In contrast, she was impaired at associative recognition of items of different kind, including integration of items and their locations, temporal positions and order, or other arbitrary bindings of, for instance, animal pictures and profession-labels, faces and voices or names, words and definitions, and pictures and sounds. Stark and Squire (2003) have also 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, Knight, Metcalfe, Wolf, & Tulving, 1996).

Thus, there is growing evidence that associative recognition can be supported by familiarity at least in some cases – as long as the to-be-associated parts of information are similar or easy to unitise, that is, they are from the same modality at least (e.g., associations of faces or face parts, Yonelinas et al., 1999; Jäger, Mecklinger, & Kipp, 2006), with other potentially relevant dimensions being relative position, size, semantic association (Rhodes & Donaldson, 2007) and repeated study presentations (Speer & Curran, submitted). Obviously, reality does not follow a simple "item versus association" dichotomy. Results show that there is no strict dissociation in a sense that the hippocampus is relevant for associative learning while the MTLCs are 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, as will be elaborated on below. Taking a connectionist perspective, differences in learning rate and sparseness of representation lead to differential aptitudes for certain tasks. This makes good evolutionary sense because multiple, differently fast learning mechanisms enable us to extract information from the environment in a highly flexible way (cf. McClelland, McNaughton, & O'Reilly, 1995). These functional differences arise from architectural differences, which most likely fall along a continuum and are not as dichotomous as a gross item versus associative distinction (Norman & O'Reilly, 2003). Rather, there seem to be more subtle differences in neurocomputational processing and information representation in hippocampus and MTLCs resulting in a dissociation between familiarity – *mainly* concerned with item memory – and recollection – *mainly* concerned with associative integration of item and context –, which, however, does not hold in every case (e.g., Mayes et al., 2001, 2004). For instance, the sparseness of hippocampal representation together with its across-domain binding abilities *inherently* implies that hippocampal processing is more sensitive to associations or conjunctions than MTLC, although there is no reason to believe that MTLC processing and thus familiarity should be acontextual *in principle* (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 arbitrary "higher-level" binding. As already stated for the prefrontal cortex (PFC), even the small regions of the MTL we are talking about probably all subserve dif-

ferent 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, Rolls, & Xiang, 2003). Furthermore, the postrhinal cortex seems to subserve quite a different function as far as associative learning is concerned, more similar to the hippocampus than to the perirhinal cortex (e.g., Norman & Eacott, 2005). The functions of other brain areas involved in episodic memory have not even been touched in this thesis; e.g., 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, Becker, King, & O'Keefe, 2002).

Another point with regard to the Stark and Squire (2003) paper is that the medial temporal region rarely "sleeps", meaning that it is often active even during non-associative tasks (baseline problem; cf. Cabeza et al., 2003). 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 cylindrical orientation of hippocampal neurons which hinders the detection of field potentials at the surface of the head. Hence, a strong test of the type-token model would have to combine ERP and fMRI methods. Yet, the experiments presented in this thesis and Experiment 4 in particular have shown that it cannot just be the "kind of information" to-be-bound that determines whether familiarity or recollection are "responsible" for integration, but that the intrinsic-extrinsic factor is just as relevant.

7.2.2 Intrinsic versus Extrinsic Binding

Thus, the above discussion of intrinsic and extrinsic features touches a very fundamental question in the study of object perception and memory. Even after decades of research it is still not entirely clear what indeed defines an object. What is intrinsic? What is extrinsic? It is hard to give a sophisticated answer to these questions without stumbling on circularity. We have noted above that concurrent attention is a likely binding mechanism and that objects are likely units of both perception *and* memory. At the intrinsic level, object colour was presented as a typical intrinsic feature. Yet, the very question whether colour counts as a typical intrinsic feature is not all that easy to answer. Previous work in our laboratory has indicated that the colour of words is not perceived as an intrinsic feature of the

word, but rather as a feature of the medium (e.g., the chalk). The colour of multi-coloured objects and – to a lesser degree – silhouettes, however, seems to be a clearly intrinsic feature: it is encoded quite automatically and recognised well above chance even after incidental study, whereas the colour of line-drawings is not (Zimmer & Steiner, submitted). The latter proposition might be the reason Friedman et al. (2005), manipulating the colour of line drawings, did not report a significant congruency effect on the mid-frontal ERP old-new effect. In this vein, the results of Park and Puglisi (1985) contradict our model. They reported that young but not elderly participants remembered the colour of pictures better than the colour of words. Assuming that age mainly affects contextual integration (Bastin & Van der Linden, 2005; Cabeza, Anderson, Houle, Mangels, & Newberg, 2000; Spencer & Raz, 1995; but see Naveh-Benjamin, 2000) and that our model is valid, the elderly should be particularly poor in remembering the colour of words. Orientation is another example of a supposedly intrinsic feature. In fact, with regard to a stand-alone object orientation seems rather intrinsic (see also Groh-Bordin et al., 2005). If, however, the orientation of an object is meaningful with regard to its context (e.g., a car facing a pedestrian), orientation may be regarded a rather extrinsic feature.

Turning to the extrinsic side, the picture becomes even more complex. On the safe side, arbitrary across-domain associations can confidently be regarded as requiring extrinsic binding and hippocampal involvement (e.g., face-name associations). Seemingly, the room or building an object is encountered in is also an extrinsic feature, although the mere size of the room might nevertheless influence perception of the object (as anyone who has ever bought a large piece of furniture in an outlet and then tried to fit it in the living room might agree). Yet, global and permanent context such as the experimental room likely influences familiarity, as will be discussed in the next paragraph. It was noted that our choice of more local contexts was motivated by the fact that this kind of global extrinsic context is very different from actual objects and we wanted to make sure that the effects we measure are not due to these basic differences. It was further stressed that this might not be the most typical way to think of context, but that it allowed us to tackle questions of item unitisation in a straightforward and rather conservative way, as it was not clear a priori whether or not and at which level the utilised contexts would be integrated or in fact treated as contextual (see especially Experiment 5). Clearly, the focus of this thesis is too narrow to conclusively answer these fundamental questions; it was successful, however, in pointing out impor-

tant commonalities of perception and memory, and in supporting our model view of differential processing and representation of object and local context features.

The question why associative information of the same kind seems to be bound in familiarity in some studies (Mayes et al., 2001, 2004; Speer & Curran, submitted) and not others (this thesis, see also Introduction) awaits further research. Concerning their patient studies, Mayes et al. (2004) have pointed out that "*no familiarity memory may exist in normal subjects for such associations*" (p. 763). In particular, further empirical research should aim at more thoroughly exploring the constraints of item or "object" unitisation and the determinants of what is considered and labelled "context". For instance, we had mentioned above that the encoding task has an important influence on retrieval processing: in two studies manipulating the supposedly intrinsic feature orientation (Curran & Cleary, 2003; Groh-Bordin et al., 2005), feature manipulation selectively affected either familiarity or recollection ERP correlates. Whereas in the former study, encoding was intentional, thus fostering an influence of perceptual manipulation on recollection, in the latter the encoding task was incidental with a strong perceptual focus (items were hard to identify), thus presumably supporting a modulation of familiarity. Further studies manipulating study intention, the amount of necessary sensory processing, and also looking at subsequent memory effects at encoding are urgently needed in order to clarify these issues. Concerning the test task, Guillem et al. (2001) have argued – in line with the type-token model – that familiarity ERP effects represent "*an integration of the intrinsic attributes of items that is directed by the goal of the task*" (p. 121). Presumably, some features such as object colour are indeed processed rather automatically (affecting familiarity), whereas the impact of other features is more task-dependent. For instance, if word pairs are to-be-recognised, the association between words may affect familiarity memory (Donaldson & Rugg, 1999), but this may not be the case if only a member of a pair is the target (cf. Tendolkar & Rugg, 1998; see also discussion of retrieval orientation in the next section). Other arbitrary context features, however, may always depend on recollection¹⁹.

7.2.3 Types of Context

Obviously, there are different *types of context*; the binding of an item with arbitrary cross-domain information (e.g., location) may be different from the bind-

¹⁹ see Appendix for an example of a supposedly extrinsic feature seemingly affecting familiarity.

ing of two similar items, although this claim could not be substantiated by the present thesis (also see below). Regarding arbitrary context binding, there is a certain focus in the literature on spatial aspects of context, somewhat neglecting temporal context. The integration of temporal context, such as order information, also relies on hippocampal function (Mayes et al., 2001; see also Eichenbaum, 2006), although perhaps to a lesser degree than spatial context, as spatial processing is a hallmark even of non-mnemonic hippocampal function. The integration of order information and temporal context integration also strongly relies on the PFC, as has been demonstrated for both animals (Hannesson, Vacca, Howland, & Phillips, 2004; Kesner & Holbrook, 1987) and humans, in which the anterior cingulate cortex and dorsolateral PFC have been associated with temporal context information retrieval (Nyberg et al., 1996; Zorrilla, Aguirre, Zarahn, Cannon, & D'Esposito, 1996). Yet, what is often termed "temporal context" is in fact recency. There are recency-sensitive cells in the perirhinal cortex (Xiang & Brown, 1998), and it has been suggested by some ERP studies that episodic familiarity is rather short-lasting (Rugg & Nagy, 1989; Nessler & Mecklinger, 2003; but see also Curran & Friedman, 2004; Wolk et al., 2006), and hence also somewhat dependent on recency information. Therefore, this particular aspect of so-called temporal context likely also has an influence on familiarity processing.

Importantly, familiarity is context-sensitive in a way as operationalised by, for instance, Mike Humphreys (Humphreys et al., 1989; Dennis & Humphreys, 2001): more or less permanent, global experimental context. In a sense, familiarity as part of episodic recognition even *needs* to be contextual, otherwise it would not be episodic. Task settings in episodic recognition experiments explicitly require subjects to judge whether or not they have *just* (i.e., in the context of the study phase) encountered a specific item. Thus, most recognition tasks are in fact tacit exclusion tasks, requiring context-dependent memory. If familiarity were acontextual in this sense, recognition memory experiments with standard font words, for example, would not yield familiarity effects, because most words are "familiar" anyway (e.g., an experimentally "new" word seen a hundred times on a sign or in the newspaper)²⁰. Somewhat problematic in this vein is the finding that effects of global context shifts (e.g., a change of room) on recognition memory are rather small and sometimes not found; McKone and French (2001) have suggested a dual process account of this result pattern, arguing that a "fluency" subprocess of

²⁰ This implies that significant font differences (holding constant long-term familiarity, e.g., upper case vs. lower case, or typed vs. handwriting) between study and test should impact on familiarity (viz. Diana et al., 2004).

recognition (akin to familiarity) is not context-sensitive, while an "elaboration" sub-process (akin to recollection) is. However, this account leaves unanswered the question concerning global contextual influence of familiarity.

A hierarchical connectionist model by Meeter et al. (2005) offers one possibility how such a contextual influence on familiarity could come about. In this model, the parahippocampal cortex (PHC) also codes for contextual features, whereas the hippocampus (HC) codes for the whole situation the organism is in (an "ensemble") and neocortical (NC) nodes code for permanent features of the environment (context) and phasic cues (stimuli). Each NC node has a strong connection to a PHC node, in addition, NC nodes send weak connections to other PHC nodes. When a phasic cue is presented together with permanent context features, NC nodes coding for context features will be coactivated with PHC nodes activated by the stimulus and there will be long-term potentiation from NC nodes to PHC nodes. Thereafter, permanent context features will weakly activate PHC nodes in the absence of the stimulus. The resulting adaptation in the PHC node will make it less responsive to its preferred input (stimulus), which produces the familiarity effect, generally assuming higher activity for a stimulus at first presentation, decreasing with repetition (in the same context). Indeed, PHC neurons have been shown to be stimulus-selective but also contextually modulated (Dusek & Eichenbaum, 1997; Suzuki, Miller, & Desimone, 1997).

Compatibly, it has been noted above that the occurrence of familiarity and the respective ERP effect has been linked to a prerequisite cognitive state referred to as "retrieval mode". Retrieval mode has been described as a tonically maintained cognitive state biasing the system towards treating external events as retrieval cues (Rugg & Wilding, 2000; Tulving, 1983). The magnitude of old/new effects has been shown to differ according to whether subjects intentionally retrieve (Düzel et al., 1999), and in a study contrasting implicit and explicit access to memory representations generated under equal conditions, Groh-Bordin et al. (2005) reported a familiarity effect in the explicit task only (but see Guillem et al., 2001). Thus, familiarity only seems to occur when the test task refers to the "context" of the study episode. In this vein, episodic familiarity is thought to arise "pseudo-automatically" – that is, it arises automatically if one is in the respective retrieval mode. A likely brain region involved in the maintenance of this state is the right PFC and frontopolar cortex (Cabeza et al., 2003; Düzel et al., 1999; Morcom & Rugg, 2002). There is even evidence that under specific conditions, familiarity may only arise when subjects are in a specific "retrieval orientation", a further frac-

tionation of the retrieval mode concept, referring to a specific form of processing applied to a retrieval cue (Rugg & Wilding, 2000; Werkle-Bergner, Mecklinger, Kray, Meyer, & Düzel, 2005). For instance, retrieval orientation would differ for attempts to retrieve phonological vs. visual information. Herron and Rugg (2003) reported that old-new effects were present for non-target words when items studied as pictures were targets, but not vice versa, pointing to the ability to use retrieval cues highly specifically when adopting a respective retrieval orientation. Yet, this asymmetry could be explained without referring to the concept of retrieval orientation: subjects were always tested with words; thus, in the word condition, a target (also studied as a word) would elicit high perceptual familiarity, not a non-target (studied as a picture). In the picture condition, a target (studied as a picture) would not elicit a high amount of perceptual familiarity, a non-target (studied as a word), however, would. Thus, the exact contribution of retrieval orientation to the moulding of familiarity/recollection and respective ERPs remains to be elucidated. One way in which this could be done is to manipulate subject's orientation towards either retrieving a specific exemplar or a more general category. Such manipulations have been employed in the literature (Koutstaal, 2006; Ranganath & Paller, 1999, 2000; Werkle-Bergner et al., 2005) mainly focussing on the flexibility of control, but a thorough investigation of (mid-frontal) old-new effects could shed more light on the question of whether or not familiarity and the ratio of perceptual/conceptual processing associated with it depend on retrieval orientation beyond basic retrieval mode.

A similar notion to retrieval mode/orientation was proposed by Simon Dennis and Mike Humphreys (Dennis & Humphreys, 2001; Humphreys et al., 2003) in their bind cue decide model of episodic memory (BCDMEM). In this model, memory storage is conceptualised as a binding operation in which item features are bound to several types of contextual features. They assume that recognition is partly based on a match between a reinstated context vector referring to the study context and a more general context retrieved on the basis of the probe item (this will also include extra-experimental context). Thereby, the reinstated context will partly depend on test instructions, that is, the reinstated context would control which specific information would emerge (of the possible information that could emerge), so visual details of an item are more likely retrieved when a visual context was reinstated. Thus, there is a directed search process, and thereby test instructions determine which information (first) emerges from memory access (i.e., the order in which information is accessed). For instance, in one of their experiments, they presented visual and auditory stimuli, and subjects first recognised

items in a "Remember/Know" paradigm, and were then given an exclusion task. When asking to accept only auditory items in test 2, the exclusion error rate (false alarms to visual items) was not higher for items that had received a "Know" vs. "Remember" response in test 1, as would be predicted by classic PDP accounts (if an item is recollected at test 1, it should be confidently rejected at test 2). However, reading a word will produce auditory information, hearing a word may produce visual information, thus, depending on instruction, when you are asked to look for auditory information, you may find auditory information even if you studied an item visually.

Taken together, task settings (instructions, global experimental context) have quite some influence on the effects under investigation, and although standard episodic memory research usually holds these factors constant, a systematic examination could prove useful in the understanding of episodic effects in a wider frame of reference, for instance, when contrasting episodic and semantic familiarity.

7.3 Episodic versus Semantic (Familiarity) Memory

By the same token, a distinction seems necessary between long-term or semantic familiarity (akin to decontextualised semantic knowledge) and experimental or episodic familiarity, which is in a sense context-specific as outlined above. It is undisputed that semantic appropriateness of context is important, in the identification of objects in particular. Interestingly, the PHC shows the largest BOLD signal difference between objects that are highly associated with a certain context and those that are not associated with a unique context (Bar & Aminoff, 2003). Multimodal inputs with only a relative small visuospatial proportion in fact indicate that MTLs bind together more than just intrinsic visual information but may also mediate semantic contextual associations. To avoid confusion, one should thus perhaps use a different term for episodic familiarity (e.g. recency), although this encounters problems at the neuronal level, at which different neurons and networks compute novelty, familiarity, and recency, although the functional significance of this remains to be proven (see below).

Rafal Bogacz and Malcolm Brown have modelled "episodic familiarity" via the computational characteristics of parahippocampal "novelty" neurons in a series of connectionist models, demonstrating that very simple 3-layer networks can discriminate by far more patterns than for instance the CA3 field of the hippocam-

pus (around the order of 10^9 vs. 10^5) with a comparable number of neurons (Bogacz & Brown, 2003; Bogacz et al., 2001). They argue that such specialised networks can be very fast and would allow the organism to store prior occurrence without changing synaptic connections within perceptual and categorisation networks to perform this function, whereas storing new and retrieving old associations of a stimulus, including its semantics and context of prior occurrence, should rely on additional systems – inherently for economic reasons –, which is why recognition memory involves two separable processes. Even more effective could be a model using long-term depression (Anti-Hebbian learning) rather than long-term potentiation, which would also offer an elegant explanation for the physiological finding of decreased firing for familiar stimuli. Bogacz et al. also discuss initial appraisal of familiarity/novelty as a trigger for new learning, thereby integrating retrieval and encoding processes (see also Fernández & Tendolkar, 2006), although they suggest that two separate specialised networks within the MTLs serve these functions.

As far as semantic memory in a broader sense is concerned, in the type-token model it is only stated that sensory types can be considered entry points to the semantic system, as they carry some conceptual information themselves (e.g., "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 (1992, 2006), semantic information is part of an object file. We have focused on the sensory information represented in an object token; however, the present results indicate that there are both perceptual and conceptual influences on familiarity appraisal. The already mentioned studies of developmental amnesia (Baddeley et al., 2001; Brizzolara, Casalini, & Montanaro, 2003; Vargha-Khadem et al., 1997) 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 information²¹. An interesting question would be what would happen if not only the hippocampus, but also the perirhinal cortex was damaged in early childhood? Most likely, development of conceptual knowledge would be far from normal. Anyway,

21 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 disoriented 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, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2001). This points to the hippocampus playing a crucial role in spatial learning and the representation of temporal order.

the topic of how and under what circumstances adult amnesics can acquire semantic knowledge remains unsolved (Bayley & Squire, 2002; Hamann & Squire, 1995; McKenna & Gerhand, 2002; Tulving, Hayman, & Macdonald, 1991). The same holds true for the role of higher brain plasticity, more efficient learning strategies, environmental support, and personality traits in the performance of developmental amnesics, restricting the direct transfer of these patient study results to healthy functioning.

Other neuropsychological work on semantic dementia (cf. Hodges & Graham, 2002) has indicated that episodic (recognition) memory and semantic memory indeed partially rely on distinct brain areas. Semantic dementia arises mainly from atrophic lesions of the left antero-lateral temporal lobe, resulting in loss of semantic knowledge, typically with a "reversed Ribot gradient", that is, relative preservation of recent memories – in contrast to retrograde amnesia. Recognition memory is largely intact in patients suffering from semantic dementia, although they seemingly rely on perceptual processing more strongly than healthy persons. That is, perceptual study-test changes will impact on recognition memory performance even more than in healthy people, especially for items which particular patients have "lost" the concept for (Graham, Simons, Pratt, Patterson, & Hodges, 2000; see also Groh-Bordin et al., 2006). Specifically, however, the preservation of recognition memory in these patients will likely vary with the extent of their lesions, especially when these extend into the parahippocampal gyrus.

