

# The encoding–retrieval relationship: retrieval as mental simulation

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**There is increasing evidence to suggest that mental simulations underlie many cognitive processes. We review results from three rapidly developing research areas suggesting that simulations underlie information retrieval. First, neuroimaging work indicates that cortical circuits that were activated during encoding are reactivated during retrieval. Second, retrieval is aided by behavioural re-enactment of processes involved in encoding, including re-enactment of encoding eye movements. Third, the time courses of encoding of visual features and the retrieval of information about those features are related. Overall, the evidence suggests that the often observed interactions between encoding and retrieval result from a cognitive system that, at least partially, reactivates processes that were involved in encoding to retrieve information.**

## Encoding and retrieval

Many cognitive tasks require the encoding of perceptual information and the later retrieval of this information. Both processes have generated a vast amount of literature. But, surprisingly, encoding and retrieval are usually studied in relative isolation of each other, and few models have been developed that attempt to integrate both processes into a comprehensive theory of information acquisition and retrieval. Modern memory theorists largely failed to appreciate the impact of encoding processes on subsequent retrieval of information (see Refs [1–3] for a review). However, during the late 1960s and 1970s, ideas about the relationship between the initial encoding event and subsequent retrieval bloomed, resulting in the documentation of several well-known phenomena, such as transfer-appropriate processing [4], contextual/state/mood dependent memory [5–7 respectively], and the encoding specificity principle [8,9]. However, although the encoding–retrieval interaction literature questioned strict abstractionist accounts of memory, it did not provide much insight into the underlying process of retrieval itself. Consequently, the causal mechanisms of encoding–retrieval interactions have remained poorly understood, and the theoretical importance of such interactions has been questioned [10].

Against this background, the work of Kolers (e.g. [11–13]) emerged as a significant new development, with its strong focus on the cognitive processes in encoding and retrieval. Kolers argued that the procedures by which information was encoded were also stored in memory,

and could be used to aid retrieval. For example, in a task in which participants were taught to read passages of text that were transformed from the canonical form (e.g. mirrored text), the ability of participants to reread previously presented text (even months after study) was improved relative to reading a novel (but still transformed) passage, even though participants did not recognize the text [12]. Here, we expand on Kolers' proceduralist viewpoint, and argue that encoding–retrieval interactions arise naturally from a cognitive system in which internal representations and the operations that manipulate them (partly) rely on the processes that encode perceptual information. Although this point of view is not new [13,14], recent evidence, such as the overlap in the neural circuitry of perception and retrieval (e.g. [15]), the re-enactment of eye movement patterns during rehearsal and retrieval of visual displays [16,17], and the relationship between the time course of encoding and the time course of retrieval [18–20] has provided important new insights into the nature of the relationship between perceptual encoding processes and subsequent information retrieval.

## Perceptual symbols and mental simulations

The main theme of Kolers' procedural account, which states that information is not merely abstracted from the environment with disregard for contextual and processing information, survives today in many theories (e.g. [14,21,22]). One influential modern approach is that of perceptual symbol systems [14,23], which suggests that perceptual information is stored in the sensory-motor neural units that were responsible for encoding the information. According to perceptual systems accounts, when participants are required to think about information in memory, they engage in a mental 'simulation' of the relevant symbols (Box 1). The notion of mental simulation is well established in cognitive psychology [22,24]. Simulation theories have been developed in relation to social cognition (especially with the discovery of mirror neurons, e.g. [25–28]), the cognitive processing of object concepts (e.g. [14,23,24,29–31]) and mental imagery (both mental rotation and mental scanning can be interpreted as simulations; e.g. [24,32]). However, the use of simulations in cue-driven retrieval has not received so much attention. Previous accounts of the encoding–retrieval interactions have not gone far enough in explaining the underlying mechanisms responsible for the observed increase in retrieval performance with increased overlap between encoding and retrieval conditions. In particular, popular

