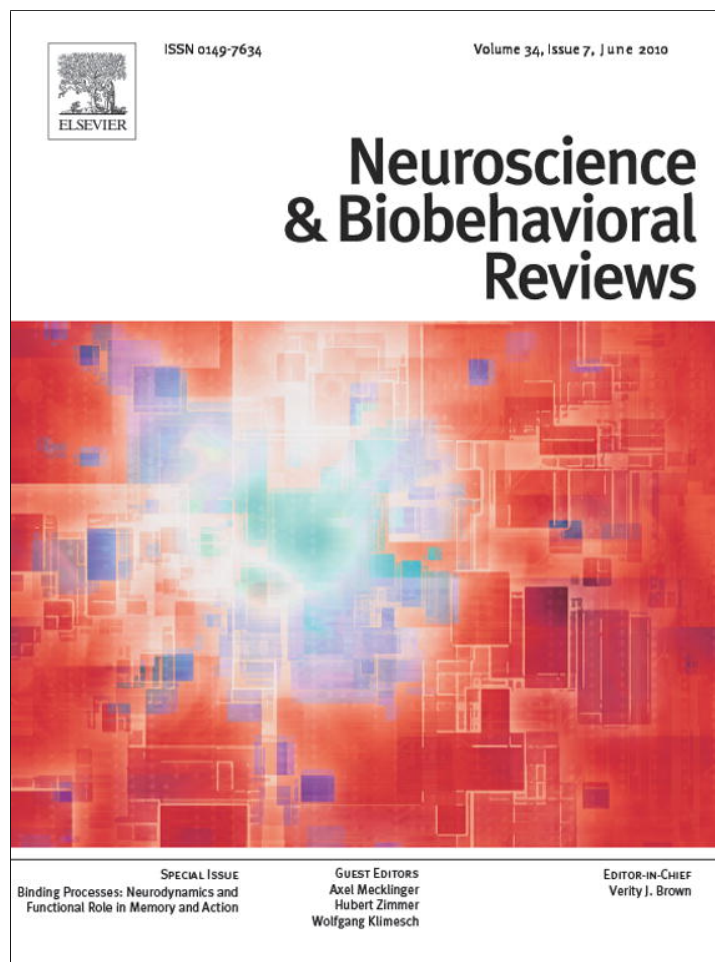


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## Review

## Remembering perceptual features unequally bound in object and episodic tokens: Neural mechanisms and their electrophysiological correlates

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## ABSTRACT

We present a neurocognitive model of long-term object memory. We propose that perceptual priming and episodic recognition are phenomena based on three distinct kinds of representations. We label these representations *types* and *tokens*. *Types* are prototypical representations needed for object identification. The network of non-arbitrary features necessary for object categorization is sharpened in the course of repeated identification, an effect that we call *type trace* and which causes perceptual priming. *Tokens*, on the other hand, support episodic recognition. Perirhinal structures are proposed to bind intrinsic within-object features into an *object token* that can be thought of as a consolidated perceptual object file. Hippocampal structures integrate object- with contextual information in an *episodic token*. The reinstatement of an *object token* is assumed to generate a feeling of familiarity, whereas recollection occurs when the reinstatement of an *episodic token* occurs. Retrieval mode and retrieval orientation dynamically modulate access to these representations. In this review, we apply the model to recent empirical research (behavioral, fMRI, and ERP data) including a series of studies from our own lab. We put specific emphasis on the effects that sensory features and their study–test match have on familiarity. The type–token approach fits the data and additionally provides a framework for the analysis of concepts like unitization and associative reinstatement.

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In everyday life, we frequently encounter objects that we have encountered before. This can result in three fundamentally different mental states that involve memory. First, one does not remember the previous encounter at all, but the object is nevertheless encoded more efficiently due to the earlier experience with the object. This phenomenon is known as *perceptual*

priming. Second, re-encountering the object results in the unspecific awareness that the object has been experienced before, but without any conscious access to details of that encounter. This is referred to as *familiarity*. Third, one remembers both the object and details of the previous encounter (such as the spatiotemporal context). This is called *recollection*. Familiarity and recollection are usually subsumed under the label *episodic recognition*.

These three memory processes and the resulting mental states have very different properties, but they all have something very important in common: When the object is re-encountered—or in scientific terms: at the time of retrieval—processing leading up to these states starts with the identical perceptual input, but then different processes take place. How does our memory system achieve this?

To answer this question, we will have to look at two levels of abstraction. First, how is information about encountered objects represented and accessed in memory? Clearly, the perceptual representation of the target item and its match with the corresponding memory representation is an important determinant of memory performance. We will argue that the distinct properties of perceptual priming, familiarity, and recollection strongly suggest that these processes are based upon distinct memory representations. For example, within episodic recognition, the representation subserving recollection contains contextual information, whereas the representation supporting familiarity does not. Moreover, in perceptual priming, the representation is not consciously accessible (hence this phenomenon is considered an *implicit* memory process). In contrast, the representations supporting familiarity and recollection allow to link the “study” (initial encounter) and “test” (subsequent encounter and retrieval) experiences, albeit with different levels of phenomenological awareness (therefore, these are considered *explicit* memory phenomena).

On a second level of abstraction, we should consider the actual implementation in the brain, that is, which neural networks

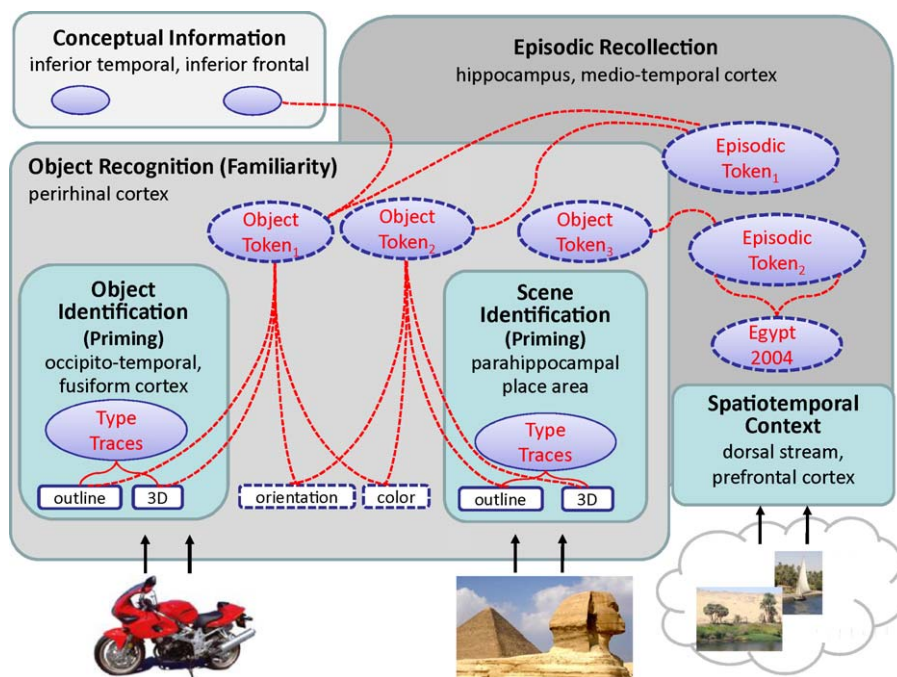
achieve the mnemonic representation of and access to object information? Neurocognitive research within the last decade has established compelling evidence that perceived objects are represented within a distributed neural network. This network comprises visual-sensory, medio-temporal, and prefrontal brain areas. Sensory areas are the storage sites of perceived items, medio-temporal structures mediate successful encoding and retrieval, and prefrontal areas host control processes of encoding, retrieval, and evaluation that are necessary to comply with task demands (Aggleton and Brown, 2006; Brown and Aggleton, 2001; Diana et al., 2007; Simons and Spiers, 2003). It will become immediately clear that the latter two mainly play a role in episodic recognition and are less important for perceptual priming.