I further claim that notions of unitary declarative memory incorporating episodic and semantic memory (e.g., Squire, 1987, 2004) in part result from the assignment of familiarity (e.g., as operationalised in the "Remember/Know" paradigm) to a semantic memory system. While we accept that familiarity (i.e., experimental or episodic familiarity) processing involves conceptual aspects, I have also stressed that there are at least functional differences between episodic and long-term semantic familiarity. These differences should not, however, be treated as evidence for two "hermetically sealed" systems, as they interact at many stages and in part rely on the same brain structures (e.g., MTLCs). For instance, Nessler et al. (2005) have shown that semantic and episodic familiarity partly rely on the same network. This is in line with our notion that perceptual and conceptual processes work hand in hand in familiarity computation, and is also consistent with the four types of neurons found within the perirhinal cortex by Xiang and Brown (1998; see also Hölscher et al., 2003): while about 30 % of neurons are visually responsive but not occurrence-selective (representation neurons), 25 %

respond differentially depending on prior occurrence and have thus been termed novelty, recency, and familiarity neurons. Notably, the familiarity effect in the Meeter et al. (2005) model occurs under a wide range of parameter settings, but both strength and time course are determined by parameters, potentially explaining the variability in the literature; that is, variations in wiring, learning rate, and weight decay may produce the four kinds of parahippocampal neurons proposed by Xiang and Brown. Note that the described findings of Düzel and colleagues (2003, 2004) of differential activation of MTLC and hippocampal regions in response to old versus new arrangements of familiar items also run somewhat counter to the adumbrated view of familiarity and novelty being sort of two sides of the same medal. While this view may be true *in a functional* sense, it is obviously not true in a strictly neuroanatomical sense. ERP effects may fall somewhere in between, as they only give quite an indirect picture of "wetware" processing, and the precise specification of familiarity/novelty effect characteristics awaits further research.

Thus, perhaps the most parsimonious way to explain these findings is to move away from static conceptions and towards more dynamic accounts of cognitive processing. As far as familiarity processing is concerned, this may involve the assumption that depending on the task demands, the cognitive system computes a novelty/familiarity signal, thereby flexibly adjusting the amount of processing concerned with perceptual and conceptual attributes and also the amount of contextual detail. In a typical laboratory old/new experiment, the spatiotemporal experimental context is incorporated, whereas it may not be in more real world settings with a demand for general, more long-term familiarity appraisal, or in situations calling for an evaluation of recency. This again would constitute a kind of task appropriate processing, and the work presented in this thesis also serves to again demonstrate some constraints of this account. That is, although claiming that certain kinds of general context influence familiarity processing, in terms of local contexts, only what is treated as a (unitised) item by the cognitive system, with accordant attention allocation and perceptual figure-ground segregation, will elicit a familiarity signal. The experiments presented here support this notion of "strictly-intrinsic" binding. Yet, the evidence seems to suggest that the association of items of the same kind can in some cases rely on familiarity, most likely depending on task settings (repeated presentation, instructions, etc.) or rather idiosyncratic processing in neuropsychological patients. This must be clarified by further research, eventually yielding the need to adjust the type-token model accordingly. The integration of arbitrary contextual information, however, remains a hall-

mark of recollection and the hippocampus proper, in cooperation with the PFC (Janowsky, Shimamura, & Squire, 1989).

7.4 One Dual Process out of Control?

7.4.1 *Where is Control – or – A Neuroanatomical Peculiarity*

I have proposed that recollective retrieval is a rather controlled process, and data from Experiments 2 and 3, and also 5, lend some support to this claim. The present thesis thus suggests that the reintegration of arbitrary contextual information is at least partially under subjects' control, in contrast to the more automatic retrieval of intrinsic features. The respective ERP data constitute a substantial contribution to the existing literature. Yet, future research should focus more strongly on differential aspects of control in retrieval processing. For instance, initiation of search, maintenance of retrieval mode/orientation, allocation of attention, criterion setting, decision making, retrieval and response monitoring are all control processes that likely unfold their influence in different ways at different stages in time. Careful examination of these processes with electrophysiological measures in well-designed experiments is needed in order to untangle these different contributions, which will blur and amalgamate in most ERP studies (viz. the broad frontal old-new effects after 500 ms in Experiment 2 and 3, in particular). This also implies that familiarity and recollection will not follow a strict controlled vs. automatic dichotomy. As noted before, familiarity seems to depend on retrieval mode, and decision processes of course also apply to familiarity – in fact, the need for smoothing out of response uncertainty may be even larger for familiarity. In terms of the type-token model, control is associated with recollection, yet this remains an oversimplification, so the model may have to be adapted to become even more overarching.

The prefrontal cortex (PFC) is usually associated with executive functions also in the context of episodic memory (Faw, 2003; Phillips, Ahn, & Floresco, 2004; Rugg et al., 1999; Smith & Jonides, 1999). Prefrontal lesions typically do not lead to dense amnesia (Alexander, Stuss, & Fansabedian, 2003), supporting the claim that key "hotspots" such as the hippocampus mediate key memory processes (such as binding) while the PFC serves modulatory functions (albeit *important* modulatory functions; Foster, 2003). But, there is evidence that anterior-posterior circuits are active at both encoding and retrieval stages of recognition memory (Kirchoff, Wagner, Maril, & Stern, 2000; Summerfield & Mangels, 2005),

and a wealth of memory studies has reported prefrontal activation in different conditions (cf. Cansino et al. 2002; Lepage, Ghaffar, Nyberg, & Tulving, 2000; Slotnick et al., 2003) consistent with a major role of the PFC especially in source integration and thus recollection. Deficits in contextual integration and source memory following PFC lesions corroborate this notion (e.g., Janowsky et al., 1989). Yet, neuroanatomically, main connections are between the PFC and the parahippocampal cortices. Despite well-documented projections from the hippocampus to the medial PFC, there are, however, virtually no direct connections from the PFC to the hippocampus (Vertes, 2006; but see Leichnetz & Astruc, 1975). At first sight, although of course MTLs provide the major input into the hippocampus, this seems a bit at odds with our notion of controlled recollective processing and more automatic familiarity appraisal. However, one should not overstate the role of "static" neuroanatomical connectivity in this case. The hippocampus, or rather the extended hippocampal-diencephalic system (Aggleton & Brown, 1999) sits at the top of the hierarchy (Norman & O'Reilly, 2003; Meeter et al., 2005; Squire & Zola-Morgan, 1991; see Figure 6) and its unique binding capabilities allow it to integrate dispersed representational information in spatiotemporal context. It is the high level of binding necessary for "mental time travel" (for a recent essay, see Tulving, 2002) that also urgently requires a high amount of executive control.

7.4.2 Global Match and Dual Processing Models

This thesis has basically assumed that there are in fact (at least) two distinct processes contributing to recognition memory (dual-process or DP models). However, although adumbrated in the introduction, it shall not be ignored that there are also elaborate single-process or "global match" (GM) accounts – embedded in a signal detection framework and frequently implemented in formal mathematical models – which account rather parsimoniously for a wide range of behavioural and – perhaps to a lesser degree – neuropsychological findings (see Clark & Gronlund, 1996; Dennis & Humphreys, 2001; Dunn, 2004; Dunn & Dennis, submitted; Gillund & Shiffrin, 1984; Humphreys et al., 1989; Murdock, 1982; Ratcliff, Van Zandt, & McKoon, 1995; Shiffrin & Steyvers, 1997; Wixted, in press).

As outlined in the introduction, in DP accounts, familiarity is usually thought of as providing little context information concerning a previous encounter, and this depends neither on task instructions nor on how memory is cued. Rather, contextual information is provided by more controlled recollection processes. In contrast,

a general assumption of GM accounts, derived from signal-detection theory, is that the strength-of-evidence distribution of old items is displaced relative to the distribution of new items and that this difference is indicative of memory strength. Based on this global match or "strength-of-evidence", decision processes operate. That is, subjects set response criteria depending on task instructions, subjective variables etc. in order to arrive at a decision. GM accounts use the term familiarity to refer to the strength-of-evidence of an item in response to a context-specific retrieval cue ("episode specific strength"). This depends on task instructions and on how memory is cued. Notably, so-called "single process" models usually incorporate additional parameters related to the representation of context, memory cues, and decision processes and should thus not be called "single-process".

As far as ERP old-new effects are concerned, GM models assume that (F)N400 effects reflect familiarity or overall memory strength, whereas LPC effects reflect decisional factors such as decision confidence, based inter alia on findings that correct rejections and hits elicit similar LPC amplitudes (Finnigan et al., 2002) and that false alarms also elicit an LPC effect (Wolk et al., 2006). Yet, the effects reported by Wolk et al. may have also been due to an overlying negativity associated with response conflict (viz. Johansson & Mecklinger, 2003). Curran (2004) and Woodruff, Hayama, and Rugg (2006) have demonstrated that decision confidence may in fact contribute to the LPC effect or a similar overlapping effect, but that this is not the whole story. In Woodruff et al.'s study, confidence effects were more right lateralised as the LPC, although being very LPC-like overall. In Curran's study, there were respective confidence effects only for old items and not for new – as should be the case when claiming the effect reflects confidence per se, because in signal detection terms, confidence differences in either case reflect distance from the response criterion. In accordance with familiarity interpretations of the FN400 effect, they also reported a symmetric mirror effect, that is, the FN400 effect was larger for high confidence responses, but confidence affected both old and new items. Curran, DeBuse, Woroch, and Hirshman (2006) showed that the drug midazolam selectively diminished the LPC effect, not affecting the FN400 effect. They argued that under a control condition, performance was based on recollection, while only with the drug did performance correlate with familiarity (study conditions fostered deep encoding and recollection). Again, LPC-drug effects were limited to old items, not new. The fact remains that the LPC covers the P300 which is known to increase with confidence in non-memory tasks (Squires, Squires, & Hillyard, 1975); thus, non-recollective aspects of confidence would be expected to exert some influence on LPC effects.

The setting of response criteria has also been associated with the LPC effect (see Finnigan et al., 2002). Yet, this is not supported by recent evidence. Herron, Quayle, and Rugg (2003) manipulated the old-new ratio of items and showed that the LPC effect is insensitive to generic probability effects, although somewhat unusually, in this study there was no effect of the ratio on decision criterion in terms of behavioural data. Azimian-Faridani and Wilding (2006) reported that instructions to adopt conservative vs. liberal response criteria yielded differences in FN400 amplitude. They argued that in the conservative condition, hits are based on a higher level of familiarity and thus there is a greater FN400 effect. Accordingly, there are behavioural data suggesting that criterion shifts should mainly impact on familiarity (Yonelinas, 2002a). Windmann, Urbach, and Kutas (2002) reported that in subjective (and standard) old-new effects, a group of conservative subjects showed a larger FN400 effect (in line with Azimian-Faridani & Wilding and a DP account), whereas there was no difference in objective FN400 effect (in line with GM models). They claimed that criterion setting can occur prior to any attempts at controlled recollection or response selection, although the temporal characteristics of bias effects will vary with task complexity. Curran, DeBuse, and Leynes (2007) used a payoff manipulation that affected criteria setting while leaving performance level unaffected. Response criteria had negligible influence on ERP old-new effects prior to 1000 ms, but affected the LPN/ERN component (Johansson & Mecklinger, 2003), thus likely reflecting changes in post-retrieval metacognitive processes (response conflict) rather than familiarity evaluation or recollection itself.

Taken together, the link of familiarity/recollection and the FN400/LPC effects seems firmly established overall (cf. Mecklinger, 2006, 2007). As reviewed in the introduction, there is quite some evidence to support the claim of dual processes, and the experiments reported in this thesis strongly add to this evidence. In particular, the finding that context as operationalised throughout this thesis does not affect the FN400 old-new effect despite being available and/or task-relevant (and dependent thereon affecting the LPC effect, cf. Experiments 2 and 3) poses a challenge for GM accounts. Experiment 4 showed that there are obviously two successive processes and that the influence of perceptual specificity on the first is quite independent of the nature of the second. That is, the differential effect of the intrinsic/extrinsic factor on familiarity holds whether or not subjects seem to capitalise on recollection – as it is typically understood – at all. Yet, terminal evidence has not yet been reported. One step towards this goal has recently been made by Yonelinas, Otten, Shaw, and Rugg (2005). After inferences derived from the PDP

and especially the “Remember/Know” procedure were severely tackled by Humphreys (e.g., Humphreys, Dennis, Chalmers, & Finnigan, 2000) and Dunn (2004), Yonelinas et al. adjusted the “Remember/Know” procedure in order to remove a confound in previous imaging and ERP studies, namely that regions or waveforms associated with recollection may have not been related to recollection per se but to the higher level of confidence associated with it. In this procedure, subjects gave either a “Remember” judgement or – if they could not recollect anything – a 5-scaled confidence rating. Thus, recollection-related regions were identified as those showing larger activity for “Remember” responses compared with confidently recognised but unrecollected items, whereas familiarity-related regions were those in which activation covaried with confidence reports. Regions associated with recollection included parahippocampal gyri and the hippocampal formation, whereas familiarity was associated with precuneus activation. There were also distinct patterns of frontal activation, but importantly, regions showed virtually no overlap (there was also no familiarity-related activity near the perirhinal cortex, see Henson et al., 2003). However, Dunn and Dennis (submitted) argued that under a GM perspective, all 5 response categories of Yonelinas et al. can be arranged on a single continuum. They modelled the data using differently shaped activation functions obtained within a signal detection framework, showing that all major results of Yonelinas et al. could be modelled within a GM account. In particular, they argued that the fact that Yonelinas et al. had found no region more active for high confidence familiarity judgements as compared to “Remember” responses was actually inconsistent with the assumption of two independent processes. Marginally, it should be noted that their account of Yonelinas et al.’s hippocampal activation data in terms of a functional association of hippocampal activity and decisional factors seems somewhat far-fetched. Similarly, Wais, Wixted, Hopkins, and Squire (2006) used receiver operating characteristics in a study on young adults, patients with limited hippocampal lesions, and matched controls, and argued that the hippocampus supports both recollection and familiarity components of recognition memory (see also Squire & Zola, 1998).

Woodruff et al. (2006) applied the procedure by Yonelinas et al. (2005) in an ERP study and reported a double dissociation between recollection and familiarity ERP correlates. The FN400 effect was sensitive to familiarity strength and importantly, when subjective familiarity strength was equated across (objectively) old and new items, the old-new effect disappeared (by the way, speaking strongly against a priming account of the FN400). Frontal effects did not differ between recollected items and those recognised via high-confidence familiarity. Yet, in this

contrast there was a standard LPC effect, speaking for a qualitative rather than a quantitative difference between recollection and familiarity. There was no LPC effect for confident-old and confident-new conditions, so it is not sensitive to familiarity strength.

Moving to behavioural findings, the study of item vs. associative memory has revealed a number of dissociations tackling GM accounts. These refer to effects of encoding instruction or strategy (incidental/intentional, separate/interactive imagery), time course of retrieval (Gronlund & Ratcliff, 1989, reporting that associative word recognition (same vs. rearranged) evolves some 100-200 ms after discrimination that can be based on item information alone; also see Doshier & Rosedale, 1991), and word-frequency and similarity (e.g., a list length effect in recall and recognition, a list strength effect only in recall; see Clark & Gronlund, 1996, for a review). These results are best explained by assuming different representational formats of item and associative information, as in the type-token model. Global matching models struggle to explain these findings and either have to assume that (a) compound cues take longer to be produced or to become memory-effective, an assumption not easily integrated into GM models, (b) associations are stored as higher order units (reminiscent of higher-level hippocampal binding) or (c) by introducing a second recall-like process to support associative retrieval. Note that if one assumes the latter it would be awkward to preclude any influence of this recall-like process in item recognition. That is, either there are dual processes or a dissociation of information (representation). For instance, concerning the latter, nonmonotonic false alarm curves to lures in response signal tasks (e.g., Hintzman & Curran, 1994) could simply reflect retrieval of contextual information linking studied items to experimental context, and this need not necessarily imply a recall-like process. McElree, Dolan, and Jacoby (1999) placed familiarity and source information in opposition by exclusion task instructions (accept heard/reject read items). The attenuation of a high initial false alarm rate could result from changes in response criteria, that is, strategic attempts to correct for high initial familiarity values (Doshier, McElree, Hood, & Rosedale, 1989). McElree et al. used a response signal procedure and reported a cross-over interaction of early and late false alarm rates: words read repeatedly initially had a higher rate ($5/3 > 1 > \text{new}$), whereas this was reversed at later points in time ($1 > 5/3 > \text{new}$), suggesting initial familiarity appraisal followed by source recovery. Familiarity emerged around 485 ms, recollection around 570 ms. This pattern of results cannot be explained by response criterion shifts. In order to resolve this, GM models propose alternative retrieval operations for overt recall (i.e., they add

a process), but alternatively, familiarity (item) and source information could be retrieved by a common mechanism through differential cueing of memory, applying different decision rules to each type of retrieved information. Such a scenario would preserve the assumption of a common retrieval mechanism acting on different familiarity values – one acontextual and one context-sensitive – which are handled with different decision rules, although this almost merges GM and DP approaches. For instance, in Dennis and Humphreys' (2001) BCDMEM outlined above, a studied item can be bound to several different types of context (associative context, list context, environmental context). The test item is used as a cue to retrieve a contextually bound representation, and the retrieved (general) context vector is matched to the reinstated (study) context vector. A dynamic approach, assuming the reinstated study-context vector has a broader (environmental) focus at first and is then narrowed (experiment...list...trial-associate) would also account for the data pattern without assuming two qualitatively distinct retrieval operations.

Despite a certain tendency in the literature to confound methods and theoretical positions – modellers tend to accept a global strength account and try to (over-) simplify things, neuropsychological researchers tend to promote the multiple process account – there is also evidence from the modelling literature favouring dual processes. For instance, Diana and Reder (2005) argue that list strength manipulations affect recollection but not familiarity and that this supports DP models. They modelled word recognition data with a localist network model (SAC) somewhat akin to the type-token model (see Reder et al., 2000, for details, and Diana, Reder, Arndt, & Park, 2006, for formal application of the model to a wider range of episodic recognition findings). Basically, at encoding, a stimulus representation is bound to experimental/list context, resulting in an "episode node". At test, the more active the episodic node after presentation of a probe, the more likely recollection. When the node presenting the item itself ("word/concept node") is more active this results in familiarity. For instance, the SAC model predicts list strength effects because increasing the strength of some items decreases the amount of available context activation for other items. In mixed (strong/weak) lists, strong items on a list have stronger connections to the experimental context node and receive more of the activation spreading from the context node when context is activated at test, so weak items draw less "Remember" responses. Strong words also have higher familiarity than weak words, but this is independent of list type (pure/mixed). Yet, familiarity is only thought to guide response if recollection fails (interdependent model). Only very few studies to date have attempted to

compare DP and GM models directly. Quamme, Frederick, Kroll, Yonelinas, and Dobbins (2002) tested source recognition in a list-discrimination task under conditions in which participants were required to discriminate between strong studied items, weak studied items, and new items. Applying ROC analyses, a DP model provided a better account of performance than did the unequal-variance GM model, even though familiarity could have been used to perform the task (often, both types of model fair equally well in this condition and DP models only have advantages if familiarity is "useless"). Moreover, results suggested that recollection was used to make recognition judgements even when assessments of familiarity were useful. In contrast, Brockdorff and Lamberts (2000) modelled data from a number of old/new recognition experiments involving response deadlines. They reported superior fits of a well-specified GM model accounting for the time course of recognition judgements when comparing it to a DP model which, however, involved questionable assumptions, namely considering "recall as perfect", so the relative contribution of each feature dimension to the decision process were constant over processing time (whereas the type-token model assumes recollection to be piecemeal).

With respect to context effects, studies by Murnane and Phelps (1993,1994) could offer a way of contrasting DP and GM models. They reported that context shifts (using stimulus/background colour and location as "context") produce a decrease in both hit and false alarm rates. GM models can account for this data, because context shifts would decrease familiarity of both targets and distractors. Yet, the critical point is that GM models predict that decreases must be parallel, that is, there should be no overall performance difference induced by context shifts (as long as context is not integrated into an "ensemble", reminiscent of an "object token", see Murnane et al., 1999).