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### Box 1. Mental simulation

Although the idea of mental simulation (or mental re-enactment) has been around for a long time [24], the exact nature of the simulations that might underlie cognitive processes such as information retrieval is still unclear. There seem to be at least two types of simulation, which map onto previous distinctions in the literature about explicit (conscious) processes and implicit (unconscious) processes. Explicit simulations would include those based on episodic information, such as in autobiographical memory tasks [53], or those that underlie analogue reasoning about complex systems [54]. Explicit simulation processes give rise to the experience of seeing with the mind's eye. Most of us are familiar with performing mental imagery tasks, and there is now a well-established literature on the neuronal mechanisms underlying mental imagery and their relation to the mechanisms underlying perception (see [32] for a review). However, simulations might also underlie other cognitive tasks that involve more implicit retrieval procedures. Tasks that do not require consciously experienced analogue reasoning or explicit episodic recall still seem to involve some form of (partial) re-enactment of encoding processes. For instance, the cognitive processes in various conceptual knowledge tasks (e.g. [14,23,24]), in language comprehension [55] and in implicit social cognition (e.g. [25–27]) all seem to rely on a form of re-enactment that is markedly different from explicit simulation. Perhaps these types of task involve a qualitatively different kind of simulation that does not give rise to the same phenomenological experience, because they rely on a different instantiation of the same general simulation mechanism [24], or because they involve a different 'format' of information [54]. There is a growing body of evidence suggesting that amodal information can also be simulated (see, e.g., [24] for a review). An important future avenue for research will be to characterize the types of simulation underlying different tasks and data types, especially those involving nonperceptual (conceptual) information. Simulations must be flexible to produce novel concepts and to adapt to task and contextual demands. This flexibility distinguishes simulation from strict process reinstatement. In a simulation, perceptual process information is used in a constructive and generative process. This constructive process might involve partial reinstatement, but should not be identified with it.

accounts, such as encoding specificity and transfer-appropriate processing, have largely ignored the time course of how encoding–retrieval interactions unfold. Simulation-based accounts are not incompatible with previous approaches. However, simulations offer an account at a lower level of analysis, which explains how the general principles of encoding specificity and transfer-appropriate processing emerge. Simulation, therefore, offers a natural temporal framework within which to understand encoding–retrieval interactions. We provide a brief review of three emerging areas that lend support to the idea that mental simulation might underlie information retrieval.