We will now focus on each of the three memory processes and associated representations in turn. To this end, we present a neurocognitive model of long-term object memory that amalgamates the two levels of representation and neural implementation—the Type-Token model (Ecker et al., 2004; Zimmer et al., 2006). A schematic illustration of the model is given in Fig. 1.

## 1. Remembering objects in the Type-Token model

### 1.1. Type traces in memory: the basis for perceptual priming

When an item is presented a second time in a cognitive task, participants' performances are usually enhanced compared to the first presentation of the item, even though the task does not refer to remembering (Schacter, 1987). Interestingly, such implicit repetition effects are intact in amnesic patients who show impaired episodic memory (e.g., Craft et al., 2007; Schacter et al., 1994a, 1994b; Vaidya et al., 1998); hence the same encoding event could lead to an implicit memory effect even though there may be no explicitly available memory for the event. This has led to the postulation of separate memory systems for explicit and implicit memory.



**Fig. 1.** An illustration of the Type-Token memory model and the neural structures that tentatively provide the information. The pictures stand for environmental input (or items), and the cloud illustrates the set of pictures experienced in a larger episode defining the spatiotemporal context (cf. Polyn and Kahana, 2008). The boxes refer to mental processes and the related neural structures. Only exemplary connections and representations are shown for illustration. For the sake of simplicity, only a selection of the feature modules (white boxes) and of connections to them are depicted (e.g., none for spatiotemporal context). The blue ellipses indicate memory representations, the turquoise boxes refer to input networks that are involved in identification. Dashed lines indicate connections generated by encoding of specific episodic information including arbitrary features.

More specifically, our model deals with one specific kind of implicit memory namely perceptual priming. Perceptual priming refers to the acceleration of encoding processes during object recognition (Schacter et al., 1990). Perceptual priming is sensory specific, which means that changes of the item's modality or exemplar reduce the priming effect (Roediger and Srinivas, 1993). However, perceptual priming is not sensitive to perceptual changes in non-diagnostic features—features that do not aid the identification of items, such as left-right orientation. To anticipate, such changes between study and test do affect episodic recognition (Biederman and Cooper, 1992; Cooper et al., 1992; Zimmer, 1995; Zimmer and Steiner, 2003). This finding was taken as evidence that memory effects in episodic recognition and perceptual priming are based on different memory traces.

To explain this selective perceptual sensitivity, we have proposed that perceptual priming is associated with slow-changing sensory types—modality-specific sensory representations that allow for the identification of objects. More specifically, perceptual priming effects result from small changes to these representations—*type traces*—that occur whenever an object is perceptually processed. Such slow memory (learning) mechanisms for category information were already postulated by O'Reilly and colleagues (McClelland et al., 1995; O'Reilly et al., 2003; O'Reilly and Norman, 2002) who also distinguished this form of memory from a faster process that provides memory of specific exemplars—a process that we will discuss in the next section. Type traces strengthen the network of category-relevant features; in Fig. 1 this is illustrated by continuous lines.

In more neuroscientific terms, perceptual priming is explained by small changes in neural identification networks caused by the sensory representation build-up during object encoding. Put simply, sensory memory of previous encoding facilitates neural processing in subsequent encoding; the perceptual system is 'tuned' for a second encoding (Schacter and Tulving, 1994; Wiggs and Martin, 1998). For pre-experimentally known stimuli, repetition suppression—reduced activity—is typically observed. These effects occur in the same category-specific regions that are active during perception/identification. For vision, this is the fusiform cortex and occipito-temporal areas (Buckner et al., 1998; Grill-Spector et al., 1999; Henson et al., 2000); for reviews see Schacter et al. (2004) and Grill-Spector et al. (2006). Correspondingly, perceptual priming does not seem to occur if occipital brain structures are damaged (Fleischman et al., 1997; Gabrieli et al., 1995; Keane et al., 1995).

### 1.2. Remembering objects via the reactivation of object tokens

To recognize a specific object as "old" (that is, encountered before), our cognitive system faces an additional challenge, namely the recognition of arbitrary feature details (e.g., the red car that I saw). Engelkamp and Zimmer (1994) therefore suggested that sensory information contributes to the episodic recognition of objects. One problem our cognitive system needs to overcome in this regard is the so-called binding problem.

Behavioral and neurophysiological results suggest that when objects are perceived, sensory features are analyzed in parallel (Livingstone and Hubel, 1988). Two streams are distinguished (Ungerleider and Mishkin, 1982): Features of the object's appearance (e.g., shape, size, color) are analyzed in a ventral stream and spatial features as well as action-related information (Chao and Martin, 2000) in a dorsal stream.

The question arises, how can we perceive let alone remember coherent entities if the processing of features is distributed? Hence, the sensory features need to be bound to mentally represent the object already in perception (the binding mechanism is most likely interregional phase-synchronization, cf. Tallon-

Baudry et al., 1996). Treisman called this bound representation an object file (see, Treisman, 2006, for review). We assume that this object file initiates the genesis of the memory trace of the specific exemplar; this trace remains when the object is removed from perception. We call the memory trace of an object file *object token*. Perception therefore generates object tokens in memory and it provides access to these tokens during episodic recognition. In Fig. 1 we indicate this network of item-specific features by dashed lines. If multiple objects are presented, consequentially multiple object tokens result. A salient landmark (such as a monument) will according to our model be encoded into a separate object token. Even though such a landmark may appear in the background of a memorized item and may hence functionally be the item's context and discussed as such in some experiments (cf. Ecker et al., 2007; Tsivilis et al., 2001), memorizing such an association is not necessarily different from memorizing an association to a second item—which will be discussed later.

Evidence for the abovementioned connection between perception and memory includes the observed overlap in neural activity between encoding and retrieval (see, e.g., Nyberg, 2006; Polyn and Kahana, 2008). It could be shown that some content-specific brain structures that are active during perception are partially also active in memory retrieval (see the discussion in Zimmer, 2008). This has been demonstrated on different levels of abstraction from the global level of sensory modality down to individual features. At the level of modality, remembering visual material (abstract shapes, pictures of objects, line drawings) typically causes activation in those brain areas that are also active in visual perception, that is, the occipito-temporal lobe and the fusiform cortex (FFC) (Garoff et al., 2005; Johnson and Rugg, 2007; Kensinger and Schacter, 2007; Schacter et al., 1995; Schacter et al., 1997; Slotnick, 2004; Slotnick and Schacter, 2004; Slotnick et al., 2005; Vaidya et al., 2002; Wheeler and Buckner, 2003; Wheeler et al., 2000; Woodruff et al., 2005). Modality-specific brain activations (matching the encoding modality) have been found during retrieval even if direct activation of these regions by the memory cue was precluded (Nyberg et al., 2000; Wheeler et al., 2000). At the feature level, direct comparisons of brain activity at encoding and retrieval of specific features have revealed common sensory brain activity; e.g. BA 18 and the lingual gyrus in case of color memory (Ueno et al., 2007), and area V5/MT+ in case of motion memory (Ueno et al., 2009). Correspondingly, electrophysiological studies have reported that event-related potentials (ERP) over sensory areas were influenced according to the specific memory content (Cycowicz et al., 2001; Gratton et al., 1997; Khader et al., 2005a, 2005b; Khader et al., 2007).