7.4.3 Resolution: Iteration. Interaction. Integration.

Oppositional views claiming there are two processes of familiarity and recollection or rather a memory strength process followed up by a decision process may not be as exclusive as assumed. For instance, Shiffrin and Steyvers (1997) have argued for a "two phase" (but single process) account of recognition, in which the nature of the information contained in the probe cue would vary across time and only at late stages include contextual information. Notably, such an account seems to merge DP and GM models. This thesis adds to the common view that there are two consecutive processes involved in recognition memory. How to

call these two processes is another question, and in particular, the resolution of the debate may in part be dependent on the definition of recollection.

As noted by Herron and Rugg (2003), beyond the retrieval of episodic information, the definition of recollection may or may not encompass the *employment* of retrieved information in the conscious control of behaviour. A smaller LPC effect in this vein could thus be interpreted in various ways. One could assume that the LPC directly reflects recollective retrieval and a smaller effect would then simply reflect less recollection and thus worse performance. In fact, this correlation can often be found (e.g., Experiment 2), but this is a rather circular way of explanation, and it says little as to *why* there is less recollection. Thence, a diminished LPC could imply that despite successful retrieval there could be less allocation of processing resources to the retrieved information (cf. dependence of the LPC on task-relevance; Herron & Rugg, 2003). Alternatively, a smaller LPC effect could be attributable to (inhibitory) "non-binding", that is, nonintegration of irrelevant features due to the ability to control the integration process. This thesis takes the latter standpoint, although the first cannot be refuted given the present evidence. Notably, however, both the control or inhibition of binding and the allocation of processing resources accounts suggest that executive functioning plays a pivotal role in recollective processing. Again taking a dynamic system viewpoint, the retrieval of detailed episodic information usually requires strategic control and it usually also impacts on behaviour, thus leading up to or affecting decisional processes. That is, I propose strategic and decisional processing to be an integral part of recollection under most circumstances. Notably, the late right frontal ERP old-new effects often associated with strategic processing usually occur *post-retrieval*, so it should actually be *demand*ed to see strategic decisional processing in the ERP earlier on. The rather broad LPC old-new effects and accompanying CSD analyses presented here support this claim, most likely reflecting recollective processing with a high demand for (prefrontal) retrieval control, assumingly due to context integration effort. Hence, the ERP results of the present thesis lend further support to the notion that a fronto-parietal network serves recollective retrieval (cf. Cabeza et al., 2003), whereby the ratio of anterior-posterior involvement will most likely vary with demands on perceptual reinstatement and contextual integration, decisional and strategic aspects depending on the task and motivational factors, as well as the information supplied by the familiarity/memory strength signal²².

²² This implies that one may think of tasks that require across domain feature integration that nominally look like a recognition task, but do not require list memory at all, but still produce similar ERP signatures (Simon Dennis, personal communication).

Concerning the latter, although familiarity and recollection are assumed to be independent processes in principle, I have pointed out that they will usually occur together. Recollection, in particular, will rarely arise without familiarity, although there is some evidence that this also occurs (see Groh-Bordin et al., 2005, 2006, for both possibilities). Although the processes leading up to familiarity may be cognitively impenetrable, there is no reason to assume that the resulting signal should not impact on further recollective/decisional processing. To lend a term from connectionist-developmental work (Elman et al., 1996): there are "*interactions all the way down*". From a neuroscientific point of view, not only does a close interaction between MTLC and hippocampal processing make sense with regard to the tight neuroanatomical connections, but this assumption has been supported by findings of phasic iterative interactions of these regions at the stage of encoding (Fell et al., 2001, 2006) and likely also in retrieval (Maguire, Mummery, & Büchel, 2000; cf. also Mormann et al., 2005).

There is also evidence in support of the claim that the cascade of processing sketched in this thesis tells us something about the more general functioning of our mnemonic system beyond recognition memory. Attention is influenced by stimulus-driven and strategic processes, leading to a representation immediately assessed in terms of identity, previous occurrence, and behavioural relevance. During this ongoing process, the system attempts to integrate and assess more and more information, until enough evidence has accrued to determine behaviour. This thesis has shown that stored object-specific information and contextual information unfold their impact at different stages of this process, very likely relying on somewhat different regions of the brain. Extending these findings and supporting a more general scope, comparable effects have been reported in short-term recognition: intrinsic facial features affect ERPs early, whereas contextual features impact later on (Guillaume & Tiberghien, 2001). Likewise, the hippocampus has been shown to be active in working memory maintenance of object-location but not object-colour associations (Piekema, Kessels, Mars, Petersson, & Fernández, 2006). In perception, and again in favour of a dynamic view of these processes, Bar (2004) has reviewed evidence (including combined fMRI-MEG evidence) for mutual influences of context and object recognition, that is, interactive processes iteratively integrating contextual information to facilitate object recognition, and using object identities to promote the understanding of a scene (cf. Kassam, Aminoff, & Bar, 2003). As adumbrated above, Cabeza et al. (2003) compared a sustained visual attention task and an episodic retrieval task and reported activity in a common fronto-parietal-cingulate-thalamic network. This im-

plies that "specific" effects in episodic memory studies may in fact rather reflect general attentional processes. For instance, post-retrieval monitoring requires continuous attention aimed at retrieval output, information recovery may imply attentional shifts and so on. Notably, Cabeza and colleagues also found some regions specifically associated with episodic recognition, including left PFC, left posterior parahippocampal cortex, frontopolar and precuneus regions, but surprisingly, some MTL regions were similarly active in both tasks. This suggests that the hippocampus subserves a function of indexing representations in the focus of consciousness, regardless whether these refer to episodic retrieval, working memory maintenance, or perceptual processing (cf. Moscovitch, 1992). Perhaps this explains why hippocampal activity is not consistently reported in imaging studies despite the fact that there is broad agreement in the scientific community regarding its pivotal role in episodic remembering: activity may simply be lost in many studies in the course of subtraction of critical and control conditions.

Somewhat related to the findings of Cabeza et al. (2003), Nosofsky (1988, 1991), Estes (1994), and Brockdorff and Lamberts (2000) have shown that perceptual classification and recognition memory can be framed within a single, exemplar-based theory, assuming a common store of exemplars in memory. However, computational models often highlight similarities in computational task requirements, whereas neuropsychological work often shows that different brain regions underlie certain tasks (eg, perceptual classification/object categorisation vs. recognition memory, see Lamberts, Brockdorff, & Heit, 2002; Squire & Knowlton, 1995). Although single-system models can also model neuropsychological dissociations (e.g., by varying a sensitivity parameter that controls exemplar discrimination, Nosofsky & Zaki, 1998), fMRI findings are more in line with a multiple systems/processes approach.

Further evidence for the notion of iterative appraisal of familiarity comes both from the modelling literature (Humphreys et al., 1989) and from ERP research carried out in our laboratory (Groh-Bordin et al., in preparation). In the latter study, when presenting different exemplars of the same concept at study and test in a subset of trials (e.g., two images of different cats), the early mid-frontal old-new effect initially only seemed to code for the conceptual old-new status (i.e., no difference between same-exemplar and different-exemplar repetitions), whereas the perceptual impact kicked in later (i.e., a larger old-new effect for same-exemplar compared to different-exemplar repetitions). Replication and more systematic investigation of this potentially iterative effect is urgently needed.

Taken together, I suggest that the system will interactively and iteratively appraise certain aspects of presented stimuli. Initial processing of identity, novelty, familiarity, and recency will mostly be automatic (reminiscent of the "generalised strength" concept promoted by Humphreys, Bain, and Burt (1989) as reflecting an amalgamation of frequency, recency, and duration of exposure), but strategic and intentional influences will shape the further line of integrational processing depending on task demands. However, top-down influences may also become active even earlier via attentional selection (cf. Experiment 5) and even implicitly (cf. Olson, Chun, & Allison (2001), who reported attentive search of simple abstract targets to be guided by implicitly learnt spatial information. Yet, as objects are the preferred units of the cognitive system, intrinsic features will in most cases be evaluated prior to extrinsic features (Experiments 1-4).

An alternative account, which could potentially explain the findings presented in this thesis within a different framework, has been proposed by Koen Lamberts and colleagues (Brockdorff & Lamberts, 2000; Heit, Brockdorff & Lamberts, 2003; Lamberts et al., 2002; Kent & Lamberts, 2006; see also Loftus & McLean, 1999). In the formulation of their "feature sampling theory of recognition" (FESTHER), they stress the importance of the temporal dimension. They propose a perceptual feature integration process over time, whereby different features or feature dimensions are sampled in parallel, but with a different time course, so they exert their influence at different points in time. Also, subjects – even without response time restrictions – may not process all features before making their (old/new) decision. Using response signal techniques and manipulating certain stimulus features, they suggest that this approach enables the modelling of old/similar-lure/new recognition memory data within a computational single-process model. Thus, FESTHER would explain differential congruency effects concerning intrinsic and extrinsic features by simply stating that intrinsic features of the *test probe* would be sampled first in perception. Congruency effects could then arise from either the reactivated mnemonic representation or the online construction of a perceptual representation. Combining response signal and ERP methodologies could prove extremely helpful in elucidating predictions of the different models. For instance, one could compare intrinsic and extrinsic stimuli of Experiment 4 in a perceptual matching task. In Experiment 4, the same feature was manipulated intrinsically vs. extrinsically, so if perceptual integration processes were not to differ between stimulus classes, the data of Experiment 4 would speak strongly for the mnemonic basis of the reported congruency effects. Yet, in line with a main proposal of this thesis, the account of Lamberts highlights the

need to move away from static concepts (the match of two representations) to more dynamic accounts of processing, concerning familiarity memory and beyond. With respect to the single- vs. dual-process debate, it should be noted for the sake of completeness that Lamberts (Brockdorff & Lamberts, 2000; Lamberts et al., 2002), despite being in favour of GM models, explicitly states that there are at least two subsequent processes involved in recognition memory, a perceptual processing stage building a representation, and a decision stage that matches perceived and stored representations, and that recognition memory is "*likely to include other fundamental processes as well*" (p.98).

Similarly, Curran et al. (2002), reported that the N1 ERP component was sensitive to learnt category membership, the LPC was sensitive to old/new status, and the FN400 was sensitive to both with no topographical differences. While underpinning the argument that conceptual and perceptual processes contribute to familiarity, this effect pattern also suggests that there might be a single process contributing to categorisation and recognition memory, best understood as a temporal sequence of events involving a transition between early sensitivity to category membership and later sensitivity to differential experience with particular exemplars. Thus, across time, there is a shift from a gross level of sensitivity to stimulus similarity (N1 in/out category effects) to intermediate levels (FN400 in/out and old/new effects) to fine-grained differences (parietal old/new effects).

Finally, I would like to address another general issue touched in the previous section. As noted there, scientists from different communities tend to focus on specific aspects of the cognitive system. For instance, neuroscientific research has recently yielded evidence that there are even three MTL processes contributing distinctively to recognition memory – recollection, familiarity, and novelty (Daselaar et al., 2006; see also Xiang & Brown, 1998). In their fMRI study, Daselaar et al. used linear and nonlinear "oldness" functions based on subjects' response confidence levels (assuming graded familiarity/novelty processes and a high-threshold and thus nonlinear recollection process) to investigate the contribution of different brain regions. MTL regions made separate and unique contributions as revealed by multiple regression analysis, suggesting relative independence of processes. Hippocampal novelty is also discussed as a trigger enhancing efficient encoding of novel stimuli via acetylcholine-regulation through efferents to the nucleus basalis of Meynert (NBM; see also Grunwald & Kurthen, 2006). The main point to be outlined here is, however, that from a behavioural or *functional* point of view, novelty and familiarity can be treated as two sides of the same

medal, whereas the fMRI data indicate that they are separable on the brain level (see also Tsivilis et al., 2001; Experiment 5). I suggest that these positions should, however, be seen as complementary rather than competing. Both the assignment of function to neural structure as well as the investigation of a functional "black box" seem far less interesting and promising in terms of scientific progress than the combination of the two. Thus, the integration of classical cognitive, neuroscientific, and connectionist/computational modelling approaches seems to offer the most auspicious way to propel the understanding of the human cognitive system.

8 Conclusion

In conclusion, the type-token model shares some resemblance to other models presented by Aggleton & Brown (1999), Mecklinger (2000, 2007), Paller (2000, 2006), Murre (1999), or Eichenbaum (for an update of his relational representation model see Eichenbaum, 2006), 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, some of which have been tested as reported in the present thesis. Furthermore, our model integrates in a rather unique way processes of perception, implicit memory, and episodic memory, it touches the question of mnemonic processing control, and can also be extended to incorporate verbal memory and phenomena of object naming and imaging (cf. Engelkamp & Zimmer, 1994, 2006).

Beyond further examination of item unitisation, associative binding, and context influences in and on recognition memory, given that single processing accounts – especially from the math modelling literature – tackle the standard dual processing view of recognition memory by stating that criterion shifts moderate a single recognition process, further research should aim at the resolution of the ongoing single versus dual processing debate in recognition memory research by integrating ERP, fMRI, and modelling approaches. The proposed view stressing interaction between subprocesses and structures and focussing on the dynamics of processing could potentially bring the two positions closer together. The ERP results presented differ slightly from much of the existing literature in that late (i.e., from 500 ms post stimulus onset onwards) old-new effects are very broad with a strong anterior component. These effects could be an indicator of control and decision processes and this is compatible with both dual-processing and mathematic GM modelling accounts. The nature of these control processes in re-

lation to familiarity and recollection needs to be investigated more thoroughly in future research.

To conclude, it should have become clear that the human brain and its exciting (mnemonic) functions do not fit into neat dichotomies, categories, boxes and arrows, waveforms, colourful brain pictures, or computational models. Yet, it is a ravishing enterprise to *try* and fit some of it and thus gradually increase our knowledge and understanding of the most complex system known to man. In the end, however, brain-processes are a lot like crocodiles: for every one you see, there are ten (or maybe one) you don't see (Figure 48). That is, nature has found impressive solutions, but these have not succeeded mainly on parsimony grounds, but depending on whether or not they *work*.



Figure 48. Australian Estuarine (Saltwater) Crocodile (*Crocodylus porosus*).

9 Appendix

Illustrating difficulties in intrinsic/extrinsic categorisation of features, hairstyle may initially be considered extrinsic as compared to facial expression. Introspection suggests, however, that the person in Figure 49 is not particularly familiar (in terms of semantic familiarity)....



Figure 49. An unfamiliar face – familiarity reduced by hairstyle.

....in contrast to the person in Figure 50 (next page).



Figure 50. A familiar face.

10 Zusammenfassung

10.1 Einleitung

Die Objekte unserer Umwelt besitzen eine Reihe verschiedener Merkmale (Form, Größe, Farbe, etc.). Diese Merkmale werden bei der Reizverarbeitung im Zuge der Wahrnehmung bereits in unterschiedlichen Gehirnarealen prozessiert (Corbetta & Miezin, 1990; Livingstone & Hubel, 1988; Zimmer, 1988, 1993) und müssen gebunden werden, um eine kohärente mentale Repräsentanz des externen Reiz zu gewährleisten (Bindungsproblem der Wahrnehmung; Herrmann, Mecklinger, & Pfeifer, 1999). Neben dem Wahrnehmen und Erkennen von Reizen ist auch das Wiedererkennen zuvor bereits „erlebter“ Reize eine höchst alltagsrelevante kognitive Fähigkeit. Sie basiert im wesentlichen auf einem Abgleich mentaler Repräsentanzen in Wahrnehmung und Gedächtnis. Es gibt überzeugende Evidenz dafür, dass verschiedene Reizmerkmale lokal dort gespeichert werden, wo sie auch primär verarbeitet werden, in funktional spezialisierten Kortexarealen (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Woodruff, Johnson, Uncapher, and Rugg, 2005). D.h., auch die zum Wiedererkennen notwendige Aktivierung einer mnestischen Repräsentanz verlangt Bindung bzw. Reintegration der lokalen Merkmalsspuren (Bindungsproblem des (episodischen) Gedächtnisses; Klimesch et al., 2001). Hinzu kommt, dass Objekte in der Realität nicht isoliert, sondern in einem raumzeitlichen Kontext eingebunden sind und dass auch die Verarbeitung eines Reizes meist in Bezug zu anderen Objekten bzw. eigenen Gedanken und Gefühlen geschieht (Bar, 2004). Die vollständige Aktivierung einer episodischen Gedächtnisspur im Sinne einer „mentalen Zeitreise“ (Tulving, 1983, 2002) setzt daher auch die Reintegration solcher Kontextmerkmale voraus.

Man geht in der Psychologie des episodischen Wiedererkennens allgemein davon aus, dass zwei unabhängige Prozesse einen Beitrag leisten: Vertrautheit und Rekollektion (Jacoby & Dallas, 1981; Mandler, 1980; Mecklinger, 2007; Yonelinas, 2002a; obwohl es auch einflussreiche sog. Ein-Prozess-Modelle gibt, vgl. Dennis & Humphreys, 2001; Gillund & Shiffrin, 1984; Humphreys, Bain, & Pike, 1989; Murdock, 1982). Vertrautheit bezeichnet dabei ein unspezifisches Gefühl, etwas schon einmal gesehen (oder gehört) zu haben, während Rekollektion den bewussten Abruf spezifischer Details der Enkodierepisode voraussetzt. Es gibt aus verschiedenen Bereichen Evidenz, dass es sich hierbei um eine valide und qualitative Unterscheidung handelt. U.a. sind die beiden Prozesse funktional dis-

sozifizierbar, zeigen sich z.B. unterschiedlich beeinflusst von Verarbeitungstiefe (Gardiner, Java, & Richardson-Klavehn, 1996) oder Retentionsintervall (Yonelinas & Levy, 2002). Problematisch bei der Untersuchung solcher behavioraler Dissoziationen sind die z.T. kontrovers diskutierten Methoden, um die Anteile der Teilprozesse zu schätzen, insbesondere zu nennen hier die introspektive „Remember/Know“ Technik (Tulving, 1985; siehe Yonelinas, 2002 und Dunn, 2004, für unterschiedliche Positionen). Moderne Verfahren wie die funktionelle Magnetresonanztomografie (fMRT) und die aus dem EEG abgeleiteten ereigniskorrelierten Potentiale (EKP), sowie neuropsychologische Studien legen jedoch nahe, dass Vertrautheit und Rekollektion auf zumindest teilweise unterschiedliche neuronale Substrate zurückgreifen. So zeigt eine Subgruppe von Amnestikern mit fokaler Läsion des Hippocampus stärkere Defizite im Bereich der Rekollektion (Aggleton & Shaw, 1996; Srinivas & Verfaellie, 2000) und schließlich sind die beiden Prozesse mit distinkten neuronalen Aktivationsmustern im fMRT (vgl. Henson, Cansino, Herron, Robb, & Rugg, 2003; Cabeza et al., 2003) bzw. distinkten elektrophysiologischen Komponenten – EKP alt-neu Effekten – assoziiert (Smith, 1993; Friedman & Johnson, 2000; Mecklinger, 2000).

Das von Hubert Zimmer und Kollegen entwickelte Type-Token Modell des Objektgedächtnisses (Ecker, Groh-Bordin, & Zimmer, 2004) ordnete u.a. den beiden Prozessen unterschiedliche Repräsentationsformate zu, das „Objekttoken“ und das „episodische Token“. Die im wesentlichen in der vorliegenden Arbeit untersuchte Hypothese war dabei, dass die intrinsischen Merkmale eines Objektes (z.B., seine Farbe) in einem Objekttoken (eine Art konsolidiertes „object file“ im Sinne Treismans, 1992, 2006) repräsentiert sind, welches die Grundlage für Vertrautheit liefert, während extrinsische Kontextmerkmale zusätzlich in einem episodischen Token repräsentiert sind, welches Rekollektion unterstützt. Die letztere Art der Repräsentation stellt höhere Ansprüche an die Bindung, welche zur raumzeitlichen Integration über Domänen hinweg erfolgen oder aber zumindest mehrere Items integrieren muss. Die Datenlage (s.o.) spricht dafür, dass solche Bindungen einen intakten Hippocampus benötigen, während intra-item Bindung wohl von den angrenzenden Kortexarealen geleistet werden kann (Buffalo, Reber, & Squire, 1999; Cansino, Maquet, Dolan, & Rugg, 2002; Mumby, Gaskin, Glenn, Schramek, & Lehmann, 2002;).