#### Perception and retrieval activate common neural systems

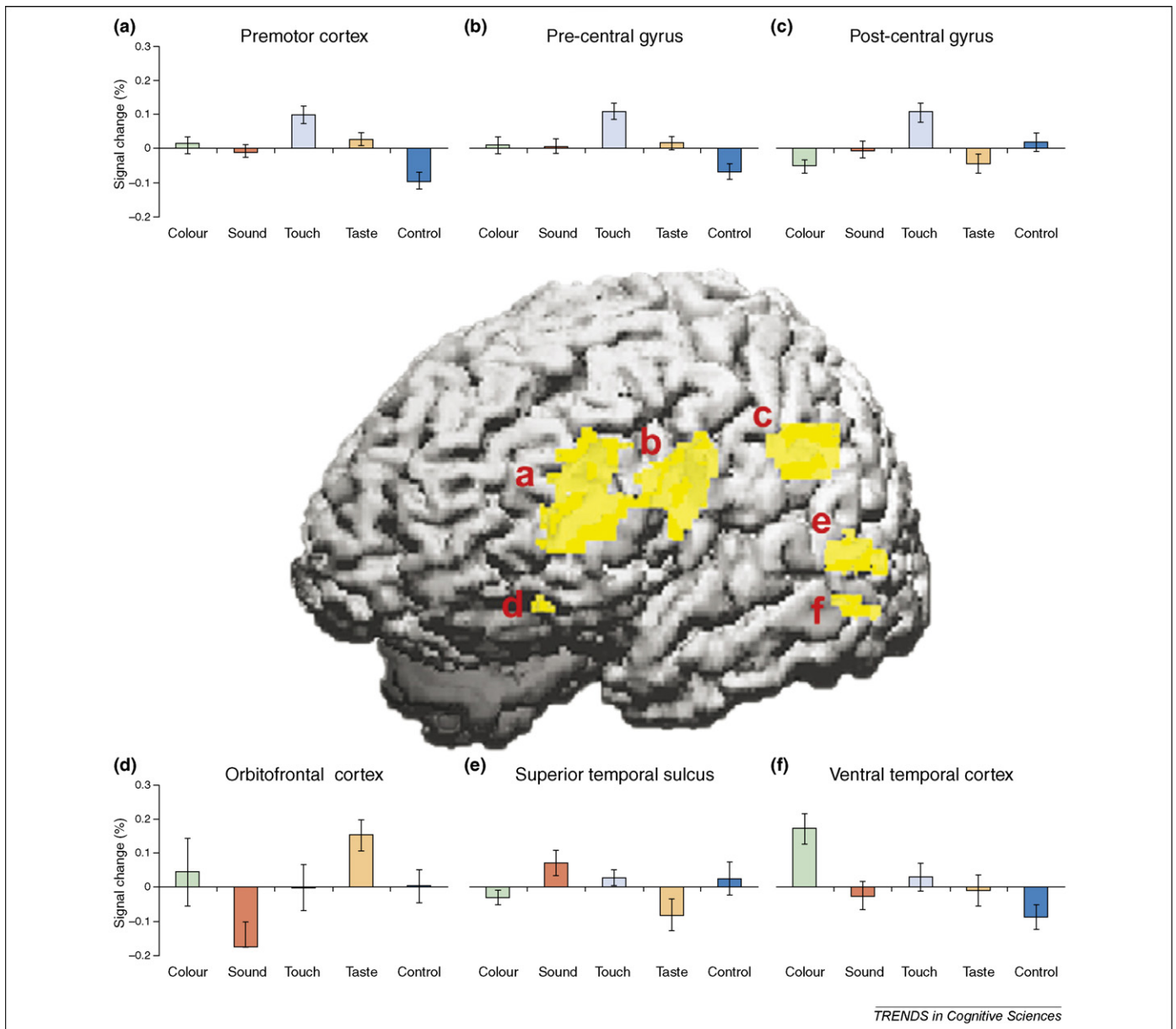
There is now a large body of evidence suggesting that perceptual information retrieval reactivates neural circuits that were originally involved in processing that information (for reviews see, e.g., [15,24,31,33]). Although most studies on this topic have focused on visual processing [15], there is good evidence that the same relationship also holds for other perceptual modalities, and that there is modality-specific cortical activation [34]. Property verification tasks have been used to demonstrate that cortical areas associated with the encoding of specific object proper-

ties (such as colour) are also active when retrieving information about these properties. For example, Goldberg *et al.* [34] carried out a functional neuroimaging study in which they asked participants whether objects had certain properties (drawn from four modalities: visual, auditory, tactile and gustatory). The results demonstrated that retrieval of information about specific modalities affected activity in the corresponding sensory areas (Figure 1). Likewise, colour perception and retrieval of information about colour (cued by verbal stimuli) have been shown to have overlapping neural correlates [35]. Using a different methodology (free recall of word lists), Polyn *et al.* [36] found striking evidence that retrieval involves category-specific (including faces, locations and objects) reinstatement of neural activity before participants initiated a free-recall response. Thus, there is evidence that reactivation of perceptual processes during retrieval is modality-, feature- and category- (or domain-) specific (see also [15]). Otten [37], like other authors [4,8,9,11–13], has highlighted the importance of considering both the encoding task and the retrieval task in studies of the neural correlates of memory. Otten [37] used a complex encoding task, in which participants viewed a series of object names, and were required to make size judgments about the objects that were named. This task produced a diverse pattern of neural activity across trials, presumably reflecting variation in the attributes (phonological, visual or semantic) that were most emphasized in the encoding of different objects. In a subsequent recognition-memory task, responses to two types of retrieval cue (either a spoken object name or a picture of an object) were recorded. A crucial finding was that the brain regions activated at encoding predicted the effectiveness of the visual and verbal retrieval cues at test. This result is compatible with the view that success of retrieval processes depends on their overlap with processes at encoding, in line with proceduralist accounts.