We acknowledge the possibility that some of these effects may be correlates of retrieval attempts rather than retrieval success (see the discussion in Friedman et al., 2005; Johansson and Mecklinger, 2003). Also, activity in a specific brain area may reveal what kind of content is processed, but not necessarily that this processing refers to an actually encoded item. Nevertheless, the perceptual specificity of episodic object recognition and the discussed feature-specific brain activity during retrieval strongly suggest that (a) sensory information is part of the memory trace of a perceived object and that (b) this information is provided by brain structures that are involved in perception (see also Slotnick, 2004). We assume that this is the sensory component of an object token. As will be discussed in later sections, however, please note that an object token may additionally contain more abstract, conceptual information.

### 1.3. Object tokens and type traces

One central aspect of the Type-Token model is the dissociation between perceptual priming and familiarity representations. Yet,

the brain regions associated with perceptual priming and familiarity both belong to the ventral stream. Also, both familiarity and perceptual priming can be elicited by the identical target item. So how are they different?

As noted above, even if the same target item is used as a cue, sensory features and their study–test match influence both kinds of process differently. For example, a study–test change in orientation, size, or color will impair episodic recognition but not priming (Biederman and Cooper, 1992; Cooper et al., 1992; Zimmer, 1995; Zimmer and Steiner, 2003; for reviews see Engelkamp et al., 2001; Schacter, 1994). Also, different neural networks and mechanisms seem to be involved.<sup>2</sup>

Implicit memory is based on type traces. These are changes in the processing route used for identification and categorization. It is associated with repetition suppression, a reduction of neural activity that is probably a consequence of sharpening: only category-relevant, diagnostic features are bound in this representation, and their interconnections are tuned according to Hebbian rules. Arbitrary features are given less weight than diagnostic features. To illustrate, for object identification (and hence perceptual priming), the (three-dimensional) shape of an object is the critical and dominant feature. For instance, we identify a car mainly by virtue of its shape. In contrast, for successful episodic object recognition, arbitrary, category-irrelevant features need to be represented as well. For this purpose, Anti-Hebbian ‘weakening’ is considered the more effective mechanism (Bogacz and Brown, 2003).

There is evidence that the perirhinal cortex (PRC) may contribute to both of these tasks (Bussey et al., 2005; Tyler et al., 2004). Accordingly, Aggleton and Brown (2006) discussed that the PRC is involved in both priming and familiarity processing, but that different cell assemblies mediate these two processes, given their different constraints. Starting with the same cue, one route may end in generic information (category), whereas the other route may end in individual information (the object token).

Another factor that may have an impact is the retrieval mode the system is in at the time of retrieval. Retrieval mode is a mind state orienting one’s thinking to the past (Rugg and Wilding, 2000). This state biases the system towards retrieval of information that matches the critical episode. Hence, successful episodic recognition is more likely to occur if one is in the appropriate retrieval mode.

#### 1.4. The distinction between object and episodic tokens

In the Type–Token model, episodic recognition can rely on two processes: familiarity and recollection. Perhaps the most important phenomenological difference between the two lies in the retrieval of contextual information, which occurs only if episodic recognition is based on recollection. Thus, recollection requires retrieval of additional information on the object’s encoding context or a consciously represented feature. In our model, this information is bound in an *episodic token* (Ecker et al., 2004). An episodic token is therefore a higher-level representation that integrates information contained in the object token with additional information, for example other tokens, a spatiotemporal context, and explicit predicates generated to the item at study, such as “I experience this as a strange exemplar”. The spatiotemporal context is potentially a more abstract representation of an episode, which is built and modified during encoding of multiple elements of the episode. The binding of episodic tokens in our model

corresponds to the context association mechanism that Polyn and Kahana (2008) discussed in their temporal context model.

Recent neuropsychological research has partially disclosed the structures that are relevant for these binding processes. Mediotemporal structures are likely candidates—the hippocampus (HC) and the surrounding entorhinal, perirhinal (PRC) and parahippocampal (PHC) cortices. These structures have different functional roles. We suggest that these roles map onto the distinct binding requirements associated with familiarity and recollection.

In particular, the PRC is considered relevant for familiarity and item memory (i.e., acontextual memory for an isolated object), whereas, in contrast, the HC and PHC areas are involved in recollection (see for review Davachi, 2006; Diana et al., 2007; Skinner and Fernandes, 2007). We assume that the introduced *object tokens* are processed within the perirhinal route and the reinstatement of an object token should cause familiarity. In contrast, the integration of object information and (spatiotemporal) context in an episodic token relies on an intact hippocampus. There are several lines of evidence that support this mapping of PRC–familiarity and HC/PHC–recollection.

In animal studies, isolated lesions of the HC impair “recollection” (e.g., the preference for familiar objects in novel vs. familiar surroundings) but leave familiarity-based memory (e.g., the preference for novel objects per se) intact (Mumby et al., 2002; Sauvage et al., 2008). Importantly, this pattern of impairment is also found in human amnesics with selective HC damage (Aggleton et al., 2005; Bowles et al., 2007).

In imaging studies, activity in the hippocampus is usually correlated with recollection and retrieval of specific information regarding the item or the study episode (e.g., Davachi et al., 2003; Ross and Slotnick, 2008; Vilberg and Rugg, 2007). The corresponding type of task is often called “relational memory task” (Cabeza, 2006; Eichenbaum, 2006) because it is not only item memory that is relevant but additionally the relations between items or between pieces of item-specific and contextual information. In addition to the HC, the PHC has been found active in relational memory tasks (Bar and Aminoff, 2003; Daselaar et al., 2006c; Kahn et al., 2004; Köhler et al., 2005). Tendolkar et al. (2008) found that activity in the PHC was linearly related to the amount of recollected sensory details.<sup>3</sup>

In contrast, memory-related effects in the PRC have been found both during encoding of subsequently recognized stand-alone items (Davachi et al., 2003; Staresina and Davachi, 2006; Tendolkar et al., 2007) and—frequently—during single-item recognition (Cansino et al., 2002; Gonsalves et al., 2005). Increasing familiarity is thereby often correlated with decreasing activity in PRC (see Henson, 2005; Henson et al., 2003) although this is not always found (Brown and Aggleton, 2001; Daselaar et al., 2006a).

The inconsistencies in imaging findings are likely due to the following two reasons. First, the hippocampus seems to constantly encode and bind all conscious experience into memory (most of which will not be consolidated or will become inaccessible due to interference; cf. Cabeza et al., 2008; Eichenbaum, 2006). This makes it difficult to reliably detect memory-related hippocampal activity with the subtraction method in fMRI studies. Second, familiarity as discussed in the episodic recognition literature is

<sup>2</sup> This is particularly astonishing if one believes that category knowledge is provided by view-point specific memory of exemplars (Tarr and Bülthoff, 1998) and not by view-point independent, abstract prototypes (e.g., Biederman et al., 1999).