Die Annahme unterschiedlicher Repräsentationsformate war im Rahmen des Type-Token Modells u.a. darauf gestützt, dass die Veränderung einiger perceptueller (intrinsischer) Objektmerkmale vom Lernen zum Testen das Wiederer-

kennen unwillkürlich beeinträchtigt (im Sinne von Reaktionszeitverlangsamung), obwohl sie gar nicht aufgabenrelevant sind (Cooper, Biederman, & Hummel, 1992; Engelkamp, Zimmer, & de Vega, 2001; Jolicoeur, 1987; Zimmer, 1995; Zimmer & Steiner, 2003), während dies für Kontextmerkmale eher nicht zutrifft (vgl. Smith & Vela, 2001). Auch in der vorliegenden Arbeit wurde vornehmlich das Paradigma der Lern-Test-Manipulation in einer alt/neu Entscheidungsaufgabe benutzt, d.h., bei einem Teil der gelernten Objekte wurde ein Merkmal in der Testphase verändert, so dass die Bedingungen „kongruent“, „inkongruent“ und „neu“ verglichen werden konnten. Auf Grundlage des Modells wurde vorhergesagt, dass sich Manipulationen intrinsischer Reizmerkmale unwillkürlich auf die Vertrautheit und damit sowohl auf die Reaktionszeiten, als auch das entsprechende EKP-Korrelat (den mid-frontalen alt/neu- oder FN400-Effekt) auswirken sollten. Andererseits sollte die Veränderung extrinsischer Kontextmerkmale einen Einfluss auf Rekollektionsprozesse und den entsprechenden parietalen alt-neu Effekt (LPC-Effekt) haben. Da davon ausgegangen wird, dass Rekollektion im Vergleich zu Vertrautheit ein eher kontrollierter Prozess ist (Herron & Rugg, 2003; Troyer & Craik, 2000), sollte dieser Effekt jedoch nur dann zu beobachten sein, wenn das entsprechende Merkmal aufgabenrelevant ist. Wichtig hierbei ist, dass eine intrinsische Manipulation laut Modell durchaus auch einen Einfluss auf spätere Rekollektionsprozesse haben kann, jedoch ein Einfluss extrinsischer Merkmale auf frühere Vertrautheitsprozesse ausgeschlossen wurde.

In diesem Zusammenhang relevante EKP Studien untersuchten meist das Quellengedächtnis (vs. Itemgedächtnis) und lieferten recht uneindeutige, da indirekte Evidenz. So berichteten Schloerscheidt und Rugg (2004) Kongruenzeffekte in Reaktionszeiten und EKP alt-neu Effekten bei einer Manipulation des Wort-/Bild-Formats. Mit einer Farbmanipulation fanden Friedman, Cycowicz, und Bersick (2005) jedoch nur signifikante Kongruenzeffekte in den Reaktionszeiten. Auch Studien, die direkt den Einfluss der perzeptuellen Manipulation untersuchten, kamen zu unterschiedlichen Ergebnissen. Curran und Cleary (2003) manipulierten z.B. die Orientierung von Bildern und berichteten einen selektiven Einfluss auf den mit Rekollektion assoziierten EKP alt/neu Effekt (in der „late positive component“ oder LPC, ca. 500-700 ms), während Groh-Bordin, Zimmer, und Mecklinger (2005) mit einer ähnlichen Manipulation einen selektiven Effekt auf die Vertrautheits- (oder FN400, um 400 ms) Komponente fanden. Mit einer Farbmanipulation fanden Groh-Bordin, Zimmer, & Ecker (2006) sogar einen Einfluss auf beide Komponenten. Erschwert wird der Vergleich dieser Studien durch unterschiedliche Anforderungen der Lern- und Testaufgaben (z.B. unterschiedliche

Betonung perzeptueller Verarbeitung beim Enkodieren oder Inklusions- vs. Exklusionsaufgaben im Test). Tsivilis, Otten, & Rugg (2001) untersuchten schließlich den Einfluss einer kontextuellen Manipulation, indem sie Objekte in einem Rekognitionstest auf mit Bezug zur Lernphase unveränderten, rekombinierten oder neuen Landschaftsszenen präsentierten. Sie fanden einen Vertrautheitseffekt im EKP nur für Objekte auf alten (gleichen oder rekombinierten) Kontexten, jedoch nicht für alte Objekte auf neuen Kontexten, was einer wesentlichen Vorhersage des Type-Token Modells widerspricht.

10.2 Experimente

Experiment 1 diente dazu, innerhalb eines Experimentes ein intrinsisches (die Objektfarbe) und ein extrinsisches Merkmal (die Form eines arbiträren grauen Hintergrundes) zu manipulieren. Der Faktor intrinsisch/extrinsisch wurde zwischen Versuchspersonen (Vpn) manipuliert. Die Vpn lernten wie in allen Experimenten intentional mit Merkmalsfokus 80 Objekte, im Test wurden sie mit 160 Objekten in einer Inklusionsaufgabe getestet (40 kongruent, 40 inkongruent, 80 neu), d.h. das jeweilige Merkmal war für die Entscheidung prinzipiell irrelevant. In jedem Trial beurteilten die Vpn nach ihrer alt/neu Entscheidung, ob sich das entsprechende Merkmal verändert hatte, um eine Schätzung darüber zu erhalten, wie gut Objekt und Merkmal assoziiert wurden. Behavioral zeigte sich der erwartete Effekt, d.h. eine irrelevante intrinsische Manipulation wirkte sich negativ auf die Leistung (Reaktionszeiten) aus, während die Kontextmanipulation keinen Einfluss hatte²³. Allerdings zeigte sich im direkten Merkmalstest, dass Vpn nur die Farbe jedoch nicht den Kontext überzufällig beurteilen konnten. Somit konnte nicht ausgeschlossen werden, dass die Kontextmanipulation nur deswegen keinen Einfluss auf die Leistung der Probanden in der alt/neu Entscheidung hatte, weil diese den Kontext gar nicht mit dem jeweiligen Objekt assoziiert hatten. Die EKP-Befunde waren ebenfalls uneindeutig, so fand sich lediglich ein breiter, eher posteriorer alt-neu Effekt um 500 ms, jedoch kein fokaler mid-frontaler alt-neu Effekt. Es fanden sich in beiden Gruppen (intrinsisch vs. extrinsisch) Kongruenzeffekte, die in der Farbgruppe jedoch deutlich früher auftraten als in der Kontextgruppe. Die Befundlage von Experiment 1 ist damit insgesamt konsistent mit der Modellannahme eines frühen Einflusses intrinsischer Verarbeitung auf den eher automatischen Ver-

²³ Im übrigen zeigte sich ein äquivalenter Effekt in einem Kontrollexperiment, in dem der intrinsisch/extrinsisch Faktor innerhalb Vpn manipuliert wurde, was Strategieunterschiede als Basis der Interaktion unwahrscheinlich macht. Die notwendige Anzahl an Trials zur Durchführung eines EKP-Experiments erforderte jedoch die zwischen-Vpn-Manipulation.

trauthheitsprozess versus einer eher späteren extrinsischen Merkmalsintegration (vgl. auch Hintzman & Curran, 1994). Die Tatsache, dass Kontextinformation jedoch von vorneherein nicht mit dem jeweiligen Objekt verknüpft werden konnte, schwächt die möglichen Schlussfolgerungen deutlich ab.

Das Ziel von Experiment 2 war demzufolge, diese Mängel zu beheben. Als Hintergründe wurden nun nicht mehr unregelmäßig geformte, arbiträre Formen, sondern geometrische Formen verwendet. Zudem wurde nun in zwei Lern-Test-Blöcken experimentiert und jedes Lernitem wurde doppelt präsentiert. Die Verhaltensdaten der alt/neu Entscheidung zeigten ein ähnliches Muster: Bei intrinsischer Manipulation gab es einen signifikanten Kongruenzeffekt sowohl in den Reaktionszeiten, als auch im eigentlichen Leistungsmaß (Pr; Snodgrass & Corwin, 1988), während die extrinsische Manipulation keinen Effekt machte (beide Interaktionen über Gruppen signifikant). Im direkten Merkmalstest unterschieden sich die Gruppen jedoch nun nicht signifikant in ihrer Leistung, d.h. sowohl Farbe als auch Kontext wurde von den Vpn mit dem jeweiligen Objekt erfolgreich assoziiert. Somit gab es selektiv einen unwillkürlichen Effekt der intrinsischen Manipulation, obwohl diese nicht relevant für die Aufgabe der Objektrekognition war und obwohl die extrinsische Information ähnlich gut verfügbar war. Im EKP der Objektentscheidung zeigte sich bzgl. der Vertrauthheitskomponente der erwartete Effekt, dass nur die intrinsische Manipulation den Effekt verkleinerte, die extrinsische Veränderung jedoch keinen Einfluss hatte, was die wesentliche Voraussage der Studie war. Die Größe des Kongruenzeffektes der Farbgruppe in den Reaktionszeiten und im mid-frontalen EKP alt-neu Effekt waren dabei korreliert, was wie erwartet ebenfalls darauf hinweist, dass die Merkmalsintegration des intrinsischen Merkmals im wesentlichen im Vertrauthheitsprozess stattfindet. Die Ergebnisse bzgl. der Rekollektionskomponente waren ähnlich, was vor dem Hintergrund des Modells so erklärt werden kann, dass auch intrinsische Merkmale rekollektiert werden können, da sie redundant im episodischen Token repräsentiert sein können²⁴ und ohnehin vom System mehr oder weniger automatisch zur Verfügung gestellt werden. Andererseits hatte die extrinsische Manipulation – das episodische Token und die darin enthaltenen extrinsischen Merkmale sind laut Modell ja Grundlage der Rekollektion – u.U. deswegen keinen Einfluss auf den LPC Effekt, da der Kontext zunächst irrelevant für die primäre Objektrekognitionsaufgabe war und erst später (bei der Merkmalsentscheidung) aufgabenrelevant wurde, und

²⁴ Offen ist dabei die Frage, ob intrinsische Merkmale gleichwertig (perzeptuell) in Objekttoken und episodischen Token repräsentiert sind, oder ob ein intrinsisches Merkmal im episodischen Token eher auf einer anderen Ebene repräsentiert ist, beispielsweise als Prädikat „der Ball war blau“.

extrinsische Integration laut Modell ein kontrollierter Prozess ist. Für diese These sprechen akzentuierte frontopolare alt/neu Effekte in einem späten Zeitfenster (800-1200 ms) in der Kontextgruppe, was für spät einsetzende, präfrontal gesteuerte Integrationsprozesse im Lichte der sekundären Merkmalsentscheidung spricht. In den ebenfalls aufgezeichneten EKPs der Merkmalsentscheidung zeigte sich dementsprechend nur in der Kontextgruppe ein signifikanter Kongruenzeffekt (bei im Vergleich zur Farbgruppe verlängerten Reaktionszeiten) – d.h., zu dem Zeitpunkt, als das extrinsische Merkmal aufgabenrelevant wurde.

Es gibt allerdings eine Alternativerklärung der Daten: Wenn es lediglich die notwendige kognitive Anstrengung ist, die intrinsische und extrinsische Merkmalsintegration unterscheiden, so könnte das Befundmuster von Experiment 2 auch durch strategische Gruppenunterschiede erklärt werden. Wenn nun die Kontextintegration nicht „unnötige Arbeit“ wäre, sondern notwendig zur Bewältigung einer Aufgabe, dann sollten Vpn versuchen, den Kontext schnellstmöglich zu integrieren. Sollten Unterschiede in der Strategie die Grundlage für das Ausbleiben eines Kongruenzeffektes auf die Vertrautheitskomponente in Experiment 2 gewesen sein, und nicht grundlegende Unterschiede in der Repräsentation, dann sollte eine Kontextmanipulation nun den FN400 Effekt im EKP beeinflussen. Wenn jedoch – wie hier behauptet – repräsentationale Unterschiede vorliegen, dann können diese auch nicht durch Strategie „überwunden“ werden, und es sollte sich selektiv ein Einfluss der Kontextmanipulation auf den späteren LPC Effekt zeigen, aber kein Einfluss auf den FN400 Effekt. Daher wurde ein weiteres Experiment durchgeführt, in dem bei einer Replikation der Kontextgruppe aus Experiment 2 die Aufgabe nun eine Exklusionsaufgabe war, d.h., es waren nur alte Objekte auf altem Kontext als „alt“ zu akzeptieren, Kontext wurde so unmittelbar aufgabenrelevant. In den Verhaltensdaten zeigte sich der wenig überraschende Effekt, dass neue Items insgesamt am schnellsten und am sichersten bewertet wurden, gefolgt von kongruenten alten Items und inkongruenten, bei denen also der Kontext verändert wurde, was zu einem gewissen Antwortkonflikt führt (Objekt alt, richtige Antwort: neu). In beiden Bedingungen lag die Performanz jedoch deutlich über Zufall. In den EKPs zeigte sich exakt das vorhergesagte Befundmuster: Die extrinsische Manipulation hatte keinen Effekt auf den ausgeprägten mid-frontalen alt-neu Effekt (Vertrautheitseffekt), während der spätere parietale LPC Effekt abgestuft war, d.h. der alt-neu Effekt war größer für kongruente Wiederholung als für inkongruente. Somit erfolgte Kontextintegration trotz gegebener Aufgabenrelevanz erst in der relativ späten Rekolektion, Vertrautheit zeigte sich also durch

Kontext nicht beeinflusst, obwohl Kontextinformation verfügbar und aufgabenrelevant war.

Die Ergebnisse von Experiment 1-3 sprechen daher für einen qualitativen Unterschied in der Repräsentation intrinsischer und extrinsischer Merkmale, wobei im Abruf frühe Vertrautheitsprozesse unabhängig von Aufgabenrelevanz und prinzipieller Verfügbarkeit unbeeinflusst von Kontext bleibt, während spätere Rekollektionsprozesse je nach Aufgabenrelevanz – also eher kontrolliert und flexibel – Kontextinformation mitintegrieren können.

In Experiment 4 sollten diese Befunde mit anderem Stimulusmaterial repliziert werden, wobei zum einen das Merkmal an sich nun konstant gehalten wurde, d.h., Farbe wurde sowohl intrinsisch (als Objektmerkmal) als auch extrinsisch (als Farbrahmen) manipuliert; zum anderen wurde untersucht, ob sich der Befund der intrinsischen Merkmalsmanipulation aus Experiment 2 auch bei gegebener Aufgabenrelevanz des Merkmals zeigt. Dementsprechend sollten Vpn in der Testphase von Experiment 4 eine Dreifach-Entscheidung treffen (alt-kongruent, alt-inkongruent, neu). Gelernt wurden 144 Objekte (halb intrinsisch gefüllt, halb extrinsisch umrahmt). Im Test gab es 72 kongruente Wiederholungen, 72 inkongruente, und 72 neue Items (je zur Hälfte intrinsisch/extrinsisch). Im intrinsischen Fall sollte eine Farbmanipulation den Vertrautheitseffekt reduzieren, im extrinsischen Fall sollte der Effekt für beide Gruppen alter Items gleich groß sein. Für den LPC-Effekt und die Verhaltensdaten galt, dass die Farbkongruenz in beiden Bedingungen (intrinsisch/extrinsisch) einen Effekt machen sollte, da Farbe entscheidungsrelevant war. In allen Bedingungen lag die Performanz über Zufall, und es zeigte sich lediglich wie erwartet ein Haupteffekt der Kongruenz. D.h. andererseits, die Leistungen waren in beiden intrinsisch/extrinsisch Bedingungen vergleichbar, EKP-Differenzen zwischen den Bedingungen können demnach nicht durch basale Performanzunterschiede erklärt werden. Erwartungsgemäß wurden erneut neue Items am schnellsten bewertet, während sich in den Latenzen der alten Items Haupteffekte der Kongruenz und des intrinsisch/extrinsisch Faktors zeigten, jedoch keine Interaktion, so dass auch diese Verhaltensdaten als Grundlage möglicher differentieller Kongruenzeffekte in den EKPs beider Bedingungen ausscheiden. Der frühe mid-frontale EKP alt-neu Effekt zeigte exakt das vorhergesagte Muster, nämlich eine Abstufung in Abhängigkeit der Kongruenz im intrinsischen Fall, und keine Beeinflussung durch Kongruenz im extrinsischen Fall. Der Kongruenzeffekt im EKP – selektiv für intrinsische Information – zeigt sich also auch dann, wenn das Merkmal entscheidungsrelevant ist. Erneut weist dies dar-

auf hin, dass Vertrautheit unbeeinflusst von kontextueller Manipulation ist, jedoch perzeptuell spezifisch bzgl. intrinsischer Merkmale. Ungewöhnlicherweise trat in Experiment 4 im Mittel über Vpn kein LPC Effekt auf, allerdings zeigte sich dieser bei fast allen Einzelversuchspersonen, lediglich bei der Hälfte der Probanden sozusagen invertiert. In der Regel zeigt die EKP-Kurve für neue Items (korrekte Zurückweisungen) einen negativeren Verlauf im Vergleich zu alten Items (Hits), in dieser Untergruppe war es genau umgekehrt. Dies ist wahrscheinlich auf Strategieunterschiede zwischen den Gruppen zurückzuführen (möglicherweise im Sinne eines "semantic novelty focus" der "inversen Gruppe", vgl. Nessler, Friedman, and Bersick, 2004), denn es fanden sich keine offensichtlichen Unterschiede zwischen den Gruppen (weder in demographischen Variablen noch in den Daten, mit Ausnahme eines größeren Kongruenzeffektes in den Reaktionszeiten der "Standardgruppe"). In der weiteren Analyse wurden also neue EKPs für die beiden Untergruppen berechnet; zentral dabei war, dass das mid-frontale Befundmuster stabil blieb, sich der Vertrautheitseffekt also unabhängig vom späteren LPC Effekt in beiden Gruppen verhielt wie zuvor beschrieben. Bzgl. des LPC Effektes zeigte sich wie erwartet gerade in der extrinsischen Gruppe eine Interaktion derart, dass unabhängig von der Polung des Effektes die alt-neu Differenz für kongruente Wiederholung größer war als für inkongruente, was als Zeichen des Merkmalszugriffs im Zuge der Rekollection interpretiert werden kann. Auch wenn also alle anderen Faktoren konstant gehalten werden (gleiche Vp-Gruppe, gleiches Merkmal, sogar gleiche Anzahl von Farbpixel in intrinsisch/extrinsisch Bedingungen), zeigt der intrinsisch/extrinsisch Faktor den erwarteten Einfluss auf Vertrautheit und Rekollection: Vertrautheit basiert u.a. auf einer Evaluation der intrinsischen Merkmale eines Objektes, extrinsische Merkmale werden erst in späteren Rekollectionsprozessen mitintegriert. Die Unabhängigkeit des frühen Effektes von der Polung des späteren spricht im übrigen deutlich für zwei unabhängige Prozesse.