Further recent evidence that the retrieval system can reactivate relevant perceptual systems includes the finding that stochastic cortical activation in certain perceptual regions biases perception of ambiguous stimuli [38], that imagery involves reactivation of content-specific cortical areas [39,40] (Box 2), and that prior knowledge can facilitate the perception of degraded stimuli by top-down activation of relevant perceptual areas [41].

#### Eye movements during retrieval are functional

There is growing evidence that behavioural re-enactment of the encoding stage benefits retrieval. Recent examples include the finding that congruent body posture [42] and reinstating effortful encoding procedures at test [43] both aid recollection. Particularly compelling evidence for the benefits of re-enactment has been obtained in eye-movement studies, which suggest that eye movements have a functional role in retrieval. Specifically, retrieval performance seems related to the degree of overlap between study eye movements and eye movements at test. Laeng and Teodorescu [16] reported two experiments in which participants first inspected a stimulus, and were then asked to engage in a task in which they imagined the stimulus. The participants were allowed to move their eyes freely across the stimuli during encoding. Their eye movements were



**Figure 1.** Activation changes as a function of sensory area and perceptual knowledge retrieval. The letters refer to sensory motor areas. Tactile knowledge in the premotor (a), motor (b) and somatosensory cortex (c), taste knowledge in the orbitofrontal cortex (d), auditory knowledge in superior temporal sulcus (e) and visual knowledge in ventral temporal cortex (f). The x-axis on the graphs gives the type of perceptual knowledge that had to be verified. Error bars represent the standard error of the mean (SEM). The extent of the activation changes suggest that the modality from which information is being retrieved influences activity at the sensory area responsible for processing that type of perceptual information. Adapted, with permission, from Ref. [34]. Copyright 2006 by the Society for Neuroscience.

also recorded in the imagery task, when they looked at a blank screen (there were also conditions in which a central fixation had to be maintained, but those are less relevant for our current argument). The results showed that scan patterns in the imagery task re-enacted those from the initial study task: The participants tended to fixate similar locations, in a similar order, in perception and in imagery. Most importantly, the correlation between scan patterns at encoding and at imagery predicted accuracy in a memory test. The results thus demonstrated that the re-enactment of scan patterns was not a mere epiphenomenon, but had a functional role in retrieval. Johansson *et al.* [44] first recorded eye movements of participants who were listening to a verbal description of a scene. When participants subsequently engaged in a recall task, in which they had to reproduce the scene description from memory, their eye

movement patterns were related to those observed at study. The effect also occurred in a condition where scenes were first visually inspected, after which the participants produced a verbal description from memory. Further evidence for the functional role of eye movements in memory comes from Tremblay *et al.* [17], who demonstrated that serial free recall of visual-spatial material was aided by eye movements that 'rehearse' the study input (serial presentations of dots in different spatial locations). Mäntylä and Holm [45] argued that eye movements mediate the nature of recollection. In their first experiment (in which participants made remember-know judgments in a face recognition task), eye movements were restricted or not either at study or at test, or at both. When eye movements were restricted (either during encoding or during retrieval) fewer 'remember' responses (which indicate explicit