<sup>3</sup> It should be noted that some of the most consistently found regions associated with recollection lie in the ventral and dorsal parietal cortex. The functional role of these activations are still debated, but coarsely speaking, it seems clear that these areas support the attentional orientation to and/or the online representation of retrieved information in the process of making a memory decision (Cabeza, 2008; Vilberg and Rugg, 2009; Yonelinas et al., 2005), for a review see Wagner et al. (2005). Importantly, the proposed functions of parietal activation do not seem to be critically (nor specifically) involved in successful recollection. Hence parietal (unlike hippocampal) lesions do not typically lead to severe memory problems. We therefore do not consider this topic further at this stage, although it will be picked up in a later section.

almost certainly only the end-product of an interactive cascade of subprocesses (Ecker, 2007; Tsivilis et al., 2001). In particular, neurons in the PRC can be sensitive to recency of occurrence, longer term familiarity, or novelty (Xiang and Brown, 1998), and the calculation of episodic familiarity as measured in the laboratory very likely utilizes all of these signals (for instance, computationally, episodic familiarity can be conceptualized as 1/novelty (cf. Bogacz and Brown, 2003).

Our model therefore assumes that intra-item features are bound within the PRC. Because of the item-specific memory effects, it is assumed that the PRC is at the top of the encoding hierarchy in the ventral stream of object processing, and that cell assemblies in this structure represent bound features of the perceived object. Taylor et al. (2006) therefore consider the PRC the “master binder” in perception, which, for example, relates sensory (object) input to semantic information. Therefore, we assume that single-item recognition via familiarity relies on the PRC. In contrast, the HC seems to be essential for inter-item and item-context binding, and hence recollection (Diana et al., 2007; Skinner and Fernandes, 2007; Wais, 2008). In this vein, hippocampal recollection mechanisms are seen to integrate information from the ventral and dorsal streams.

To summarize, our Type-Token model (Ecker et al., 2004; Zimmer et al., 2006) proposes three kinds of representation: Type traces are the basis for perceptual priming; these are changes in neural networks within the ventral pathway, caused by the sensory representation build-up during object identification. Object tokens represent single items, and access to this kind of representation is assumed to be related to familiarity. Finally, episodic tokens represent item-context associations and are related to recollection. Our research has focused on the generation of and access to these representations in the course of episodic recognition, and the associated electrophysiological correlates, which will be discussed next.

### 1.5. Electrophysiological correlates of episodic recognition and perceptual priming

The three different memory states—episodic familiarity, episodic recollection, and perceptual priming—are not only associated with different neural structures but also with different electrophysiological correlates in event-related potentials (ERPs).

Familiarity and recollection are assumed to be reflected in two ERP old–new effects. An early frontal positivity between 300 and 500 ms for old compared to new items—the mid-frontal (old–new) effect from here on—is considered the correlate of familiarity, while a corresponding late (600–800 ms) posterior-parietal positivity—the parietal (old–new) effect from here on—has been associated with recollection (see for reviews, Curran et al., 2006; Friedman and Johnson, 2000; Mecklinger, 2000). A number of observations support this assumption.

For example, item memory alone seems sufficient to elicit the mid-frontal old–new effect, whereas the parietal effect is enhanced if context memory is available (Allan et al., 1998; Curran, 2000; Rugg et al., 1998; Schloerscheidt and Rugg, 2004; Senkfor and van Petten, 1998; Wilding and Rugg, 1996). Consistent with this a patient with hippocampal impairment did show the mid-frontal but not the parietal old–new effect (Düzel et al., 2001). Based on these results (see Rugg and Curran, 2007), we therefore assume that the size of the mid-frontal and parietal old–new effects varies with familiarity and recollection, respectively.<sup>4</sup>

<sup>4</sup> It should be noted that other opinions about the functional role of the mid-frontal old–new effect have been put forward. For instance, Paller and co-workers have argued that the mid-frontal effect reflects conceptual priming (cf., Paller et al., 2007; Voss and Paller, 2007). We will deal with this assumption after presenting our own research in the following section.

Other ERP components with different timing and topography are discussed as correlates of perceptual priming. Most frequently, repeated stimuli are found to elicit a positive-going waveform relative to new items (Berman et al., 1990; Friedman and Cycowicz, 2006; Gruber et al., 2006; Henson et al., 2004; Kazmerski and Friedman, 1997; Kazmerski et al., 1995; Rugg et al., 1998; Schendan and Kutas, 2003; Swick and Knight, 1997). This positivity is observed in a time window between approximately 300 and 700 ms, and it has a rather broad topography with a centro-parietal maximum. However, also other topographies and time windows have been reported. Curran and Dien (2003) reported an early frontopolar effect in the P2 component which they associated with perceptual priming, whereas others have reported occipital topographies for the modulation of P2 (Schendan and Kutas, 2007a, 2007b); speculatively, these effects may represent activation patterns associated with the same dipole).

Despite the inconsistencies, these data suggest it should be possible to dissociate the electrophysiological correlates of perceptual priming from those of episodic recognition. Therefore, the investigation of these ERP effects allowed us to test some specific predictions of our Type-Token model. We took the mid-frontal and parietal old–new effects observed in episodic recognition as suitable indicators of familiarity and recollection. Furthermore, both effects should be distinguishable from old–new effects in perceptual priming. The size of these respective effects should therefore be sensitive to variations in the associated process components and specifically these effects should be differently modulated by the match of perceptual information between study and test.

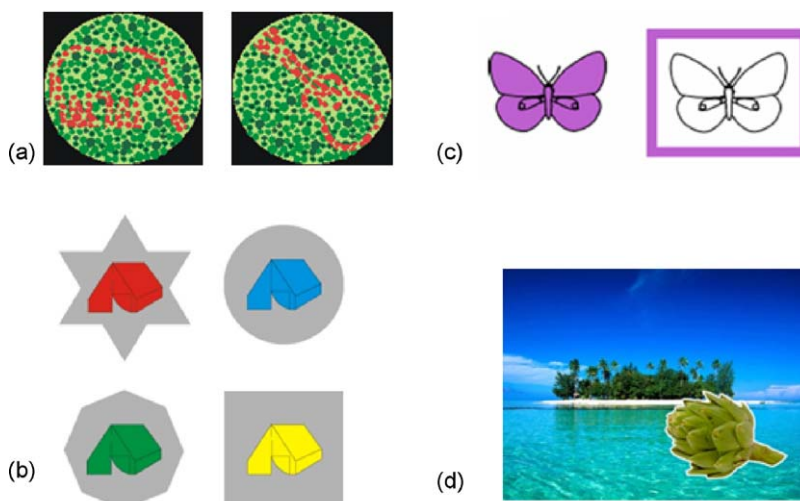
## 2. Electrophysiological correlates of processing types and tokens in memory—testing the Type-Token model

As mentioned above, we assume that an object token is the basis of item memory (as opposed to relational memory). It is automatically accessed if an old item is processed in an episodic recognition task, and its reinstatement should cause familiarity. We assume that familiarity is a graded signal that increases with the number of perceived *intra-item* features that match the object token. Hence, familiarity and consequentially the mid-frontal old–new effect should be a function of the sensory match between the study and test item.

In contrast, an episodic token integrates item and context information, and reinstatement of an episodic token should elicit recollection. We assume that retrieval of context information is more deliberate (Herron and Rugg, 2003). Consequentially, the degree of recollection and the corresponding parietal old–new effect should be influenced only by the match or mismatch of those context and item features that are accessed in complying with task demands.