Insbesondere ein eingangs erwähnter Befund von Tsivilis et al. (2001) spricht nun aber gegen die Annahme, Vertrautheit sei kontextunabhängig, denn dort wurde in einer Inklusionsaufgabe ein mid-frontaler alt-neu Effekt nur für alte Items auf alten Hintergründen berichtet. In dieser Studie wurden jedoch hochsaliente Landschaftsszenen als Kontexte benutzt. Es ist somit eine plausible Alternativerklärung, dass in einem Teil der Trials der initiale Aufmerksamkeitsfokus nicht auf dem eigentlichen Target lag, sondern dass die Landschaftsszenen das "Rennen" um Repräsentation und bewusste Wahrnehmung gewonnen haben (Brockdorff & Lamberts, 2000; Hickey, McDonald, & Theeuwes, 2006) und somit der Hintergrund eher als Objekt verarbeitet wurde und dementsprechend selbst

ein Vertrautheitssignal auslöste, bevor top-down ein Aufmerksamkeitsshift hin zum zu beurteilenden Objekt erfolgen konnte. In anderen Worten könnte der Effekt von Tsivilis et al. nicht einen direkten Einfluss des Kontexts auf die Objektvertrautheit widerspiegeln, sondern die Vertrautheit des Kontextes selbst (bzw. fehlende Vertrautheit bei neuem Kontext). Dies wurde in einem Zwei-Gruppen-Design in Experiment 5 untersucht. In einer Gruppe wurde die Tsivilis et al. Studie im wesentlichen repliziert, während den Probanden der anderen Gruppe in jedem Testtrial vor dem Target ein Cue präsentiert wurde. Dabei handelte es sich um einen Rahmen, der exakt dem Umriss des folgenden Objektes entsprach und somit als Hilfe zur Aufmerksamkeitsfokussierung im Sinne eines "spotlights" (Cave & Kosslyn, 1989) diente. Der wesentliche Befund war, dass das FN400 Datenmuster von Tsivilis et al. in einer Gruppe exakt repliziert werden konnte (alt-neu Effekt nur für kongruente und inkongruent-rekombinierte Wiederholung, also im Fall "beide Stimuluskomponenten alt", nicht jedoch bei altem Objekt auf neuem Hintergrund), der Effekt in der Cue-Gruppe jedoch für alle drei Bedingungen mit altem Objekt äquivalent auftrat. Dies spricht deutlich für die Annahme, dass der von Tsivilis et al. berichtete Effekt kein Kontexteffekt auf Vertrautheit war, sondern eher ein Vertrautheitseffekt des Kontextes. Des weiteren zeigte sich in Experiment 5 wie bei Tsivilis et al. ein Kontexteffekt auf die Verhaltensdaten, und zwar auch in der Cue-Gruppe. Auffällig war weiterhin, dass die Latenzen in der Cue-Gruppe nicht wie erwartet kürzer, sondern insgesamt sogar länger waren. Die EKP-Daten legten nahe, dass Vertrautheit im System in der Cue-Gruppe zwar in der Tat früher zur Verfügung stand, dass sich die Vpn jedoch scheinbar nicht auf dieses "verkapselte" Signal verließen, sondern versuchten, zusätzlich den Kontext als Abruf-Cue für rekollektive Prozesse zu nutzen. Dementsprechend gab es in den EKP-peak-Latenzen eine signifikante Interaktion derart, dass die Vertrautheitskomponente in der Cue-Gruppe früher, der LPC Effekt jedoch relativ später auftrat, in Einklang mit den verlängerten Reaktionszeiten. Es bleibt festzuhalten, dass der Kongruenzeffekt des Kontextes auf die Performanzdaten jedenfalls mit hoher Wahrscheinlichkeit nicht auf Vertrautheit, sondern auf Rekolektion zurück zu führen ist.

10.3 Diskussion

Die Befunde sind in Einklang mit zentralen Vorhersagen des Type-Token Modells. Allgemeiner formuliert sind wesentliche Ergebnisse dieser Arbeit:

1. Vertrautheit ist unter bestimmten Voraussetzungen perzeptuell spezifisch. Einige Befunde in der Literatur (Curran, 2000; Curran & Cleary,

2003) sprechen dafür, dass perzeptuelle Manipulation Vertrautheit nicht beeinflusst und eher rein konzeptuelle Abgleichprozesse die Grundlage für die Berechnung des Vertrautheitssignals liefern. Diese Befunde waren möglicherweise dadurch bedingt, dass die Veränderungen der Items zu geringfügig waren, um Vertrautheit als eher mäßig sensitiven Prozess zu beeinflussen (Holdstock et al., 2002). Andererseits muss auch im Sinne eines "task-appropriate processing" (TAP; Roediger, Weldon, & Challis, 1989) beim Enkodieren und auch im Test die relevante perzeptuelle Information womöglich einen gewissen Anteil an der Verarbeitung haben (vgl. Curran & Cleary, 2003 vs. Groh-Bordin et al., 2005). Dieses Prinzip ist eingeschränkt (constrained TAP; Ecker et al., 2004) durch die neurokognitive Architektur, d.h., die Daten sprechen für die Modellannahme, dass nur intrinsische Objektmerkmale die Objektvertrautheit beeinflussen, Vertrautheit beinhaltet also "intrinsische Bindungskapazität".

2. Dementsprechend implizieren die Daten dieser Arbeit, dass Vertrautheit ein im wesentlichen kontextinsensitiver Prozess ist. Hier ist jedoch auf die eingeschränkte Gültigkeit aufgrund der hier gewählten Operationalisierung von "Kontext" hinzuweisen. Kontext wurde in dieser Arbeit eher im Sinne einer Figur-Hintergrund Entität behandelt. Natürlich muss Vertrautheit gerade in einem experimentellen Setting insofern kontextsensitiv sein, als dass das Auftreten eines Stimulus' in einem spezifizierten raumzeitlichen "Kontext" (der Lernphase) abgefragt wird. Weiter gibt es Evidenz, dass Vertrautheit in der Tat auch assoziativ sein kann, z.B. reduziert sein kann für rekombinierte Paare von Items (Speer & Curran, submitted; siehe auch Yonelinas et al., 1999; Jäger, Mecklinger, & Kipp, 2006). Voraussetzung für "assoziative Vertrautheit" scheint dabei zu sein, dass die Teilkomponenten leicht zu integrieren sind ("unitisation"), wobei auch andere Faktoren wie wiederholte Darbietung und Einzigartigkeit der Verknüpfung (in der vorliegenden Studie wurden Kontexte immer mit mind. zwei Objekten in Lern- und Testphase präsentiert, was m.E. eine ökologisch validere Konzeptualisierung von "Kontext" ist) zu nennen sind.
3. Vertrautheit ist ein recht automatischer Prozess (jedoch wohl abhängig von einer gewissen Abrufhaltung, vgl. Rugg & Wilding, 2000; Tulving, 1983). Bei gegebenem Anteil perzeptueller Verarbeitung beeinflusst

perzeptuelle Manipulation unwillkürlich die Vertrautheit, auch wenn das Merkmal irrelevant für die Aufgabe ist. Andererseits scheint in der Rekollection nur die perzeptuelle Reizinformation reintegriert zu werden, die für das Lösen der Aufgabe nötig ist, Rekollection ist daher ein kontrollierter und flexibler Prozess. Die breiten frontalen Effekte nach 500 ms post-stimulus-onset in fast allen extrinsischen Bedingungen der vorgestellten Experimente weisen auf Kontroll- und Steuerungsprozesse hin, die für diese flexible Integrationsleistung und entsprechende Entscheidungsprozesse notwendig sind.

4. Im wesentlichen sprechen die Befunde dieser Studie für die Annahme zweier unabhängiger Rekognitionsprozesse. Inwiefern der zweite Prozess dabei als Rekollection verstanden werden kann, hängt nicht unwesentlich von der Definition von Rekollection ab (vgl. Herron & Rugg, 2003), z.B., ob Steuerungs- und Entscheidungsprozesse als integraler Bestandteil der Rekollection verstanden werden. Auch einflussreiche sog. "Ein-Prozess-Modelle" gehen in der Regel nicht von einem isolierten "global matching" Prozess aus, sondern implementieren zusätzliche Parameter und Teilprozesse, so dass die zwei Herangehensweisen nur oberflächlich betrachtet wirklich gegenläufig sind. Die vorliegende Studie legt nahe, dass die episodische Rekognition (ähnlich wie andere höhere kognitive Funktionen wie z.B. die Wahrnehmung, vgl. Brockdorff & Lamberts, 2000) ein iterativer Prozess ist, bei dem im Prinzip unabhängige, aber durch gemeinsamen "Ursprung" (das Enkodieren) verbundene Teilprozesse, die auf z.T. unterschiedlichen Gehirnarealen beruhen, in Wechselwirkung treten. In der Regel werden dabei intrinsische Objektmerkmale vor extrinsischen Kontextmerkmalen evaluiert, wobei eine Zuordnung zu Vertrautheits- und Rekollectionsprozessen, die auf unterschiedlich strukturierte Repräsentationen (Objekttoken vs. episodisches Token im Type-Token Modell) zugreifen, nahe liegt.

11 References

- Aggleton, J. P., & Brown, M. W. (1999). Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. *Behavioral and Brain Sciences*, 22, 425-444.
- Aggleton, J. P., & Shaw, C. (1996). Amnesia and recognition memory: A reanalysis of psychometric data. *Neuropsychologia*, 34, 51-62.
- Alexander, M. P., Stuss, D. T., & Fansabedian, N. (2003). California Verbal Learning Task: Performance by patients with focal frontal and non-frontal lesions. *Brain*, 126, 1493-1503.
- Allen, M. T., Padilla, Y., Myers, C. E., & Gluck, M. A. (2002). Selective hippocampal lesions disrupt a novel cue effect but fail to eliminate blocking in rabbit eyeblink conditioning. *Cognitive, Affective, and Behavioral Neuroscience*, 2, 318-328.
- Asch, S., Ceraso, J., & Heimer, W. (1960). Perceptual conditions of association. *Psychological Monographs*, 74, 1-48.
- Azimian-Faridani, N., & Wilding, E. L. (2006). The influence of criterion shifts on electrophysiological correlates of recognition memory. *Journal of Cognitive Neuroscience*, 18, 1075-1086.
- Baddeley, A., Vargha-Khadem, F., & Mishkin, M. (2001). Preserved recognition in a case of developmental amnesia: implications for the acquisition of semantic memory? *Journal of Cognitive Neuroscience*, 13, 357-369.
- Bar, M. (2004). Visual objects in context. *Nature Reviews Neuroscience*, 5, 617-629.
- Bar, M., & Aminoff, E. (2003). Cortical analysis of visual context. *Neuron*, 38, 347-358.
- Bastin, C., & Van der Linden, M. (2005). Memory for temporal context: Effects of ageing, encoding instructions, and retrieval strategies. *Memory*, 13, 95-109.
- Bayley, P. J., & Squire, L. R. (2002). Medial temporal lobe amnesia: Gradual acquisition of factual information by nondeclarative memory. *Journal of Neuroscience*, 22, 5741-5748.
- Beck, D. M., & Kastner, S. (2005). Stimulus context modulates competition in human extrastriate cortex. *Nature Neuroscience*, 8, 1110-1116.
- Biederman, I., & Cooper, E. E. (1992). Size invariance in visual object priming. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 121-133.
- Bogacz, R., & Brown, M. W. (2003). Comparison of computational models of familiarity discrimination in the perirhinal cortex. *Hippocampus*, 13, 494-524.
- Bogacz, R., Brown, M. W., & Giraud-Carrier, C. (2001). Model of familiarity discrimination in the perirhinal cortex. *Journal of Computational Neuroscience*, 10, 5-23.
- Bowers, J. S., & Schacter, D. L. (1993). Priming of novel information in amnesic patients: Issues and data. In P. Graf, & M. E. J. Masson (Eds.), *Implicit memory: New directions in cognition, development and neuropsychology* (pp. 303-326). Hillsdale, NJ: Erlbaum.
- Brinkmann, T. A., & Ecker, U. K. H. (in preparation). Combined fMRI and intracranial ERP investigation of recognition memory in red versus green gummibears – evidence for triple dissociation between familiarity, novelty, and recollection, or just zero activity? *Neurogelatinia*.

- Brizzolara, D., Casalini, C., & Montanaro, D. (2003). A case of amnesia at an early age. *Cortex*, 39, 605-625.
- Brockdorff, N., & Lamberts, K. (2000). A feature sampling account of the time course of old-new recognition judgments. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 26, 77-102.
- Brown, M. W., & Aggleton, J. P. (2001). Recognition memory: What are the roles of the perirhinal cortex and hippocampus? *Nature Reviews. Neuroscience*, 2, 151-161
- Buckner, R. L., Goodman, J., Burock, M., Rotte, M., Koutstaal, W., Schacter, D., Rosen, B., & Dale, A.M. (1998). Functional-anatomic correlates of object priming in humans revealed by rapid presentation event-related fMRI. *Neuron*, 20, 285-296.
- Buffalo, E. A., Reber, P. J., & Squire, L. R. (1999). The human perirhinal cortex and recognition memory. *Hippocampus*, 8, 330-339.
- Burgess, N., Becker, S., King, J. A., & O'Keefe, J. (2002). Memory for events and their spatial context: Models and experiments. In A. Baddeley, M. A. Conway, & J. P. Aggleton (Eds.), *Episodic memory: New directions in research* (pp. 249-268). London: Oxford University Press.
- Busch, N. A., Groh-Bordin, C., Zimmer, H. D., Herrmann, C. S. (submitted). Modes of memory: performance-dependent electrophysiological repetition suppression and recognition enhancement.
- Cabeza, R. (2006). Prefrontal and medial temporal lobe contributions to relational memory in young and older adults. In H. D. Zimmer, A. Mecklinger, & U. Lindenberger (Eds.), *Handbook of binding and memory: Perspectives from cognitive neuroscience* (pp. 595-626). Oxford: Oxford University Press.
- Cabeza, R., Anderson, N. D., Houle, S., Mangels, J. A., & Newberg, L. (2000). Age-related differences in neural activity during item and temporal-order memory retrieval: A positron emission tomography study. *Journal of Cognitive Neuroscience*, 12, 197-206.
- Cabeza, R., Dolcos, F., Prince, S. E., Rice, H. J., Weissman, D. H., & Nyberg, L. (2003). Attention-related activity during episodic memory retrieval: A cross-function fMRI study. *Neuropsychologia*, 41, 390-399.
- Cansino, S., Maquet, P., Dolan, R. J., & Rugg, M. D. (2002). Brain activity underlying encoding and retrieval of source memory. *Cerebral Cortex*, 12, 1048-1056.
- Cave, K. R., & Kosslyn, S. M. (1989). Varieties of size-specific visual selection. *Journal of Experimental Psychology: General*, 118, 148-164.
- Cave, C. B., & Squire, L. R. (1992). Intact and long-lasting repetition priming in amnesia. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 18, 509-520.
- Cer, D. M. & O'Reilly, R. C. (2006). Neural mechanisms of binding in the hippocampus and neocortex: Insights from computational models. In H. D. Zimmer, A. Mecklinger, & U. Lindenberger (Eds.), *Handbook of binding and memory: Perspectives from cognitive neuroscience* (pp. 193-220). Oxford: Oxford University Press.
- Ceraso, J. (1985). Unit formation in perception and memory. *The Psychology of Learning & Motivation*, 19, 179-210.
- Ceraso, J. (1990). Perceptual organization affects both the learning and integration of object properties. In I. Rock (Ed.), *The Legacy of Solomon Asch: Essays in Cognition and Social Psychology* (pp. 113-125). Hillsdale, NJ: Lawrence Erlbaum.

- Chun, M. M. & Phelps, E. A. (1999). Memory deficits for implicit contextual information in amnesic subjects with hippocampal damage. *Nature Neuroscience*, 2, 844-847.
- Clark, S. E., & Gronlund, S. D. (1996). Global matching models of recognition memory: How the models match the data. *Psychonomic Bulletin & Review*, 3, 37-60.
- Cooper, E. E., Biederman, I., & Hummel, J. E. (1992). Metric invariance in object recognition: A review and further evidence. *Canadian Journal of Psychology*, 46, 191-214.
- Corbetta, M., & Miezin, F. M. (1990). Attentional modulation of neural processing of shape, color, and velocity in humans. *Science*, 248, 1556-1559.
- Crottaz-Herbette, S., & Menon, V. (2006). Where and when the Anterior Cingulate Cortex modulates attentional response: Combined fMRI and ERP evidence. *Journal of Cognitive Neuroscience*, 18, 766-780.
- Curran, T. (2000). Brain potentials of recollection and familiarity. *Memory & Cognition*, 28, 923-938.
- Curran, T. (2004). Effects of attention and confidence on the hypothesized ERP correlates of recollection and familiarity. *Neuropsychologia*, 42, 1088-1106.
- Curran, T., & Cleary, A. M. (2003). Using ERPs to dissociate recollection from familiarity in picture recognition. *Cognitive Brain Research*, 15, 191-205.
- Curran, T., DeBuse, C., & Leynes, P. A. (2007). Conflict and criterion setting in recognition memory. *Journal of Experimental Psychology: Learning Memory and Cognition*, 33, 2-17.
- Curran, T., DeBuse, C., Woroch, B., & Hirshman, E. (2006). Combined pharmacological and electrophysiological dissociation of familiarity and recollection. *Journal of Neuroscience*, 26, 1979-1985.
- Curran, T., & Dien, J. (2003). Differentiating amodal familiarity from modality-specific memory processes: An ERP study. *Psychophysiology*, 40, 979-988.
- Curran, T., & Friedman, W. J. (2003). Differentiating location- and distance-based processes in memory for time: An ERP study. *Psychonomic Bulletin & Review*, 10, 711-717.
- Curran, T., & Friedman, W. J. (2004). ERP old/new effects at different retention intervals in recency discrimination tasks. *Cognitive Brain Research*, 18, 107-120.
- Curran, T. & Schacter, D. L. (1997). Implicit memory: What must theories of amnesia explain? *Memory*, 5, 37-47.
- Curran, T., Tanaka, J. W., & Weiskopf, D. M. (2002). An electrophysiological comparison of visual categorization and recognition memory. *Cognitive, Affective, & Behavioral Neuroscience*, 2, 1-18.
- Curran, T., Tepe, K. L., & Piatt, C. (2006). ERP explorations of dual processes in recognition memory. In H. D. Zimmer, A. Mecklinger, & U. Lindenberger (Eds.), *Handbook of binding and memory: Perspectives from cognitive neuroscience* (pp. 467-492). Oxford: Oxford University Press.
- Cycowicz, Y. M., & Friedman, D. (2003). Source memory for the color of pictures: Event-related brain potentials (ERPs) reveal sensory-specific retrieval-related activity. *Psychophysiology*, 40, 455-464.
- Cycowicz, Y. M., Friedman, D., & Snodgrass, J. G. (2001). Remembering the color of objects: An ERP investigation of source memory. *Cerebral Cortex*, 11, 322-334.

- Damasio, A. R. (1989). Time-locked multiregional retroactivation: A system-level proposal for the neuronal substrates of recall and recognition. *Cognition*, 33, 25-62.
- Damasio, H., Grabowski, T. J., Tranel, D., Hichwa, R. D., & Damasio, A. R. (1996). A neural basis for lexical decision. *Nature*, 380, 499-505.
- Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2006). Triple dissociation in the medial temporal lobes: Recollection, familiarity, and novelty. *Journal of Neurophysiology*, 96, 1902-1911.
- Davachi, L., Mitchell, J. P., & Wagner, A. D. (2003). Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 2157-2162.
- Dennis, S., & Humphreys, M. S. (2001). A context noise model of episodic word recognition. *Psychological Review*, 108, 452-478.
- Dewhurst, S. A., Holmes, S. J., Brandt, K. R., & Dean, G. M. (2006). Measuring the speed of the conscious components of recognition memory: Remembering is faster than knowing. *Consciousness and Cognition*, 15, 147-162.
- Diana, R. A., Peterson, M. J., & Reder, L. M. (2004). The role of spurious feature familiarity in recognition memory. *Psychonomic Bulletin & Review*, 11, 150-156.
- Diana, R. A., & Reder, L. M. (2005). The list strength effect: a contextual competition account. *Memory & cognition*, 33, 1289-1302.
- Diana, R. A., Reder, L. M., Arndt, J., & Park, H. (2006). Models of recognition: A review of arguments in favor of a dual-process account. *Psychonomic Bulletin and Review*, 13, 1-21.
- Dien, J., & Santuzzi, A. M. (2005). Application of repeated measures ANOVA to high-density ERP datasets: A review and tutorial. In T. C. Handy (Ed.), *Event-related potentials: A methods handbook* (pp. 33-56). Cambridge: MIT Press.
- Dobbins, I. G., Kroll, N. E., & Yonelinas, A. P. (2004). Dissociating familiarity and recollection using rote rehearsal. *Memory & Cognition*, 32, 932-944.
- Donaldson, D. I., & Rugg, M. D. (1999). Event-related potential studies of associative recognition and recall: Electrophysiological evidence for context dependent retrieval processes. *Cognitive Brain Research*, 8, 1-16.
- Dosher, B. A., McElree, B., Hood, R. M., & Rosedale, G. (1989). Retrieval dynamics of priming in recognition memory: Bias and discrimination analysis. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 15, 868-886.
- Dosher, B. A., & Rosedale, G. (1991). Judgments of semantic and episodic relatedness: Common time-course and failure of segregation. *Journal of Memory and Language*, 30, 125-160.
- Düzel, E., Cabeza, R., Picton, T. W., Yonelinas, A. P., Scheich, H., Heinze, H. J., & Tulving, E. (1999). Task-related and item-related brain processes of memory retrieval. *Proceedings of the National Academy of Sciences of the United States of America*, 96, 1794-1799.
- Düzel, E., Habib, R., Guderian, S., & Heinze, H. J. (2004). Four types of novelty-familiarity responses in associative recognition memory of humans. *European Journal of Neuroscience*, 19, 1408-1416.
- Düzel, E., Habib, R., Rotte, M., Guderian, S., Tulving, E., & Heinze, H. J. (2003). Human hippocampal and parahippocampal activity during visual associative recognition memory for spatial and nonspatial stimulus configurations. *Journal of Neuroscience*, 23, 9439-9444.