### Box 2. Neurological systems underlying simulation

Although the neurological systems responsible for simulation are likely to be numerous and widely distributed, there is mounting and converging evidence to suggest that the parietal cortex and top-down (content-specific) activation from the prefrontal cortex to lower-level perceptual systems in the sensory cortex are central to simulation (e.g. [39–41,56]). For example, Mechelli *et al.* [40] demonstrated that visual perception of items varying in category membership (faces, houses and chairs) involved category-selective activation of the extrastriate cortex, which was mediated by content-sensitive feed-forward connections from early visual areas. In turn, visual imagery of the same categories involved top-down content-sensitive activations from the prefrontal cortex to the extrastriate cortex. This pattern of results suggests that information is stored in the perceptual and motor systems and can be reactivated by top-down activation from the prefrontal cortex. We propose that this reactivation process corresponds to a mental simulation that piggy-backs on the sensory-motor encoding neural circuits. It will be important to establish what differences in neural circuitry give rise to the explicit-implicit divide in mental simulations (see Box 1). In general, the data from ERP studies seem to support the idea that prefrontal cortical areas provide top-down activation of sensory-motor (posterior) areas [57,58]. However, ERP recordings from various source-monitoring recognition experiments present a mixed picture of the possible neural processes underlying simulation-based retrieval (see [57–59] for a review of ERP data on encoding-retrieval effects). In particular, a larger late posterior negativity (LPN) effect for old stimuli (compared with new stimuli) has been reported (e.g. [57,58,60]). Based on its locus and time course, the LPN effect has been taken as evidence for the retrieval of perceptual and procedural information in recollection of study details (e.g. [57]). However, Friedman *et al.* [60] reported no differences at recognition between the LPN for perceptually similar and perceptually dissimilar objects. They argued that the LPN reflected general source-specifying information retrieval. More recently, Mecklinger *et al.* [58] have reported a positive relation between the depth of encoding and the magnitude of the LPN effect. However, they also found a relation between encoding depth and activation over parietal areas, supporting the tentative conclusion that the LPN reflects both sensory-specific retrieval and more general retrieval mechanisms, such as search and feature binding [58,60]. This pattern of specific and general activation is consistent with a simulation involving multiple sources of information that acts to reconstruct an encoding event [57].

recollection) were given, whereas the ‘know’ responses (which measure familiarity) were not affected by eye movement restrictions. In a second experiment by Mäntylä and Holm [45], explicit recollection responses were associated with a greater degree of relatedness between gaze patterns at study and at test, providing further evidence that the recollective experience of an event is aided by the reactivation of processes related to encoding.