Finally, although the electrophysiological signature of perceptual priming is less clear, priming-related ERP effects should be dissociable from episodic recognition effects. In particular, perceptual manipulations of arbitrary item features that are known to affect episodic recognition but not perceptual priming should show analogue effects on the associated ERP components. According to our model, this is because priming is based on types—representations that code mainly for diagnostic object features such as (three-dimensional) shape and outline.

Hence, our model assumptions provided us with some clear testable hypotheses: First, perceptual manipulations of arbitrary *intra-item* features (such as an object's left–right orientation) should have no effect on the ERP effects associated with perceptual priming because types code only for diagnostic information. Second, these perceptual *intra-item* manipulations should reduce the mid-frontal old–new effect because this information should be



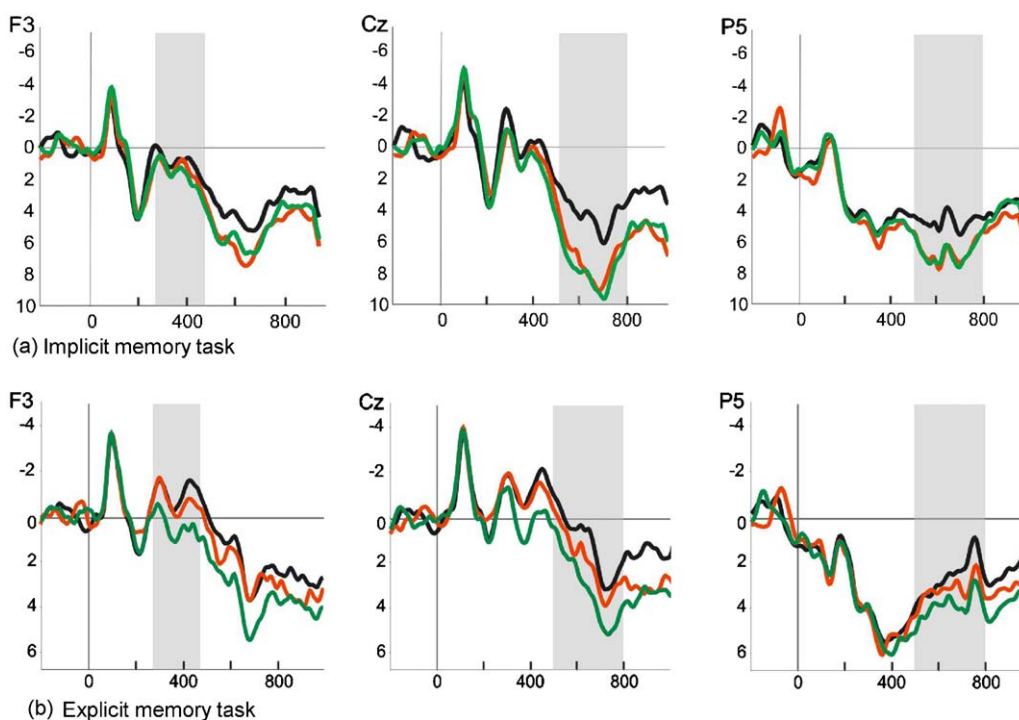
**Fig. 2.** Examples of stimuli that were used in the different recognition experiments: (a) Groh-Bordin et al. (2005); (b) Ecker et al. (2007a); (c) Ecker et al. (2007b); (d) Ecker et al. (2007c).

contained in the object token, which is automatically reactivated on target presentation (these intra-item changes could also affect the parietal old–new effect because the episodic token contains this information as well if it was explicitly encoded). Third, contextual study–test manipulations should affect only the parietal old–new effect (because context retrieval is more controlled this may only happen if the context information is task-relevant), but should under no circumstances affect the mid-frontal effect.

To test these predictions, in a number of studies we manipulated the match between study and target item by changing sensory features (e.g., arbitrary color, left-right orienta-

tion, shape; see Fig. 2). In most experiments, participants performed an inclusion task, that is, they were required to accept both unchanged old items and old items with changed features as “old”. In all studies we analyzed the ERP old–new effects as a function of sensory match.

In an initial study (Groh-Bordin et al., 2005), we contrasted perceptual priming with episodic recognition directly. We used stimuli that were difficult to identify (stimuli consisting of red and green dots, similar to the disks of the Ishihara color test) and therefore presumably enhanced perceptual processing. Like many behavioral studies before (see Engelkamp et al., 2001, for review), we found that changing an arbitrary sensory feature—in this case



**Fig. 3.** Influence of the items' sensory match between study and test on mid-frontal (electrode F3) and parietal (electrode P5) ERP old–new effects. ERPs to new items, old-congruent (unchanged), and old-incongruent (perceptually changed) items are shown in black, green, and red lines, respectively. Panels show correlates of an implicit (a) and explicit (b) memory task (Groh-Bordin et al., 2005). Because in the implicit task we got the strongest effect at Cz, this electrode is additionally shown. ERPs are time-locked to test stimulus onset; the gray bars indicate the time windows that we analyzed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)



**Fig. 4.** Influence of the items' sensory match between study and test on mid-frontal (electrode F3) and parietal (electrode P5) ERP old–new effects. ERPs to new items, old-congruent (unchanged), and old-incongruent (perceptually changed) items are shown in black, green, and red lines, respectively. The left column shows the ERP effects when an intrinsic item-feature (object color) was changed from study to test; the right column shows the effects when a context feature (shape of the background) was changed (Ecker et al., 2007a). ERPs are time-locked to test stimulus onset; the gray bars indicate the time windows that we analyzed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

left-right orientation—from first to second repetition did not reduce priming effects in an animacy task. Critically, the perceptual manipulation did not affect the priming-related occipito-parietal ERP old–new effect either.<sup>5</sup> In contrast, episodic recognition performance and the familiarity-related mid-frontal ERP effect were strikingly reduced. In fact, the mid-frontal effect even disappeared when mirror-reversing items; that is, the familiarity-related component elicited by old but reversed pictures was indistinguishable from the waveform elicited by new pictures, even though these old-incongruent pictures were well recognized (cf. Fig. 3).

Further studies focused on the effects of sensory manipulations on episodic recognition. We consistently found that study–test changes of intra-item features (e.g., the arbitrary color of objects) reduced the mid-frontal old–new effect (e.g., Groh-Bordin et al., 2006) but that changes of contextual features (such as the shape or color of the item background) did not.

In particular, we found this pattern even if direct feature memory for intrinsic and contextual features was comparable (Ecker et al., 2007a). In the latter study, we asked subjects not only to make old/new judgments regarding the objects (irrespective of any feature changes, i.e., an inclusion task), but also to indicate directly whether the color of the object (intra-item feature) or the shape of an abstract gray background (context feature) had changed from study to test. Results indicated that intra-item feature information and contextual information were bound to the object and accessible to the same degree. Nevertheless, only a manipulation of intra-item information (color) reduced the mid-frontal old–new effect associated with familiarity (cf. Fig. 4).

<sup>5</sup> In an as-yet unpublished study, changing the actual exemplar eliminated the priming-related ERP effect, as predicted by our model (Groh-Bordin et al., submitted for publication).