- Düzel, E., Vargha-Khadem, F., Heinze, H. J., & Mishkin, M. (2001). Brain activity evidence for recognition without recollection after early hippocampal damage. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 8101-8106.
- Düzel, E., Yonelinas, A. P., Mangun, G. R., Heinze, H. J., & Tulving, E. (1997). Event-related brain potential correlates of two states of conscious awareness in memory. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 5973-5978.
- Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General*, 113, 501-517.
- Duncan, J., Martens, S., & Ward, R. (1997). Restricted attentional capacity within but not between sensory modalities. *Nature*, 387, 808-810.
- Duncan, J., & Nimmo-Smith, I. (1996). Objects and attributes in divided attention: Surface and boundary systems. *Perception & Psychophysics*, 58, 1076-1084.
- Dunn, J. C. (2004). Remember-Know: A matter of confidence. *Psychological Review*, 111, 524-542.
- Dunn, J. C., & Dennis, S. (submitted). Separating the brain regions involved in recollection and familiarity in recognition memory: A comment on Yonelinas, Otten, Shaw & Rugg (2005).
- Dusek, J. A., & Eichenbaum, H. (1997). The hippocampus and memory for orderly stimulus relations. *PNAS*, 94, 7109-7114.
- Ecker, U. K. H. (2002). Implicit colour-congruency effects in object priming – a study on token construction in amnesics. Unpublished master thesis, Saarland University, Saarbruecken.
- Ecker, U. K. H., Groh-Bordin, C., & Zimmer, H. D. (2004). Electrophysiological correlates of specific feature binding in remembering – Introducing a neurocognitive model of human memory. In A. Mecklinger, H. D. Zimmer, & U. Lindenberger (Eds.), *Bound in Memory – Insights from Behavioral and Neuropsychological Studies* (pp.159-193). Aachen, Germany: Shaker.
- Ecker, U. K. H., Zimmer, H. D., & Groh-Bordin, C. (in press). Color and context: An ERP study on intrinsic and extrinsic feature binding in episodic memory. *Memory & Cognition*.
- Ecker, U. K. H., Zimmer, H. D., & Groh-Bordin, C. (under revision). The influence of object and background color manipulations on the electrophysiological indices of recognition memory. *Brain Research*.
- Ecker, U. K. H., Zimmer, H. D., Groh-Bordin, C., & Mecklinger, A. (2007). Context effects on familiarity are familiarity effects of context – An electrophysiological study. *International Journal of Psychophysiology*, 64, 146-156.
- Eichenbaum, H. (2006). Mechanisms of relational representation. In H. D. Zimmer, A. Mecklinger, & U. Lindenberger (Eds.), *Handbook of binding and memory: Perspectives from cognitive neuroscience* (pp. 25-52). Oxford: Oxford University Press.
- Eldridge, L. L., Knowlton, B. J., Furmanski, C. S., Bookheimer, S. Y., & Engel, S. A. (2000). Remembering episodes: A selective role for the hippocampus during retrieval. *Nature Neuroscience*, 3, 1149-1152.
- Elger, C. E., Grunwald, T., Lehnertz, K., Kutas, M., Helmstaedter, C., Brockhaus, A., Van Roost, D., & Heinze, H. J. (1997). Human temporal lobe potentials in verbal learning and memory processes. *Neuropsychologia*, 35, 657-667.

- Elman, J. L., Bates, E. A., Johnson, M. H., Karmiloff-Smith, A., Parisi, D., & Plunkett, K. (1996). Rethinking innateness – A connectionist perspective on development. Cambridge, MA: MIT Press.
- Engelkamp, J., & Zimmer, H. D. (1994). The human memory: A multimodal approach. Seattle, WA: Hogrefe & Huber.
- Engelkamp, J., & Zimmer, H. D. (2006). Lehrbuch der Kognitiven Psychologie. Göttingen, Germany: Hogrefe.
- Engelkamp, J., Zimmer, H. D., & de Vega, M. (2001). Pictures and words in memory: The role of visual-imaginal information. In M. Denis, C. Cornoldi, R. H. Logie, M. de Vega & J. Engelkamp (Eds.), *Imagery, language and visuo-spatial thinking* (pp. 59-80). Hove: Psychology Press.
- Estes, W. K. (1994). *Classification and cognition*. Oxford: Oxford University Press.
- Fan, J., Snodgrass, J. G., & Bilder, R. M. (2003). Functional magnetic resonance imaging of source versus item memory. *Neuroreport*, 17, 2275-2281.
- Faw, B. (2003). Pre-frontal executive committee for perception, working memory, attention, long-term memory, motor control, and thinking: A tutorial review. *Consciousness and Cognition*, 12, 83-139.
- Fell, J., Fernández, G., Klaver, P., Axmacher, N., Mormann, F., Haupt, S., & Elger, C. E. (2006). Rhinal-hippocampal coupling during declarative memory formation: Dependence on item characteristics. *Neuroscience Letters*, 407, 37-41.
- Fell, J., Klaver, P., Lehnertz, K., Grunwald, T., Schaller, C., Elger, C. E., & Fernández, G. (2001). Human memory formation is accompanied by rhinal-hippocampal coupling and decoupling. *Nature Neuroscience*, 4, 1259-1264.
- Fernández, G., Effern, A., Grunwald, T., Pezer, N., Lehnertz, K., Dümpelmann, M., Van Roost, D., & Elger, C. E. (1999). Real-time tracking of memory formation in the human rhinal cortex and hippocampus. *Science*, 285, 1582-1585.
- Fernández, G., Klaver, P., Fell, J., Grunwald, T., & Elger, C. E. (2002). Human declarative memory formation: Segregating rhinal and hippocampal contributions. *Hippocampus*, 12, 514-519.
- Fernández, G., & Tendolkar, I. (2006). The rhinal cortex: 'gatekeeper' of the declarative memory system. *Trends in Cognitive Sciences*, 10, 358-362.
- Finnigan, S., Humphreys, M. S., Dennis, S., & Geffen, G. (2002). ERP 'old/new' effects: Memory strength and decisional factor(s). *Neuropsychologia*, 40, 2288-2304.
- Foster, J. K. (2003). Editorial. Special issue on memory: Anatomical regions, physiological networks and cognitive interactions. *Cortex*, 39, 555-565.
- Friedman, D., Cycowicz, Y. M., & Bersick, M. (2005). The late negative episodic memory effect: The effect of recapitulating study details at test. *Cognitive Brain Research*, 23, 185-198.
- Friedman, D., Cycowicz, Y. M., & Gaeta, H. (2001). The novelty P3: An event-related brain potential (ERP) sign of the brain's evaluation of novelty. *Neuroscience and Biobehavioral Reviews*, 25, 355-373.
- Friedman, D., & Johnson, R. Jr. (2000). Event-related potential (ERP) studies of memory encoding and retrieval: A selective review. *Microscopy Research and Technique*, 51, 6-28.

- Gabrieli, J. D. E., Fleischman, D. A., Keane, M. M., Reminger, S. L., & Morell, F. (1995). Double dissociation between memory systems underlying explicit and implicit memory in the human brain. *Psychological Science*, 6, 76-82.
- Gardiner, J. M., Java, R. I., & Richardson-Klavehn, A. (1996). How level of processing really influences awareness in recognition memory. *Canadian Journal of Experimental Psychology*, 50, 114-122.
- Garner, W. R. (1974). *The processing of information and structure*. Potomac, MD: Lawrence Erlbaum.
- Gevins, A., Cutillo, B., Du Rousseau, D., Le, J., Leong, H., & Smith, M. (1994). High-resolution evoked potential technology for imaging neural networks of cognition. In R. W. Thatcher, M. Hallett, T. A. Zeffiro, E. R. John, M. Huerta (Eds.), *Functional Neuroimaging: Technical Foundations* (pp. 223-231). San Diego, CA: Academic Press.
- Gillund, G., & Shiffrin, R. M. (1984). A retrieval model for both recognition and recall. *Psychological Review*, 91, 1-67.
- Giovanello, K. S., Schnyer, D. M., & Verfaellie, M. (2004). A critical role for the anterior hippocampus in relational memory: Evidence from an fMRI study comparing associative and item recognition. *Hippocampus*, 14, 5-8.
- Godden, D., & Baddeley, A. (1980). When does context influence recognition memory? *British Journal of Psychology*, 71, 99-104.
- Goodale, M. A., & Humphrey, G. K. (1998). The objects of action and perception. *Cognition*, 67, 181-207.
- Gooding, P. A., Mayes, A. R., & Meudell, P. R. (1997). Indirect memory performance is not sensitive to a shift of local context. *European Journal of Cognitive Psychology*, 9, 289-312.
- Graham, K. S., Simons, J. S., Pratt, K. H., Patterson, K., & Hodges, J. R. (2000). Insights from semantic dementia on the relationship between episodic and semantic memory. *Neuropsychologia*, 38, 313-324.
- Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, 55, 468-484.
- Greenhouse, W. W., & Geisser, S. (1959). On methods in the analysis of profile data. *Psychometrika*, 24, 95-112.
- Groh-Bordin, C., Zimmer, H. D., & Ecker, U. K. H. (2006). Has the butcher on the bus dyed his hair? When color changes modulate ERP correlates of familiarity and recollection. *NeuroImage*, 32, 1879-1890.
- Groh-Bordin, C., Zimmer, H. D., & Ecker, U.K.H. (in preparation). A rose is not a rose is not a rose: Electrophysiological correlates of exemplar-specific processes in implicit and explicit memory.
- Groh-Bordin, C., Zimmer, H. D., & Mecklinger, A. (2005). Feature binding in perceptual priming and in episodic object recognition: Evidence from event-related brain potentials. *Cognitive Brain Research*, 24, 556-567.
- Gronlund, S. D., & Ratcliff, R. (1989). Time course of item and associative information: Implications for global memory models. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 15, 846-858.

- Grunwald, T., Beck, H., Lehnertz, K., Blümcke, I., Pezer, N., Kurthen, M., Fernández, G., Van Roost, D., Heinze, H. J., Kutas, M., & Elger, C. E. (1999). Evidence relating human verbal memory to hippocampal N-methyl-D-aspartate receptors. *Proceedings of the National Academy of Sciences of the United States of America*, 96, 12085-12089.
- Grunwald, T., & Kurthen, M. (2006). Novelty detection and encoding for declarative memory within the human hippocampus. *Clinical EEG and Neuroscience*, 37, 309-314.
- Guillaume, F., & Tiberghien, G. (2001). An event-related potential study of contextual modifications in a face recognition task. *NeuroReport*, 12, 1209-1216.
- Guillem, F., Bicu, M., & Debruille, J. B. (2001). Dissociating memory processes involved in direct and indirect tests with ERPs to unfamiliar faces. *Cognitive Brain Research*, 11, 113-125.
- Guo, C., Voss, J. L., & Paller, K. A. (2005). Electrophysiological correlates of forming memories for faces, names, and face-name associations. *Cognitive Brain Research*, 22, 153-164.
- Habib, R. (2001). On the relation between conceptual priming, neural priming, and novelty assessment. *Scandinavian Journal of Psychology*, 42, 187-195.
- Hahn, B., Ross, T. J., & Stein, E. A. (2006). Neuroanatomical dissociation between bottom-up and top-down processes of visuospatial attention. *NeuroImage*, 32, 842-853.
- Hamann, S. B., & Squire, L. R. (1995). On the acquisition of new declarative knowledge in amnesia. *Behavioral Neuroscience*, 109, 1027-1044.
- Handy, T. C. (Ed.) (2005). *Event-related potentials – A methods handbook*. Cambridge, MA: MIT Press.
- Hannesson, D. K., Vacca, G., Howland, J. G., & Phillips, A. G. (2003). Medial prefrontal cortex is involved in spatial temporal order memory but not spatial recognition memory in tests relying on spontaneous exploration in rats. *Behavioural Brain Research*, 153, 273-285.
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, 293, 2425-2430.
- Hayman, C. A. G., & Rickards, C. (1995). A dissociation in the effects of study modality on tests of implicit and explicit memory. *Memory & Cognition*, 23, 95-112.
- Heit, E., Brockdorff, N., & Lamberts, K. (2003). Adaptive changes of response criterion in recognition memory. *Psychonomic Bulletin and Review*, 10, 718-723.
- Henson, R. N. A., Cansino, S., Herron, J. E., Robb, W. G. K., & Rugg, M. D. (2003). A familiarity signal in human anterior medial temporal cortex? *Hippocampus*, 13, 301-304.
- Henson, R. N. A., Hornberger, M., & Rugg, M. D. (2005). Further dissociating the processes involved in recognition memory: An fMRI study. *Journal of Cognitive Neuroscience*, 17, 1058-1073.
- Henson, R. N. A., Rugg, M. D., Shallice, T., Josephs, O., & Dolan, R. J. (1999). Recollection and familiarity in recognition memory: An event-related functional magnetic resonance imaging study. *Journal of Neuroscience*, 19, 3962-3972.
- Henson, R. N. A., Shallice, T., Gorno-Tempini, M. L., & Dolan, R. J. (2002). Face repetition effects in implicit and explicit memory tests as measured by fMRI. *Cerebral Cortex*, 12, 178-186.
- Herrmann, C. S., Mecklinger, A., & Pfeifer, E. (1999). Gamma responses and ERPs in a visual classification task. *Clinical Neurophysiology*, 110, 636-642.

- Herrmann, C. S., Munk, M. H. J., & Engel, A. K. (2004). Cognitive functions of gamma-band activity: memory match and utilization. *Trends in Cognitive Science*, 8, 347-355.
- Herron, J. E., Quayle, A. H., & Rugg, M. D. (2003). Probability effects on event-related potential correlates of recognition memory. *Cognitive Brain Research*, 16, 66-73.
- Herron, J. E., & Rugg, M. D. (2003). Strategic influences on recollection in the exclusion task: Electrophysiological evidence. *Psychonomic Bulletin & Review*, 10, 703-710.
- Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of Cognitive Neuroscience*, 18, 604-613.
- Hintzman, D. L., & Curran, T. (1994). Retrieval dynamics of recognition and frequency judgments: Evidence for separate processes of familiarity and recall. *Journal of Memory and Language*, 33, 1-18.
- Hodges, J. R., Graham, K. S. (2002). Episodic memory: Insights from semantic dementia. In A. Baddeley, M. A. Conway, & J. P. Aggleton (Eds.), *Episodic memory: New directions in research* (pp. 132-152). London: Oxford University Press.
- Hölscher, C., Rolls, E. T., & Xiang, J. (2003). Perirhinal cortex neuronal activity related to long-term familiarity memory in the macaque. *European Journal of Neuroscience*, 18, 2037-2046.
- Holdstock, J. S. (2005). The role of the human medial temporal lobe in object recognition and object discrimination. *Quarterly Journal of Experimental Psychology B: Comparative and Physiological Psychology*, 58, 326-339.
- Holdstock, J. S., Mayes, A. R., Roberts, N., Cezayirli, E., Isaac, C. L., O'Reilly, R. C., & Norman, K. A. (2002). Under what conditions is recognition spared relative to recall after selective hippocampal damage in humans? *Hippocampus*, 12, 341-351.
- Holm, S. (1979). A simple sequential rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6, 65-70.
- Humphreys, M. S., Bain, J. D., Burt, J. S. (1989). Episodically unique and generalized memories: Applications to human and animal amnesics. In S. Lewandowsky, J. C. Dunn, & K. Kirsner, *Implicit memory: Theoretical issues*. (pp. 139-156). Hillsdale: Lawrence Erlbaum Associates.
- Humphreys, M. S., Bain, J. D., & Pike, R. (1989). Different ways to cue a coherent memory system: A theory for episodic, semantic, and procedural tasks. *Psychological Review*, 96, 208-233.
- Humphreys, M. S., Dennis, S., Chalmers, K. A., & Finnigan, S. (2000). Dual processes in recognition: Does a focus on measurement operations provide a sufficient foundation? *Psychonomic Bulletin & Review*, 7, 593-603.
- Humphreys, M. S., Dennis, S., Maguire, A. M., Reynolds, K., Bolland, S. W., & Hughes, J. D. (2003). What you get out of memory depends on the question you ask. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 29, 797-812.
- Jacoby, L. L., & Dallas, M. (1981). On the relationship between autobiographical memory and perceptual learning. *Journal of Experimental Psychology: General*, 110, 306-340.
- Jacoby, L. L., & Hay, J. F. (1998). Age-related deficits in memory: Theory and application. In M. A. Conway, S. E. Gathercole, & C. Cornoldi (Eds.), *Theories of memory* (Vol. II, pp. 111-134). Psychology Press.
- Jäger, T., Mecklinger, A., & Kipp, K. H. (2006). Intra- and inter-item associations doubly dissociate the electrophysiological correlates of familiarity and recollection. *Neuron*, 52, 535-545.

- Janowsky, J. S., Shimamura, A. P., & Squire, L. R. (1989). Source memory impairment in patients with frontal lobe lesions. *Neuropsychologia*, 27, 1043-1056.
- Johansson, M., & Mecklinger, A. (2003). The late posterior negativity in ERP studies of episodic memory: Action monitoring and retrieval of attribute conjunctions. *Biological Psychology*, 64, 91-117.
- Johnson, M. K., & Chalfonte, B. L. (1994). Binding complex memories: The role of reactivation and the hippocampus. In D. L. Schacter & E. Tulving (Eds.), *Memory Systems 1994*. Cambridge, MA: MIT Press.
- Johnson, R. Jr., Kreiter, K., Russo, B., & Zhu, J. (1998). A spatio-temporal analysis of recognition-related event-related brain potentials. *International Journal of Psychophysiology*, 29, 83-104.
- Jolicoeur, P. (1987). A size congruency effect in memory for visual shape. *Memory & Cognition*, 15, 531-543.
- Jolicoeur, P., Sessa, P., Dell'Acqua, R., & Robitaille, N. (2006). Attentional control and capture in the attentional blink paradigm: Evidence from human electrophysiology. *European Journal of Cognitive Psychology*, 18, 560-578.
- Jones, T. C. (2005). Study repetition and the rejection of conjunction lures. *Memory*, 13, 499-515.
- Kassam, K. S., Aminoff, E., & Bar, M. (2003). Spatial-temporal cortical processing of contextual associations. *Society of Neuroscience Abstracts*, 28, 8.
- Kellenbach, M. L., Brett, M., & Patterson, K. (2001). Large, colorful, or noisy? Attribute- and modality-specific activations during retrieval of perceptual attribute knowledge. *Cognitive, Affective and Behavioral Neuroscience*, 1, 207-221.
- Kelley, C. M., Jacoby, L. L., & Hollingshead, A. (1989). Direct versus indirect tests of memory for source: Judgments of modality. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 15, 1101-1108.
- Kent, C., & Lamberts, K. (2006). Modeling the time course of feature perception and feature information retrieval. *Journal of Memory and Language*, 55, 553-571.
- Kesner, R. P., & Holbrook, T. (1987). Dissociation of item and order spatial memory in rats following medial prefrontal cortex lesions. *Neuropsychologia*, 25, 653-664.
- Kimura, M., Katayama, J., & Murohashi, H. (2006). An ERP study of visual change detection: Effects of magnitude of spatial frequency changes on the change-related posterior positivity. *International Journal of Psychophysiology*, 62, 14-23.
- Kinoshita, S., & Wayland, S. V. (1993). Effects of surface features on word-fragment completion in amnesic subjects. *American Journal of Psychology*, 106, 67-80.
- Kirchoff, B. A., Wagner, A. D., Maril, A., & Stern, C. E. (2000). Prefrontal circuitry for episodic encoding and subsequent memory. *Journal of Neuroscience*, 20, 6173-6180.
- Kirsner, K. (1974). Modality differences in recognition memory for words and their attributes. *Journal of Experimental Psychology*, 102, 579-584.
- Klimesch, W., Doppelmayr, M., Yonelinas, A., Kroll, N. E. A., Lazzara, M., Roehm, D., & Gruber, W. (2001). Theta synchronization during episodic retrieval: Neural correlates of conscious awareness. *Cognitive Brain Research*, 12, 33-38.
- Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews*, 53, 63-88.