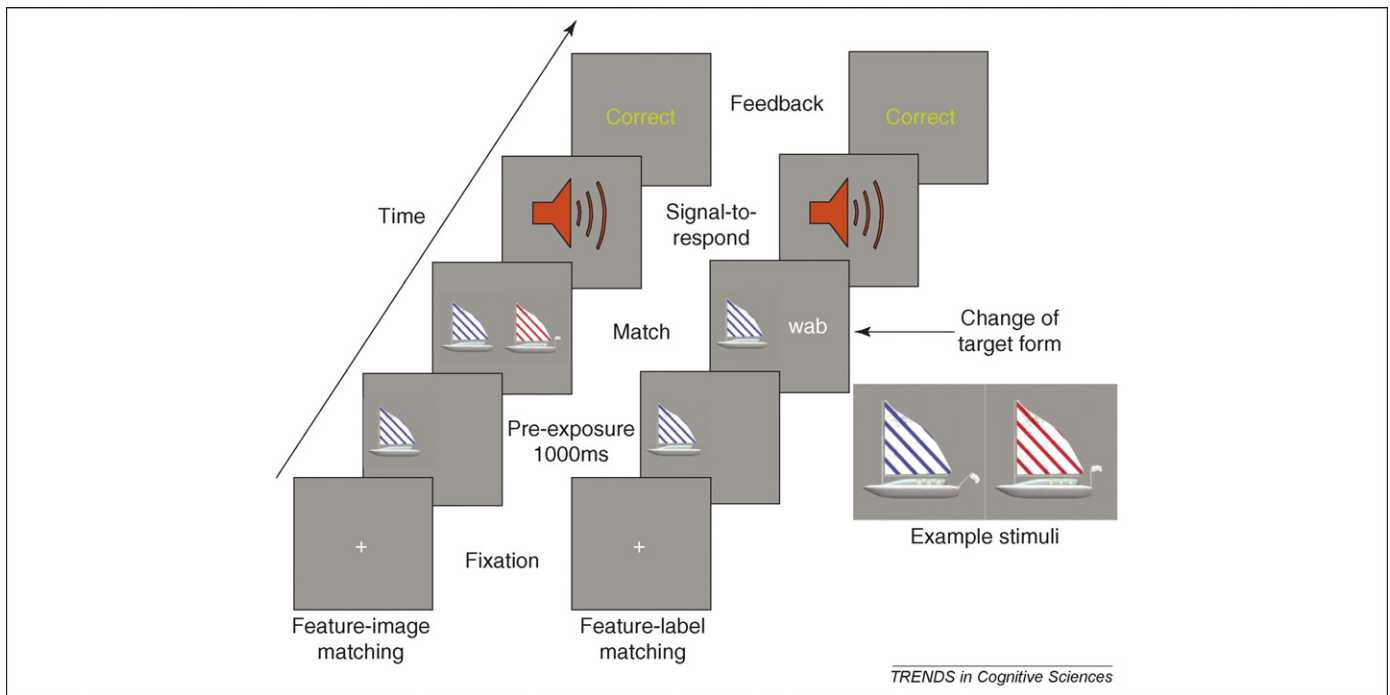
### The relationship between the time courses of encoding and retrieval

The evidence we have reviewed thus far indicates that there is a strong link between retrieval and perception: not only do retrieval mechanisms reactivate processes related to encoding, but also sensory-motor encoding procedures are stored and can aid retrieval when they are re-enacted. However, the exact nature of process reactivation and re-enactment remains unclear. It seems reasonable to assume that processes without direct sensory input cannot be entirely identical to processes that act on sensory information, but it remains unclear precisely which aspects of perceptual processing are preserved in simulations.

Recent research has started to address this question, by asking how the process characteristics of perception and retrieval are related. Understanding a cognitive process is tantamount to understanding its time course. If retrieval processes rely on perception processes, the time course of perception and the time course of retrieval must be related. For example, a strict reinstatement of the processes of encoding at retrieval would imply that the time course of retrieval should match that of encoding, such that information about a particular episode is retrieved in the same order in which it was originally acquired. However, given the strong evidence for the stochastic nature of perception and retrieval processes [46], it is unlikely that retrieval deterministically reinstates the order of encoding (see also [47] for event-related potential (ERP) evidence against deterministic reinstatement). Yet, the absence of a strictly deterministic relationship does not imply that there are no regularities in the relation between the time course of encoding and the time course of retrieval, and a