In contrast, sensory changes of the background-shape influenced only the parietal old–new effect associated with recollection, and they did so only when the contextual feature was task-relevant. That is, when the context feature was irrelevant for the old/new decision (i.e., in an inclusion task), a contextual manipulation did not affect the parietal effect (cf. Fig. 4). However, changing the task demands led to the expected pattern of results: Using exactly the same stimuli in an exclusion task—in which old items on a changed background were to be rejected—the contextual change led to a reduction of the parietal old–new effect related to recollection, comparable to the effect reduction found with a colour-change (Ecker et al., 2007a).

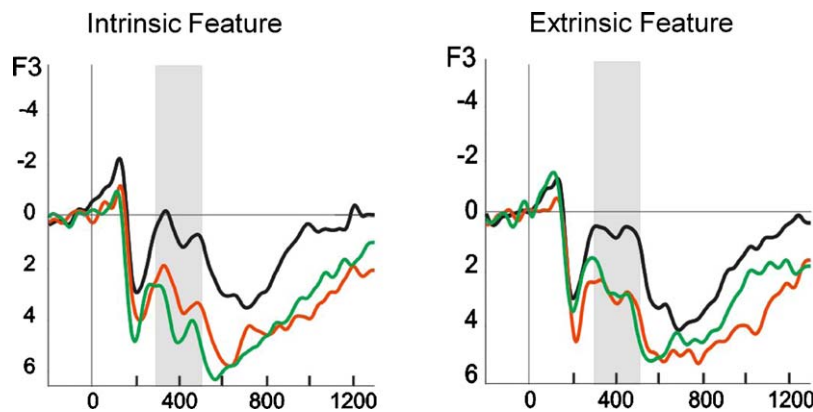
Rebutting concerns that this pattern of effects was influenced by our choice of item and context features, a highly similar result was obtained when the same feature (here color) was manipulated as either an intrinsic or a contextual feature (i.e., a colored frame Ecker et al., 2007b). In this study, a study–test manipulation of color reduced the mid-frontal old–new effect if color was an intrinsic object feature but not when it was a context feature. A summary of ERP effects is shown in Fig. 5.

### 3. Advancing the Type-Token model

#### 3.1. Dynamic access to types and tokens

Our aims were threefold: We wanted to address the questions (a) how information about encountered objects is represented and accessed in memory, (b) which neural networks achieve mnemonic representation of and access to object information, and finally (c) how—starting from the same memory cue—different memory representations can be addressed during retrieval in explicit and implicit memory tasks. To address these questions we





**Fig. 5.** Influence of the items' color match between study and test on the mid-frontal ERP old-new effect (electrode F3). ERPs to new items, old-congruent (unchanged), and old-incongruent (perceptually changed) items are shown in black, green, and red lines, respectively. The left column shows the effect when the items' intrinsic color was changed from study to test; the right column shows the effect when the color context (frame) was changed (Ecker et al., 2007b). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

proposed the Type-Token model and we outlined the presumed underlying neural network.

Our initial studies largely confirmed core predictions derived from this model. Yet, other episodic recognition studies have yielded results that seem incompatible with it. In particular, some studies (1) failed to find that sensory target qualities modulated the mid-frontal old-new effect; in others, (2) contextual or relational information did influence this ERP component.

Regarding point (1), Curran and co-workers have reported that changing the number of words (i.e., adding or removing a plural -s) or their modality of presentation (spoken vs. written words) from study to test had no influence on the mid-frontal old-new effect (Curran, 2000; Curran and Cleary, 2003; see also Curran et al., 2002). In an experiment with easily recognizable figures, presenting mirror-reversed pictures reduced the mid-frontal old-new effect slightly, but the difference was not significant (Curran and Cleary, 2003). These results were interpreted as support of the assumption that familiarity is based on global and rather abstract information, and that sensory details are not evaluated.

Concerning point (2), the effects of context on familiarity, Tsivilis et al. (2001) reported that changing context information can reduce the early familiarity effect. They presented to-be-remembered objects on landscape backgrounds and found that an old object presented on a novel background elicited no mid-frontal old-new effect. Moreover, several other groups have found that associations between items can affect familiarity (Rhodes and Donaldson, 2007; Mayes et al., 2007; Bader et al., 2010).

This contradictory state of affairs can probably be resolved by looking at the mechanisms by which memory is cued, and the modulation of these processes by specific experimental details. In the following, we will present some more recent experiments from our lab that were designed to address these inconsistencies, and we will suggest some ideas on how the Type-Token model can be modified to explain the overall pattern of findings.

However, before dealing with these apparently inconsistent findings, we would first like to address another objection, namely the proposal that the mid-frontal old-new effect does not reflect familiarity in the first place, but rather conceptual priming (Voss and Paller, 2006; Yovel and Paller, 2004), and that conceptual priming may in fact support familiarity (Paller et al., 2007). In our view, there are several reasons not to believe this to be the case. First, if the effect were purely conceptually driven, purely perceptual manipulations (of orientation or arbitrary color) should not affect its magnitude—an effect that has been frequently observed (Ecker et al., 2007a, 2007b; Groh-Bordin et al., 2006;

Groh-Bordin et al., 2005; Nyhus and Curran, 2009; Schloerscheidt and Rugg, 2004). Second, we have found that even completely meaningless stimuli elicit a mid-frontal old-new effect (Groh-Bordin et al., 2006). In contrast, however, Voss and Paller (2007) argue that this is an effect of meaningfulness if it is ideosyncratically measured. This controversy is not yet resolved. However, to date, there has been no convincing demonstration of an influence of conceptual priming on the mid-frontal old-new effect with familiarity held constant (Grove and Wilding, 2009). In contrast, there is evidence that effects caused by semantic knowledge (fame) and episodic experience (frequency) can be dissociated (Stenberg et al., 2009).

We acknowledge that episodic familiarity and conceptual priming may have similar ERP signatures, but the effect associated with conceptual priming seems to occur somewhat earlier and has a slightly different topography (Ecker and Zimmer, 2009; Voss and Paller, 2006; for a related claim see also Voss et al. (2008) and for compatible fMRI evidence see Buckner et al., 2000; Meister et al., 2007). Having dealt with this objection, we will now return to the two critical issues identified above.

### 3.1.1. Perceptual vs. conceptual processing in familiarity

We turn first to our above point (1)—the studies in which sensory congruence did not influence the mid-frontal old-new effect. Curran's results imply that an object token does not only (and not always) represent sensory information. It is more likely a vector of various types of information including perceptual and semantic information and this information is not always encoded and used in the same way. The task renders some components more important and it attenuates others. It follows that during memory access, task-relevant information is given higher weight than task-irrelevant information. The same memory cue can therefore (re)address a representation in different ways or it can even address different representations (cf. also the principle of encoding specificity, e.g., Vaidya et al., 2002).

We reported above that the perceptual specificity effect on the familiarity component varied somewhat across experiments, that is, it was largest when the task was more strongly perceptually driven (using Ishihara-like stimuli, Groh-Bordin et al., 2005). In a further experiment, we used different exemplars of the same semantic category (e.g., two different pictures of an African elephant) as stimuli. At test, we presented new items intermixed with studied exemplars (identical repetition) and perceptually different exemplars of a studied category (e.g., a different African elephant). Participants were instructed to accept the new exemplar as “old” even though this specific exemplar had not

been seen before. These new exemplars elicited (somewhat attenuated) mid-frontal old–new effects even though they were perceptually different from study items (Ecker and Zimmer, 2009). However, if subjects were told to accept as “old” only the exact exemplar studied—that is, when they were led to focus on the perceptual study–test match—same exemplars elicited a mid-frontal old–new effect but different exemplars did not (Ecker and Zimmer, 2009). Hence familiarity in this latter instance seemed to be purely perceptually driven.