- Koutstaal, W. (2006). Flexible remembering. *Psychonomic Bulletin & Review*, 13, 84-91.
- Kroll, N. E. A., Knight, R. T., Metcalfe, J., Wolf, E. S., & Tulving, E. (1996). Cohesion failure as a source of memory illusions. *Journal of Memory and Language*, 35, 176-196.
- Lamberts, K. (1998). The time course of categorization. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 24, 695-711.
- Lamberts, K., Brockdorff, N., & Heit, E. (2002). Perceptual processes in matching and recognition of complex pictures. *Journal of Experimental Psychology: Human Perception & Performance*, 28, 1176-1191.
- Lampinen, J. M., Odegard, T. N., & Neuschatz, J. S. (2004). Robust recollection rejection in the memory conjunction paradigm. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 30, 332-342.
- Leichnetz, G. R., & Astruc, J. (1975). Preliminary evidence for a direct projection of the prefrontal cortex to the hippocampus in the squirrel monkey. *Brain, Behavior and Evolution*, 11, 355-364.
- Lepage, M., Ghaffar, O., Nyberg, L., & Tulving, E. (2000). Prefrontal cortex and episodic memory retrieval mode. *Proceedings of the National Academy of Sciences of the United States of America*, 97, 506-511.
- Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, 24, 740-749.
- Loftus, G. R., & McLean, J. E. (1999). A front end to a theory of picture recognition. *Psychonomic Bulletin & Review*, 6, 394-411.
- Luck, S. J., & Hillyard, S. A. (1994). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, 31, 291-308.
- Luck, S. J., Vogel, E. K., & Shapiro, K. L. (1996). Word meanings can be accessed but not reported during the attentional blink. *Nature*, 383, 616-618.
- Maguire, E. A., Mummery, C. J., & Büchel, C. (2000). Patterns of hippocampal-cortical interaction dissociate temporal lobe memory systems. *Hippocampus*, 10, 475-482.
- Mandler, G. (1980). Recognizing: The judgment of previous occurrence. *Psychological Review*, 87, 252-271.
- Mayes, A. R., Holdstock, J. S., Isaac, C. L., Hunkin, N. M., & Roberts, N. (2002). Relative sparing of item recognition memory in a patient with adult-onset damage limited to the hippocampus. *Hippocampus*, 12, 325-340.
- Mayes, A. R., Holdstock, J. S., Isaac, C. L., Montaldi, D., Grigor, J., Gummer, A., Cariga, P., Downes, J. J., Tsivilis, D., Gaffan, D., Gong, Q., & Norman, K. A. (2004). Associative recognition in a patient with selective hippocampal lesions and relatively normal item recognition. *Hippocampus*, 14, 763-784.
- Mayes, A. R., Isaac, C. L., Downes, J. J., Holdstock, J. S., Hunkin, N. M., Montaldi, D., Downes, J. J., MacDonald, C., Cezayirli, E., & Roberts, J. N. (2001). Memory for single items, word pairs, and temporal order of different kinds in a patient with selective hippocampal lesions. *Cognitive Neuropsychology*, 18, 97-123.
- McCarthy, R. A., & Warrington, E. K. (1990). *Cognitive neuropsychology – A clinical introduction*. San Diego, CA: Academic Press.

- McCarthy, G., & Wood, C. C. (1985). Scalp distributions of event-related potentials: an ambiguity associated with analysis of variance models. *Electroencephalography & Clinical Neurophysiology*, 62, 203-208.
- McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychological Review*, 102, 419-457.
- McElree, B., Dolan, P. O., & Jacoby, L. L. (1999). Isolating the contributions of familiarity and source information to item recognition: A time course analysis. *Journal of Experimental Psychology: Learning Memory, & Cognition*, 25, 563-582.
- McKenna, P., & Gerhand, S. (2002). Preserved semantic learning in an amnesic patient. *Cortex*, 38, 37-58.
- McKenzie, W. A., & Tiberghien, G. (2004). Context effects in recognition memory: The role of familiarity and recollection. *Consciousness and Cognition*, 13, 20-38.
- McKone, E., & French, B. (2001). In what sense is implicit memory 'episodic'? The effect of reinstating environmental context. *Psychonomic Bulletin & Review*, 8, 806-811.
- Mecklinger, A. (1998). On the modularity of recognition memory for object form and spatial location. *Neuropsychologia*, 36, 441-460.
- Mecklinger, A. (2000). Interfacing mind and brain: A neurocognitive model of recognition memory. *Psychophysiology*, 37, 565-582.
- Mecklinger, A. (2006). Electrophysiological measures of familiarity memory. *Clinical EEG & Neuroscience*, 37, 292-299.
- Mecklinger, A. (2007). Elektrophysiologie des Wiedererkennens. In T. Goschke, & M. Eimer (Eds.), *Kognitive Neurowissenschaften. Enzyklopädie der Psychologie, Serie II, Band 5*. Göttingen, Germany: Hogrefe.
- Mecklinger, A., & Pfeifer, E. (1996). Event-related potentials reveal topographical and temporal distinct neuronal activation patterns for spatial and object working memory. *Cognitive Brain Research*, 4, 211-224.
- Meeter, M., Myers, C. E., & Gluck, M. A. (2005). Integrating incremental learning and episodic memory models of the hippocampal region. *Psychological Review*, 112, 560-585.
- Meiser, T., & Bröder, A. (2002). Memory for multidimensional source information. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 28, 116-137.
- Meiser, T., & Sattler, C. (2007). Boundaries of the relation between conscious recollection and source memory for perceptual details. *Consciousness and Cognition*, 16, 189-210.
- Meiser, T., & Sattler, C. (submitted). Binding of multidimensional context information as a distinctive characteristic of conscious recollection.
- Morcom, A. M., & Rugg, M. D. (2002). Getting ready to remember: The neural correlates of task set during recognition memory. *Neuroreport*, 13, 149-152.
- Mormann, F., Fell, J., Axmacher, N., Weber, B., Lehnertz, K., Elger, C. E., & Fernández, G. (2005). Phase/amplitude reset and theta-gamma interaction in the human medial temporal lobe during a continuous word recognition memory task. *Hippocampus*, 15, 890-900.
- Moscovitch, M. (1992). Memory and working-with-memory: A component process model based on modules and central systems. *Journal of Cognitive Neuroscience*, 4, 257-267.

- Müller, N. G., Bartelt, O. A., Donner, T. H., Villringer, A., & Brandt, S. A. (2003). A physiological correlate of the "zoom lens" of visual attention. *Journal of Neuroscience*, 23, 3561-3565.
- Mumby, D. G., Gaskin, S., Glenn, M. J., Schramek, T. E., & Lehmann, H. (2002). Hippocampal damage and exploratory preferences in rats: Memory for objects, places, and contexts. *Learning and Memory*, 9, 49-57.
- Murdock, B. B. (1982). A theory for the storage and retrieval of item and associative information. *Psychological Review*, 89, 609-626.
- Murnane, K., & Phelps, M. P. (1993). A global activation approach to the effect of changes in environmental context on recognition. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 19, 882-894.
- Murnane, K., & Phelps, M. P. (1994). When does a different environmental context make a difference in recognition? A global activation model. *Memory & Cognition*, 22, 584-590.
- Murnane, K., Phelps, M. P., & Malmberg, K. (1999). Context-dependent recognition memory: The ICE theory. *Journal of Experimental Psychology: General*, 128, 403-415.
- Murre, J. (1999). Interaction of cortex and hippocampus in a model of amnesia and semantic dementia. *Reviews of Neuroscience*, 10, 267-278.
- Musen, G., & Squire, L. R. (1993). On the implicit learning of novel associations by amnesic patients and normal subjects. *Neuropsychology*, 7, 119-135.
- Naveh-Benjamin, M. (2000). Adult age differences in memory performance: Tests of an associative deficit hypothesis. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 26, 1170-1187.
- Naveh-Benjamin, M. (2006). Binding of memories: Adult-age differences and the effects of divided attention in young adults on episodic memory. In H. D. Zimmer, A. Mecklinger, & U. Lindenberger (Eds.), *Handbook of binding and memory: Perspectives from cognitive neuroscience* (pp. 627-656). Oxford: Oxford University Press.
- Nessler, D., Friedman, D., & Bersick, M. (2004). Classic and false memory designs: An electrophysiological comparison. *Psychophysiology*, 41, 679-687.
- Nessler, D., & Mecklinger, A. (2003). ERP correlates of true and false recognition after different retention delays: Stimulus and response related processes. *Psychophysiology*, 40, 1-14.
- Nessler, D., Mecklinger, A., & Penney, T.B. (2005). Perceptual fluency, semantic familiarity, and recognition-related familiarity: An electrophysiological exploration. *Cognitive Brain Research*, 22-2, 265-288.
- Norman, G., & Eacott, M. J. (2005). Dissociable effects of lesions to the perirhinal cortex and the postrhinal cortex on memory for context and objects in rats. *Behavioral Neuroscience*, 119, 557-566.
- Norman, K. A., & O'Reilly, R. C. (2003). Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. *Psychological Review*, 110, 611-646.
- Nosofsky, R. M. (1988). Exemplar-based accounts of relations between classification, recognition, and typicality. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 14, 700-708.

- Nosofsky, R. M. (1991). Tests of an exemplar model for relating perceptual classification and recognition memory. *Journal of Experimental Psychology: Human Perception & Performance*, 17, 3-27.
- Nosofsky, R. M., & Zaki, S. R. (1998). Dissociations between categorization and recognition in amnesic and normal individuals: An exemplar-based interpretation. *Psychological Science*, 9, 247-255.
- Nyberg, L. (2002). Levels of processing: A view from functional brain imaging. *Memory*, 10, 345-348.
- Nyberg, L., McIntosh, A. R., Cabeza, R., Habib, R., Houle, S., & Tulving, E. (1996). General and specific brain regions volved in encoding and retrieval of events: What, where and when. *Proceedings of the National Academy of Sciences of the United States of America*, 93, 11280-11285.
- O'Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature*, 401, 584-587.
- Ogden, J. A. (1993). Visual object agnosia, prosopagnosia, achromatopsia, loss of visual imagery, and autobiographical amnesia following recovery from cortical blindness: Case M.H. *Neuropsychologia*, 31, 571-589.
- Olson, I. R., Chun, M. M., & Allison, T. (2001). Contextual guidance of attention: Human intracranial event-related potential evidence for feedback modulation in anatomically early temporally late stages of visual processing. *Brain*, 124, 1417-1425.
- Paller, K. A. (2000). Neural measures of conscious and unconscious memory. *Behavioural Neurology*, 12, 127-141.
- Paller, K. A. (2006). Binding memory fragments together to form declarative memories depends on cross-cortical storage. In H. D. Zimmer, A. Mecklinger, & U. Lindenberger (Eds.), *Handbook of binding and memory: Perspectives from cognitive neuroscience* (pp. 527-544). Oxford: Oxford University Press.
- Paller, K. A., & Gross, M. (1998). Brain potentials associated with perceptual priming vs explicit remembering during the repetition of visual word-form. *Neuropsychologia*, 36, 559-571.
- Paller, K. A., Hutson, C. A., Miller, B. B., & Boehm, S. G. (2003). Neural manifestations of memory with and without awareness. *Neuron*, 38, 507-516.
- Paller, K. A., & Kutas, M. (1992). Brain potentials during memory retrieval provide neurophysiological support for the distinction between conscious recollection and priming. *Journal of Cognitive Neuroscience*, 4, 375-391.
- Park, D. C., & Puglisi, J. T. (1985). Older adults' memory for the color of pictures and words. *Journal of Gerontology*, 40, 198-204.
- Park, D. C., Puglisi, J. T., & Lutz, R. (1982). Spatial memory in older adults: Effects of intentionality. *Journal of Gerontology*, 37, 330-335.
- Park, D. C., Puglisi, J. T., & Sovacool, M. (1983). Memory for pictures, words, and spatial location in older adults: Evidence for pictorial superiority. *Journal of Gerontology*, 38, 582-588.
- Pascual-Marqui, R. D. (2002). Standardized low resolution brain electromagnetic tomography (sLORETA): technical details. *Methods & Findings in Experimental & Clinical Pharmacology*, 24, 5-12.

- Paul, L., & Schyns, P. G. (2003). Attention enhances feature integration. *Vision Research*, 43, 1793-1798.
- Penick, S., & Solomon, R. (1991). Hippocampus, context, and conditioning. *Behavioral Neuroscience*, 105, 611-617.
- Phillips, A. G., Ahn, S., & Floresco, S. B. (2004). Magnitude of dopamine release in medial prefrontal cortex predicts accuracy of memory on a delayed response task. *The Journal of Neuroscience*, 24, 547-553.
- Picton, T. W., Bentin, S., Berg, P., Donchin, E., Hillyard, S. A., Johnson, R. Jr., Miller, G. A., Ritter, W., Ruchkin, D. S., Rugg, M. D., & Taylor, M. J. (2000). Guidelines for using human event-related potentials to study cognition: Recording standards and publication criteria. *Psychophysiology*, 37, 127-152.
- Picton, T. W., Lins D. O., & Scherg, M. (1995). The recording and analysis of event-related potentials. In F. Boller & J. Grafman (Eds.), *Handbook of Neuropsychology*, Vol. 8, (pp. 63-131). Amsterdam: Elsevier Science Publishers.
- Piekema, C., Kessels, R. P. C., Mars, R. B., Petersson, K. M., Fernández, G. (2006). The right hippocampus participates in short-term maintenance of object-location associations. *NeuroImage*, 33, 374-382.
- Posner, M. I., Snyder, C. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, 109, 160-174.
- Praamstra, P., Boutsen, L., & Humphreys, G. W. (2005). Frontoparietal control of spatial attention and motor intention in human EEG. *Journal of Neurophysiology*, 94, 764-774.
- Quamme, J. R., Frederick, C., Kroll, N. E. A., Yonelinas, A. P., & Dobbins, I. G. (2002). Recognition memory for source and occurrence: The importance of recollection. *Memory & Cognition*, 30, 893-907.
- Rajaram, S. (1996). Perceptual effects on remembering: Recollective processes in picture recognition memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 22, 365-377.
- Ranganath, C., & Paller, K. A. (1999). Frontal brain potentials during recognition are modulated by requirements to retrieve perceptual details. *Neuron*, 22, 605-613.
- Ranganath, C., & Paller, K. A. (2000). Neural correlates of memory retrieval and evaluation. *Cognitive Brain Research*, 9, 209-222.
- Ranganath, C., Johnson, M. K., & D'Esposito, M. (2000). Left anterior prefrontal activation increases with demands to recall specific perceptual information. *Journal of Neuroscience*, 20:RC108, 1-5.
- Ranganath, C., Yonelinas, A. P., Cohen, M. X., Dy, C. J., Tom, S. M., & D'Esposito, M. D. (2004). Dissociable correlates of recollection and familiarity within the medial temporal lobes. *Neuropsychologia*, 42, 2-13.
- Ratcliff, R., Van Zandt, T., & McKoon, G. (1995). Process dissociation, single-process theories, and recognition memory. *Journal of Experimental Psychology: General*, 124, 352-374.
- Reder, L. M., Nhouyvanisvong, A., Schunn, C. D., Ayers, M. S., Angstadt, P., & Hiraki, K. (2000). A mechanistic account of the mirror effect for word frequency: A computational model of remember-know judgments in a continuous recognition paradigm. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 26, 294-320.

- Reinitz, M. T. (2003). Feature binding in episodic memory: Roles of conscious awareness and intention. In T. Bajo, & J. Lupianez (Eds.), *Abstracts of the 13th conference of the European Society of Cognitive Psychology in Granada, Spain, September 17-20* (pp. 123-124). Monachil, Granada, Spain: Imprenta Santa Rita.
- Reinitz, M. T., & Hannigan, S. L. (2001). Effects of simultaneous stimulus presentation and attention switching on memory conjunction errors. *Journal of Memory and Language*, 44, 206-219.
- Reinitz, M. T., & Hannigan, S. L. (2004). False memories for compound words: Role of working memory. *Memory & Cognition*, 32, 463-473.
- Rhodes, S. M., & Donaldson, D. I. (2007). Electrophysiological evidence for the influence of unitization on the processes engaged during episodic retrieval: Enhancing familiarity based remembering. *Neuropsychologia*, 45, 412-424.
- Roediger, H. L., & Blaxton, T. A. (1987). Effects of varying modality, surface features, and retention interval on priming in word-fragment completion. *Memory & Cognition*, 15, 379-388.
- Roediger, H. L., Weldon, M. S., & Challis, B. H. (1989). Explaining dissociations between implicit and explicit measures of retention: A processing account. In H. L. Roediger, & F. I. M. Craik (Eds.), *Varieties of memory and consciousness – Essays in honour of Endel Tulving* (pp. 3-41). Hillsdale, NJ: Erlbaum.
- Rotello, C. M., & Heit, E. (1999). Two-process models of recognition memory: Evidence for recall-to-reject? *Journal of Memory and Language*, 40, 432-453.
- Rotello, C. M., & Heit, E. (2000). Associative recognition: a case of recall-to-reject processing. *Memory & Cognition*, 28, 907-922.
- Rugg, M. D., & Coles, M. G. H. (1996). *Electrophysiology of mind*. Oxford: Psychological Series.
- Rugg, M. D., Fletcher, P. C., Chua, P. M. L., & Dolan, R. J. (1999). The role of the prefrontal cortex in recognition memory and memory for source: An fMRI study. *NeuroImage*, 10, 520-529.
- Rugg, M. D., & Nagy, M. E. (1989). Event-related potentials and recognition memory for words. *Electroencephalography and Clinical Neurophysiology*, 72, 395-406.
- Rugg, M. D., Schloerscheidt, A. M., & Mark, R. E. (1998). An electrophysiological comparison of two indices of recollection. *Journal of Memory and Language*, 39, 47-69.
- Rugg, M. D., Walla, P., Schloerscheidt, A. M., Fletcher, P. C., Frith, C. D., & Dolan, R. J. (1998). Neural correlates of depth of processing effects on recollection: evidence from brain potentials and positron emission tomography. *Experimental Brain Research*, 123, 18-23.
- Rugg, M. D., & Wilding, E. L. (2000). Retrieval processing and episodic memory. *Trends in Cognitive Sciences*, 4, 108-115.
- Ryan, J. D., Althoff, R. R., Whitlow, S. & Cohen, N. J. (2000). Amnesia is a deficit in relational memory. *Psychological Science*, 11, 454-461.
- Schacter, D. L., (1992). Understanding implicit memory – A cognitive neuroscience approach. *American Psychologist*, 47, 559-569.
- Schacter, D. L., Cooper, L. A., & Delaney, S. M. (1990). Implicit memory for unfamiliar objects depends on access to structural descriptions. *Journal of Experimental Psychology: General*, 119, 5-24.
- Schacter, D. L., Church, B., & Bolton, E. (1995). Implicit memory in amnesic patients: Impairment of voice-specific priming. *Psychological Science*, 6, 20-25.