Continuing the above line of thought, apparently the influence of sensory features on familiarity is a function of the importance of sensory features for the memory task. Familiarity is only slightly reduced or even unaffected if the mismatch is due to low-weighted features; it is more strongly reduced if the weights are higher, and the mid-frontal familiarity effect is even absent if the sensory change hinders direct access to the object token. For example, the core representation of a word is its meaning (cf. levels-of-processing effects) and for isolated words the word's number is rather unimportant. Hence, the “address” of an object token established by a verbal input is predominantly the meaning of the word. This may explain why changing the number of a word from “dog” to “dogs” had no effect on familiarity (Curran, 2000). Similarly, for easily recognized pictures and line drawings, changing arbitrary features reduces familiarity, but it does not eliminate the effect (Curran and Cleary, 2003; Ecker et al., 2007b; Groh-Bordin et al., 2006). In contrast, mirror-reversing unusual and difficult-to-recognize Ishihara-like figures eliminates the mid-frontal old–new effect for changed pictures (Groh-Bordin et al., 2005). This very likely happens because at first the changed picture does not address the memory entry because the system is tuned to give more weight to perceptual features. Only later, after identifying what is depicted, is memory accessed. On the other hand, if participants are required to accept even different exemplars of the same category as old, memory is tuned to work on the categorical level, hence giving sensory features minimal weights. Consequentially, even a different picture from an old category may elicit a clear mid-frontal old–new effect (Ecker and Zimmer, 2009).

The discussed results, however, question the degree to which familiarity is in fact an automatic—purely bottom-up triggered—process and not influenced by task demands and retrieval strategies. The results of Ecker and Zimmer (2009) indicate that subjects can tune their familiarity processing to be more specific and exemplar-focused (i.e., perceptually driven) or more general and category-focused (i.e., conceptually driven), and they can do so even on a trial-by-trial basis. This is clearly a strategic top-down influence of retrieval orientation (Herron and Wilding, 2004; Wilding and Rugg, 1997) on familiarity processing. We therefore consider our original familiarity conception as too static and too strongly focused on bottom-up processing. We originally assumed that in contrast to relational processes, familiarity processes are rather automatic and mainly triggered by the memory cue. We still assume that familiarity is automatically calculated, but that it can nevertheless be modulated or tuned by top-down processes. The top-down process adjusts reinstatement of memory entries to the requirements of the memory task, rendering memory access more flexible, for instance by adjusting the weighting of features and the associated ratio of perceptual and conceptual processing as detailed in the previous section.

Another aspect of recognition that in our view has not been sufficiently considered but influences the familiarity effect is the temporal extent of memory access. It is not an instantaneous but a gradual process following the time course of feature extraction—see for example the sequential activation of different neural networks in the course of word recognition (Mainy et al., 2008). We know that analyses of visual features differ in perceptual speed

(e.g., Moutoussis and Zeki, 1997). Accordingly, it has been shown that the temporal characteristics of both episodic recognition and categorization depend on the speed of feature extraction (Brockdorff and Lamberts, 2000; Lamberts et al., 2002). If the same perceptual process that drives episodic recognition also governs identification, both tasks should follow the same time-course. In fact, this has been demonstrated for immediate and delayed matching tasks (i.e., perception and memory): apparently, there are “slow” features that take longer to be either perceived or retrieved from memory as compared to “fast” features (Kent and Lamberts, 2006a, 2006b).

It follows that different features match or mismatch at different moments of the recognition process (Ratcliff et al., 1999). Due to these variations, perceived familiarity changes over time. Memory access is therefore a dynamic event. First, it depends on the relative accessibility of features in the object token defined by perceptual qualities of the item. Salient features should therefore have a higher impact on processing and familiarity than low-key features. Second, aspects of the memory task itself—for instance the demanded general or specific retrieval orientation—modulate the importance of features.

### 3.1.2. Relational binding in familiarity

At retrieval, several processes run in parallel. While the target is processed by one set of neurons within the visual cortex, a different set of neurons represents the context or other present objects. Both representations can influence memory processes. Returning to our above point (2), this may explain effects that context has been found to have on the mid-frontal familiarity component. For example, in the study of Tsivilis et al. (2001), context changes influenced the mid-frontal old–new effect. However, the context stimuli that Tsivilis et al. used were very salient landscape images. It is therefore likely that the “context” was often processed first and hence more like a target item. To test this, we replicated the Tsivilis et al. study, extending the design (Ecker et al., 2007c). Objects were presented on background landscapes, and the study–test match was manipulated. In the replication condition, we also replicated the effect pattern that Tsivilis et al. had found: old objects on novel backgrounds did not elicit a reliable mid-frontal old–new effect—at first glance, a clear context effect on familiarity and hence a violation of our model assumptions. However, in another experimental condition, we cued the target-item positions on the landscapes (prior to each target item, a cue was presented at the exact position where the item was due to appear on the landscape) in order to draw subjects' attention to the to-be-recognized target item. We thereby gave the target an advantage in processing, and as a consequence, the context effect on familiarity vanished.

It is an essential determination in the Type-Token model what the unit of memory is and what information is bound in this unit. The above example makes clear that the memory effects that one expects depend strongly on the way information is integrated during perception (of both the study item and the test probe), that is, whether features are bound in an object token or in an episodic token. During encoding, features are bound into perceptual units, and these units constitute object tokens. Hence a multi-object display will lead to the generation of multiple object tokens. Likewise, at test, it is critical which unit is perceived (first) and used as a memory cue. We do not have a final answer to the question of how memory units are formed, but we have some ideas about aspects that are critical. One central role is attributed to perception and another to attention.

Visual grouping is important for memory (Ceraso, 1985). A common assumption is that features are more likely remembered together if they belong to the same perceptual unit (Ceraso et al., 1998). In support of this, color, for example, is better remembered

if it belongs to a to-be-recognized object (surface color) rather than the background (Walker and Cuthbert, 1998; Wilton, 1989). This holds already at the transition from perception or iconic memory to short-term memory (Delvenne and Bruyer, 2004). Importantly, it was suggested even in this context that the mnemonic function of this integrated percept is provided by the lateral occipital cortex (Ferber et al., 2005). It is therefore very likely that we always refer to the same neural representation when we talk about object representations in perception and memory; we do so only in different time domains (see to this point the thorough discussion in Zimmer, 2008).

In this vein, according to our model, object tokens are remainders of object files that are generated by perception. Hence, when asking how the formation of object tokens takes place it seems important to look at how units are formed when a scene is perceived. This is a widely discussed topic in theories of perception. It is clear that the process involves binding of features represented in distributed networks. Many factors have been identified that influence how units are formed during perception, but no simple factor is causative. In contrast, many variables appear to make unit formation more or less likely.

First, unit formation in perception is influenced by the stimulus features and their salience. Relevant explanatory approaches range from models of low-level figure-ground separation (Craft et al., 2007) to the rules of Gestalt psychology (for a review see Palmer et al., 2002). Also, features are not all equally important in unit formation, and the role of a specific feature can depend on other features of the stimulus (cf. the distinction between integral and separable dimensions, Garner, 1974).