- Schloerscheidt, A. M., & Rugg, M. D. (2004). The impact of change in stimulus format on the electrophysiological indices of recognition. *Neuropsychologia*, 42, 451-466.
- Senkfor, A. J., & Van Petten, C. (1998). Who said what? An event-related potential investigation of source and item memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 24, 1005-1025.
- Shapiro, K., Driver, J., Ward, R., & Sorensen, R. E. (1997). Priming from the attentional blink: A failure to extract visual tokens but not visual types. *Psychological Science*, 8, 95-100.
- Shiffrin, R. M., & Steyvers, M. (1997). A model for recognition memory: REM – retrieving effectively from memory. *Psychonomic Bulletin and Review*, 4, 145-166.
- Slotnick, S. D., Moo, L. R., Segal, J. B., & Hart, J. Jr. (2003). Distinct prefrontal cortex activity associated with item memory and source memory for visual shapes. *Cognitive Brain Research*, 17, 75-82.
- Smith, M. E. (1993). Neurophysiological manifestations of recollective experience during recognition memory judgments. *Journal of Cognitive Neuroscience*, 5, 1-13.
- Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science*, 283, 1657-1661.
- Smith, S. M., & Vela, E. (2001). Environmental context-dependent memory: A review and meta-analysis. *Psychonomic Bulletin & Review*, 8, 203-220.
- Snodgrass, J. G., & Corwin, J. (1988). Pragmatics of measuring recognition memory: applications to dementia and amnesia. *Journal of Experimental Psychology: General*, 117, 34-50.
- Snodgrass, J. G., Hirshman, E., & Fan, J. (1996). The sensory match effect in recognition memory: Perceptual fluency or episodic trace? *Memory & Cognition*, 24, 367-383.
- Speer, N. K., & Curran, T. (submitted). ERP correlates of familiarity and recollection processes in visual associative recognition.
- Spencer, W. D., & Raz, N. (1995). Differential effects of aging on memory for content and context: A meta-analysis. *Psychology and Aging*, 10, 527-539.
- Spiers, H. J., Burgess, N., Hartley, T., Vargha-Khadem, F., & O'Keefe, J. (2001). Bilateral hippocampal pathology impairs topographical and episodic memory but not visual pattern matching. *Hippocampus*, 11, 715-725.
- Squire, L. R. (1987). *Memory and brain*. NY: Oxford University Press.
- Squire, L. R. (1992). Memory and hippocampus: A synthesis from findings with rats, monkeys, and humans. *Psychological Review*, 99, 195-231.
- Squire, L. R. (2004). Memory systems of the brain: A brief history and current perspective. *Neurobiology of Learning and Memory*, 82, 171-177.
- Squire, L. R., & Knowlton, B. J. (1995). Memory, hippocampus, and brain systems. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences*. (pp. 825-837). Cambridge, MA: MIT Press.
- Squire, L. R., & Zola, S. M. (1998). Episodic memory, semantic memory, and amnesia. *Hippocampus*, 8, 205-211.
- Squire, L. R., & Zola-Morgan, S. (1991). The medial temporal lobe memory system. *Science*, 253, 1380-1386.

- Squires, K. C., Squires, N. K., & Hillyard, S. A. (1975). Decision-related cortical potentials during an auditory signal detection task with cued observation intervals. *Journal of Experimental Psychology: Human Perception & Performance*, 1, 268-279.
- Srinivas, K., & Verfaellie, M. (2000). Orientation effects in amnesics' recognition memory: Familiarity-based access to object attributes. *Journal of Memory and Language*, 43, 274-290.
- Stark, C. E. L., & Squire, L. R. (2003). Hippocampal damage equally impairs memory for single items and memory for conjunctions. *Hippocampus*, 13, 281-292.
- Summerfield, C., & Mangels, J. A. (2005). Functional coupling between frontal and parietal lobes during recognition memory. *NeuroReport*, 16, 117-122.
- Suzuki, W. A., Miller, E. K., & Desimone, R. (1997). Object and place memory in the macaque entorhinal cortex. *Journal of Neurophysiology*, 78, 1062-1081.
- Tallon-Baudry, C., Bertrand, O., Delpuech, C., & Pernier, J. (1996). Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. *Journal of Neuroscience*, 16, 4240-4249.
- Tendolkar, I., & Rugg, M. D. (1998). Electrophysiological dissociation of recency and recognition memory. *Neuropsychologia*, 36, 477-490.
- Tiberghien, G. (1986). Contextual effects in face recognition: Some theoretical problems. In H. D. Ellis, M. A. Jeeves, F. Newcombe, & A. W. Young (Eds.), *Aspects of face processing* (pp. 88-105). Dordrecht: Martinus Nijhoff.
- Trautner, P., Dietl, T., Staedtgen, M., Mecklinger, A., Grunwald, T., Elger, C. E., & Kurthen, M. (2004). Recognition of famous faces in the medial temporal lobe: An invasive ERP study. *Neurology*, 63, 1203-1208.
- Treisman, A. M. (1992). Perceiving and re-perceiving objects. *American Psychologist*, 47, 862-875.
- Treisman, A. M. (2006). Object tokens, binding, and visual memory. In H. D. Zimmer, A. Mecklinger, & U. Lindenberger (Eds.), *Handbook of binding and memory: Perspectives from cognitive neuroscience* (pp. 315-338). Oxford: Oxford University Press.
- Treisman, A. M., & Kanwisher, N. G. (1998). Perceiving visually presented objects: Recognition, awareness and modularity. *Current Opinion in Neurobiology*, 8, 218-226.
- Trinkler, I., King, J., Spiers, H., & Burgess, N. (2006). In H. D. Zimmer, A. Mecklinger, & U. Lindenberger (Eds.), *Handbook of binding and memory: Perspectives from cognitive neuroscience* (pp. 53-84). Oxford: Oxford University Press.
- Trott, C. T., Friedman, D., Ritter, W., & Fabiani, M. (1997). Item and source memory: Differential age effects revealed by event-related potentials. *Neuroreport*, 8, 3373-3378.
- Troyer, A. K., & Craik, F. I. M. (2000). The effect of divided attention on memory for items and their context. *Canadian Journal of Experimental Psychology*, 54, 161-70.
- Tsivilis, D., Otten, L. J., & Rugg, M. D. (2001). Context effects on the neural correlates of recognition memory: An electrophysiological study. *Neuron*, 31, 497-505.
- Tsivilis, D., Otten, L. J., & Rugg, M. D. (2003). Repetition effects elicited by objects and their contexts: An fMRI study. *Human Brain Mapping*, 19, 145-154.
- Tulving, E. (1983). *Elements of episodic memory*. Oxford: Oxford University Press.

- Tulving, E. (1985). Memory and consciousness. *Canadian Psychology*, 26, 1–12.
- Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Reviews of Psychology*, 53, 1-25.
- Tulving, E., Hayman, C. A., & Macdonald, C. A. (1991). Long-lasting perceptual priming and semantic learning in amnesia: A case experiment. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 17, 595-617.
- Tulving, E., & Thomson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review*, 80, 352-373.
- Ungerleider, L. G., & Haxby, J. V. (1994). 'What' and 'where' in the human brain. *Current Opinion in Neurobiology*, 4, 157-165.
- Urbach, T. P., & Kutas, M. (2002). The intractability of scaling scalp distributions to infer neuroelectric sources. *Psychophysiology*, 39, 791-808.
- Van Petten, C., Luka, B. J., Rubin, S. R., & Ryan, J. P. (2002). Frontal brain activity predicts individual performance in an associative memory exclusion task. *Cerebral Cortex*, 12, 1180-1192.
- Van Petten, C., Senkfor, A. J., & Newberg, W. M. (2000). Memory for drawings in locations: Spatial source memory and event-related potentials. *Psychophysiology*, 37, 551-564.
- Vargha-Khadem, F., Gadian, D. G., Watkins, K. E., Connelly, A., Van Paesschen, W., & Mishkin, M. (1997). Differential effects of early hippocampal pathology on episodic and semantic memory. *Science*, 277, 376-380.
- Verfaellie, M., Cook, S. P., & Keane, M. M. (2003). Absence of size congruency effects in amnesic patients' recognition: A failure of perceptually based recollection. *Neuropsychology*, 17, 108-114.
- Verfaellie, M., Gabrieli, J. D. E., Vaidya, C. J., Croce, P., & Reminger, S. L. (1996). Implicit memory for pictures in amnesia: Role of etiology and priming task. *Neuropsychology*, 10, 517-528.
- Verfaellie, M., Martin, E., Page, K., Parks, E., & Keane, M. M. (2006). Implicit memory for novel conceptual associations in amnesia. *Cognitive, Affective & Behavioral Neuroscience*, 6, 91-101.
- Vertes, R. P. (2006). Interactions among the medial prefrontal cortex, hippocampus and midline thalamus in emotional and cognitive processing in the rat. *Neuroscience*, 142, 1-20.
- Voss, J. L., & Paller, K. A. (2006). Fluent conceptual processing and explicit memory for faces are electrophysiologically distinct. *Journal of Neuroscience*, 26, 926-933.
- Wagner, A. T., Stebbins, G. T., Masciari, F., Fleischman, D. A., & Gabrieli, J. D. E. (1998). Neuropsychological dissociation between recognition familiarity and perceptual priming in visual long-term memory. *Cortex*, 34, 493-511.
- Walker, P., & Cuthbert, L. (1998). Remembering visual feature conjunctions: Visual memory for shape-color associations is object-based. *Visual Cognition*, 5, 409-455.
- Wan, H., Aggleton, J. P., & Brown, M. W. (1999). Different contributions of the hippocampus and perirhinal cortex to recognition memory. *Journal of Neuroscience*, 19, 1142-1148.
- Wais, P. E., Wixted, J. T., Hopkins, R. O., & Squire, L. R. (2006). The hippocampus supports both the recollection and the familiarity components of recognition memory. *Neuron*, 49, 459-466.

- Werkle-Bergner, M., Mecklinger, A., Kray, J., Meyer, P., & Düzel, E. (2005). The control of memory retrieval: Insights from event-related potentials. *Cognitive Brain Research*, 24, 599-614.
- Wilding, E. (2004). Electrophysiological evidence for the strategic control of recollection. Paper presented at the 14th Evoked Potential International Conference, Leipzig, Germany, March 28-31, 2004.
- Wilding, E. L., Doyle, M. C., & Rugg, M. D. (1995). Recognition memory with and without retrieval of context: An event-related potential study. *Neuropsychologia*, 33, 743-767.
- Wilding, E. L., Fraser, C. S., & Herron, J. E. (2005). Indexing strategic retrieval of colour information with event-related potentials. *Cognitive Brain Research*, 25, 19-32.
- Wilding, E. L., & Rugg, M. D. (1996). An event-related potential study of recognition memory with and without retrieval of source. *Brain*, 119, 889-905.
- Wilton, R. N. (1989). The structure of memory: Evidence concerning the recall of surface and background color of shapes. *Quarterly Journal of Experimental Psychology A, Human Experimental Psychology*, 41, 579-598.
- Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current Opinion in Neurobiology*, 8, 227-233.
- Windmann, S., Urbach, T. P., & Kutas, M. (2002). Cognitive and neural mechanisms of decision biases in recognition memory. *Cerebral Cortex*, 12, 808-817.
- Wixted, J. T. (in press). Dual-process theory and signal-detection theory of recognition memory. *Psychological Review*.
- Wolk, D. A., Schacter, D. L., Lygizos, M., Sen, N. M., Holcomb, P. J., Daffner, K. R., & Budson, A. E. (2006). ERP correlates of recognition memory: Effects of retention interval and false alarms. *Brain Research*, 1096, 148-162.
- Woodruff, C. C., Johnson, J. D., Uncapher, M. R., & Rugg, M. D. (2005). Content-specificity of the neural correlates of recollection. *Neuropsychologia*, 43, 1022-1032.
- Woodruff, C. C., Hayama, H. R., & Rugg, M. D. (2006). Electrophysiological dissociation of the neural correlates of recollection and familiarity. *Brain Research*, 1100, 125-135.
- Xiang, J. Z., & Brown, M. W. (1998). Differential neuronal encoding of novelty, familiarity and recency in regions of the anterior temporal lobe. *Neuropharmacology*, 37, 657-676.
- Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: Voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception & Performance*, 16, 121-134.
- Yonelinas, A. P. (2002a). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, 46, 441-517.
- Yonelinas, A. P. (2002b). Components of episodic memory: The contribution of recollection and familiarity. In A. Baddeley, M. A. Conway, & J. P. Aggleton (Eds.), *Episodic memory: New directions in research* (pp. 31-52). Oxford: Oxford University Press.
- Yonelinas, A. P., Hopfinger, J. B., Buonocore, M. H., Kroll, N. E. A., & Baynes, K. (2001). Hippocampal, parahippocampal and occipital-temporal contributions to associative and item recognition memory: An fMRI study. *Neuroreport*, 12, 359-363.

- Yonelinas, A. P., & Jacoby, L. L. (1995). The relation between remembering and knowing as bases for recognition: Effects of size congruency. *Journal of Memory and Language*, 34, 622-643.
- Yonelinas, A. P., Kroll, N. E. A., Dobbins, I. G., & Soltani, M. (1999). Recognition memory for faces: When familiarity supports associative recognition judgments. *Psychonomic Bulletin & Review*, 6, 654-661.
- Yonelinas, A. P., & Levy, B. J. (2002). Dissociating familiarity from recollection in human recognition memory: Different rates of forgetting over short retention intervals. *Psychonomic Bulletin & Review*, 9, 575-582.
- Yonelinas, A. P., Otten, L. J., Shaw, K. N., & Rugg, M. D. (2005). Separating the brain regions involved in recollection and familiarity in recognition memory. *Journal of Neuroscience*, 25, 3002-3008.
- Yovel, G., & Paller, K. A. (2004). The neural basis of the butcher-on-the-bus phenomenon: When a face seems familiar but is not remembered. *NeuroImage*, 21, 789-800.
- Zimmer, H. D. (1988). Formkonzepte und Bildmarken: Zwei verschiedene Repräsentationen für visuell-sensorische Merkmale? *Sprache und Kognition*, 7, 40-50.
- Zimmer, H. D. (1993). Modalitätsspezifische der Repräsentation und Verarbeitung von Information. *Zeitschrift für Psychologie*, 201, 203-235.
- Zimmer, H. D. (1995). Size and orientation of objects in explicit and implicit memory: A reversal of the dissociation between perceptual similarity and type of test. *Psychological Research*, 57, 260-273.
- Zimmer, H. D., Mecklinger, A., & Lindenberger, U. (Eds.). (2006a). *Handbook of binding and memory: Perspectives from cognitive neuroscience*. Oxford: Oxford University Press.
- Zimmer, H. D., Mecklinger, A., & Lindenberger, U. (2006b). Levels of binding: types, mechanisms, and functions of binding in remembering. In H. D. Zimmer, A. Mecklinger, & U. Lindenberger (Eds.), *Handbook of binding and memory: Perspectives from cognitive neuroscience* (pp. 3-24). Oxford: Oxford University Press.
- Zimmer, H. D., & Steiner, A. (2003). Color specificity in episodic and in object recognition with enhanced color impact. *European Journal of Experimental Psychology*, 15, 349-370.
- Zimmer, H. D., & Steiner, A. (submitted). Memory of colours as a function of the style of pictures and the deliberateness of colour encoding.
- Zimmer, H. D., Steiner, A., & Ecker, U. K. H. (2002). How 'implicit' are implicit color effects in memory? *Experimental Psychology*, 49, 120-131.
- Zorrilla, L. T., Aguirre, G. K., Zarahn, E., Cannon, T. D., & D'Esposito, M. (1996). Activation of the prefrontal cortex during judgments of recency: A functional MRI study. *Neuroreport*, 4, 2803-2806.

Abbreviations

ANOVA	analysis of variance
BCDMEM	bind cue decide model of episodic memory
BOLD	blood oxygenation level dependent
CR	correct rejection
CS	conditioned stimulus
CSD	current source density
cTAP	constrained task appropriate processing
DP	dual process(ing)
EEG	electroencephalogram
ERP	event-related potential
FA	false alarms
FESTHER	feature sampling theory of recognition
fMRI	functional magnetic resonance imaging
FN400	frontal negativity at ca. 400 ms
GM	global match
HC	hippocampus
LPC	late positive component
MANOVA	multivariate analysis of variance
MEG	magnetoencephalography
ms	milliseconds
MSE	mean standard error
MT	middle temporal visual cortex area (MT or V5)
MTL	medial temporal lobe
MTLC/MTLCs	medial temporal lobe cortex/cortices
MST	medial superior temporal visual cortex area
NBM	nucleus basalis of Meynert
NC	neocortex/neocortical
PDP	process dissociation procedure
PFC	prefrontal cortex
PHC	parahippocampal cortex
ROI	region of interest
RT	reaction time
SAC	source of activation confusion (model)
SDT	signal detection theory
T	Tesla
TAP	transfer appropriate processing
US	unconditioned stimulus

Annotation

Some of the experiments reported in this thesis are also included in the following manuscripts:

Experiment 2 & 3

Ecker, U. K. H., Zimmer, H. D., & Groh-Bordin, C. (in press).

Color and context: An ERP study on intrinsic and extrinsic feature binding in episodic memory. *Memory & Cognition*.

Experiment 4

Ecker, U.K.H., Zimmer, H.D., & Groh-Bordin, C. (under review). The influence of object and background color manipulations on the electrophysiological indices of recognition memory. *Brain Research*.

Experiment 5

Ecker, U. K. H., Zimmer, H. D., Groh-Bordin, C., & Mecklinger, A. (2007).

Context effects on familiarity are familiarity effects of context – An electrophysiological study. *International Journal of Psychophysiology*, 64, 146-156.

Danksagung

Mein Dank gilt in erster Linie meinem Mentor, Prof. Dr. Hubert D. Zimmer, nicht nur für die vorbildliche Anleitung zum analytischen Denken und die Heranführung an die Wissenschaft, sondern insbesondere auch dafür, im wissenschaftlichen Betrieb immer auch Mensch geblieben zu sein – ich bedanke mich für das Verständnis, ohne das diese Arbeit und meine bisherige wissenschaftliche Karriere nicht möglich gewesen wären.

Des weiteren bedanke ich mich bei Prof. Dr. Axel Mecklinger, der mich dem Gehirn näher gebracht hat (im abstrakten Sinne), sowie Dr. Bertram Opitz, Prof. Dr. Wolfgang Klimesch, Prof. Dr. Ulman Lindenberger und Dr. Simon Dennis für ihre Unterstützung und wertvolle Diskussionen.

Letztlich bedanke ich mich bei meinen studentischen Hilfskräften Anna Arend und Kirstin Fluck, sowie meinen lieben Kollegen, insbesondere Dr. Christian Groh-Bordin, Dr. Christian Frings, Günther Lehnert, Katja Umla-Runge, Nicola Ferdinand und Thorsten Brinkmann, für stete Hilfsbereitschaft, Motivation und Inspiration.

Curriculum vitae

Name: Ullrich K. H. Ecker
Geburtsdatum: 10. Januar 1978 in St.Ingbert
Familienstand: Verheiratet, 1 Kind

Bildung

2007

Dr. phil. (1.0 - *magna cum laude*), Psychologisches Institut, Universität des Saarlandes

2003

Psychologie Diplom (1.0), Universität des Saarlandes

Diplomarbeitstitel: Implicit colour-congruency effects in object priming – A study on token construction in amnesics

1982-1996

Schulbildung in Homburg/Saar, Ottweiler/Saar und Brisbane, Australien; Abitur am Gymnasium Johanneum, Homburg/Saar (1.4)

Berufliche Erfahrung

seit 2004

Psychologischer Sachverständigengutachter für Familiengerichte (Arbeitsgemeinschaft rechtspsychologische Begutachtung, Saarlouis)

seit 2003

Wissenschaftlicher Mitarbeiter im Projekt "Memory-Effective Feature Binding", Brain & Cognition Unit, Universität des Saarlandes (Projektleiter: Prof. Hubert D. Zimmer)

seit 2003

Lektor aller englischsprachigen Manuskripte versch. Arbeitseinheiten des Psychologischen Instituts

2004-2005

Wissenschaftliche Hilfskraft am Neuroimaging Labor der Universitätsklinik für Psychiatrie, Homburg/Saar (Projektleiter: Prof. Oliver Gruber)

2002

Praktikum an der Universitätsklinik für Psychiatrie, Homburg/Saar

1999-2003

Wissenschaftliche Hilfskraft an der Arbeitseinheit Experimentelle Kognitive Psychologie, Universität des Saarlandes (Projektleiter: Prof. Hubert D. Zimmer)

1996-1997

Zivildienst an einer neurologischen Rehabilitationsklinik (Reha-Med-Kliniken), Homburg/Saar