Second, top-down processes and experience with the type of input are relevant. Some units are “natural” due to extended practice (e.g., faces; Yonelinas et al., 1999); in other cases a known concept unitizes two separate components (Rhodes and Donaldson, 2007). Expectations can shape perception (Bar, 2004), and attention modulates perceptual processes. For example, switching attention between two objects increases the likelihood of conjunction errors between features from these different objects (Hannigan and Reinitz, 2000; Reinitz and Hannigan, 2001). One can also change the size of the perceptual focus and attend to the whole figure or a small detail. In other words, the task will co-determine what features are intrinsic to the perceptual unit and will consequently be bound in the object token.

Hence, there may well be a default mode of what is perceived as a unit (e.g., a car is typically perceived and memorized as a car and not as a composite of parts), but this is affected by both experience and task demands. Different sizes of focal attention will cause different contents of object files. We suspect that effects of nonmatching relational context on familiarity are caused by this mechanism (Ecker et al., 2007c; Tsivilis et al., 2001). For example, Speer and Curran (2007) observed that recognition of pairs of fractals was apparently based on familiarity. We suggest this was because the two fractals formed a perceptual unit. We know from research on interactive imagery that the visual system is very efficient in generating such units (Paivio, 1986). Correspondingly, Rhodes and Donaldson (2008) were able to enhance the mid-frontal old–new effect to semantic word pairs, e.g., cow–goat, by interactive imagery instructions.

In light of such findings, hippocampus-independent unitization has been discussed as a potential alternative relational memory mechanism to hippocampal binding. There are reports of amnesic patients with hippocampal damage that show nearly normal within-modality associative recognition (Mayes et al., 2004; Mayes et al., 2007; Stark and Squire, 2003). Even in healthy people, two separate items can apparently be associated in familiarity memory under some circumstances (Mayes et al., 2007; Taylor et al., 2006). It seems clear that such unitization can

only occur within a given modality (e.g., faces or face parts, Jäger et al., 2006; Yonelinas et al., 1999). Also, it is likely that the constituent items need to be perceived as equal “partners” (Speer and Curran, 2007) rather than as figure and background (Ecker et al., 2007a). Other potentially relevant factors include relative position and proximity, size, and—at least for words—even pre-experimental semantic association (of word pairs; Rhodes and Donaldson, 2007) or the availability of a unitizing semantic concept (for novel compounds; Bader et al., 2010). Finally, repeated study presentation arguably fosters unitization (Speer and Curran, 2007), as do explicit mental imagery instructions (van Petten et al., 2002).

In this vein Cohn and Moscovitch (2007) argued in favor of an associative reinstatement based on units that were generated during encoding and mediated by the perirhinal cortex. In our terms this is the generation of an object token. Even though we may not have the ultimate answer to the question of what factors determine the creation of object tokens, the discussed encoding processes apparently set the boundary conditions for the genesis of object tokens.

In summary, task demands and sensory stimulus qualities interactively influence access to an object token. This memory access determines object familiarity and as a consequence the size of the mid-frontal old–new effect and its reliance on sensory features.

### 3.2. Interactive biased competition as an early retrieval mechanism

Given all these influences, what is a sensible model for memory access? We assume that biased competition (Desimone, 1996) is a likely neural mechanism also for retrieval. The information present in a test display is processed in parallel. Objects (and features of objects and context) compete for representation in visual cortices during identification, leading to the generation of object files. One of these units attracts focal attention, which may occur due to its perceptual salience or a task-specific (top-down) selection. This unit (or depending on the task a weighted part of it) is selected for evaluation and used as a memory cue, and sends input into the PRC. In resonance with this structure, an object token will be reinstated. This process provides a familiarity signal which varies in size depending on the match between the cue and the memory entry. The mid-frontal old–new effect should be a correlate of this signal. If the object file matches an object token the input and retrieved information is fused and an updated object token is represented in working memory. This token can then be used as a modified cue in a second retrieval attempt that if successful enriches the active working memory representation with further retrieved details. These details can be contextual if information is fed forward to the hippocampus and an episodic token is successfully addressed. Consequentially, an object or episodic token is reinstated in working memory and the more information is retrieved the more features are represented within working memory.

Recently, it has been discussed that ventral and dorsal parts of the parietal cortex are also involved in memory (see, Vilberg and Rugg, 2008; Wagner et al., 2005). Cabeza (2008) argued that these structures serve an attentional function during retrieval, and suggested dual attention processes in memory: The dorsal parietal cortex is involved in top-down control of retrieval. It modulates retrieval according to the goal, and activity goes up with effort. In contrast, the ventral part of the parietal cortex plays a role in bottom-up attention. He speculated that activity occurs “whenever an interesting memory enters consciousness and overtakes attentional resources” (p. 1815). Hence, the ventral parietal cortex is involved in the recovery of episodic memories and the monitoring of output of medio-temporal lobe structures. This idea is very similar to those we have outlined above. Many of the

discussed parietal structures are part of the network supporting working memory for objects (see Zimmer, 2008).

It is therefore likely that the parietal cortex is involved in any memory task because it serves as a working memory network during retrieval. One may think of this as a work-space of object reinstatement, providing a window of attention to the bound features. Retrieval mode and retrieval orientation are mental states that modify its content. Biased competition is a likely mechanism to give objects files or specific features different weights and to prioritize them for representation in working memory.

Extending these thoughts to implicit priming effects, it seems reasonable to assume that priming (e.g., enhancement of categorization during identification) and episodic recognition processes (e.g., making attempts to access an object token) always run in parallel (cf. Voss and Paller, 2008). The task requirements determine which of these processes has an influence on behavior. If participants are in an explicit memory task they are in a retrieval mode and they intentionally use the items to cue their memory. In this case familiarity and recollection dominate behavior. If they are not in such a mode the perceptual qualities of the item in resonance with top-down influences will determine whether an object token is involuntarily reinstated or additional contextual information is retrieved via the episodic token. Therefore, explicit retrieval will occur even in an implicit task—based purely on bottom-up processes—if an unusual or otherwise unique exemplar of a category addresses an object token. This would cause involuntary memory (cf. Cabeza, 2008).

In this “competition”, the perirhinal cortex may have a further function. It has been suggested to serve as a gate-keeper (cf. Fernández and Tendolkar, 2006), “deciding” whether a new object token is opened—further processing resources may then be focused on the encoding of a novel item (see also Lewandowsky and Farrell, 2008)—or whether an old token is reactivated—further processing resources may then be focused on attempts to recollect and evaluate information associated with a familiar item. Support for such an idea can be seen in the observation of two neural signals within the MTL that were inversely related to familiarity and novelty (Daselaar et al., 2006b). These neural structures may thus participate in a gating mechanism that regulates how during retrieval an item is processed in working memory.

#### 4. Conclusion

We have presented a neurocognitive model of long-term object memory, proposing three different kinds of memory representation subserving different memory functions. These are type-traces supporting implicit perceptual priming effects, object tokens supporting episodic familiarity, and episodic tokens supporting episodic recollection. Our model shares attributes with other models including those presented by Aggleton and Brown (1999, 2006) and Eichenbaum and Yonelinas (Diana et al., 2007; Eichenbaum, 2006; Eichenbaum et al., 2007). Our model has been fruitful in establishing the important distinction between the roles of intra-item and extrinsic contextual features in episodic recognition. It is unique in that it applies to both perceptual priming and episodic recognition and relates the two. Perhaps most importantly, it focuses on the intermediate level of representations, bridging the gap between neural structures and cognitive processes.

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