### Box 3. Measuring the time courses of encoding and retrieval

Kent and Lamberts [19] developed a technique to measure the time course of feature encoding and the time course of retrieval of feature information (based on the perceptual matching and recognition experiments described in Refs [18,20,50]). The paradigm involved participants learning to associate unique labels with a set of visual objects (in Ref. [19] this involved associating non-word consonant-vowel-consonant (CVCs) with eight objects constructed from three binary dimensions; for example, a sail boat that could differ in the colour of the sail, the orientation of a flag, and the shape of the portholes; see Figure 2). Once participants had learned the associations, they performed a series of simple matching tasks that required them to determine whether a single cued feature (e.g. a blue sail) matched the corresponding feature of a target object. The target presented was either the object itself (Feature-Image matching) or the associated label (Feature-Label matching) (Figure 2). A signal-to-respond procedure was used to limit the amount of processing time available in the matching tasks. At an unpredictable time after both the cue and the target were displayed a signal instructed the participant to respond immediately. The signal-to-respond method enabled us to measure how information had accumulated over time (Figure 3), and to estimate the speed of feature encoding or the speed of feature information retrieval. The Feature-Image matching tasks were assumed to involve only perceptual processes, which encoded the feature cue (in some tasks this cue was pre-exposed, as in Figure 2, enabling encoding before the matching task) and which encoded the target image for matching. The data from this task provided information about the rate at which stimulus information was encoded. The Feature-Label matching tasks were assumed to involve both a perceptual process, which encoded the feature cue (and the label), and a retrieval process, which recovered the feature information associated with the label. The Feature-Label matching task thus provided information about the rate of feature encoding and about the rate of feature information retrieval. The results from Ref. [19] showed that there were differences between the speeds at which different features were encoded (e.g. with the sail boat stimuli, the colour of the sail was encoded faster than the orientation of the flag, which was encoded faster than the shape of the portholes). We also demonstrated, for the first time, that information about the different features of an object was retrieved at different speeds. Further, the rate at which information was retrieved was linearly (positively) related to the rate at which it was encoded, such that features that were encoded relatively quickly were retrieved relatively quickly (see Figure 3).



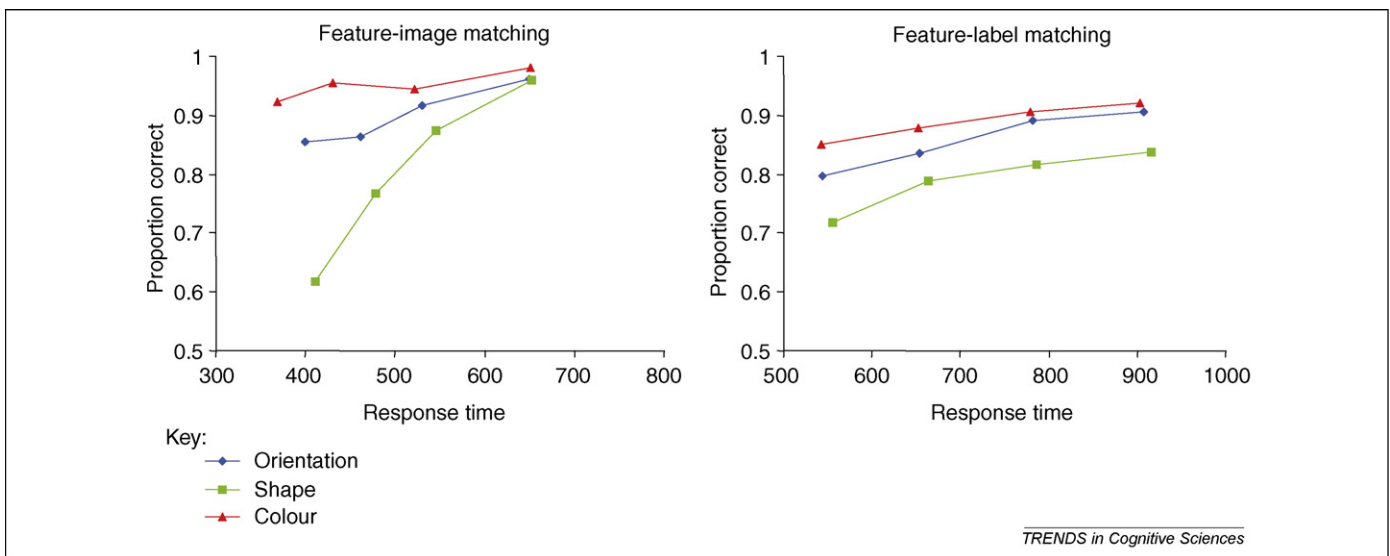
**Figure 2.** The trial structure of the Feature–Image matching trials and the Feature–Label matching trials used by Kent and Lamberts [19] (see Box 3). Kent and Lamberts [19] used an additional trial type in which the cued feature was simultaneously presented with the target (the pre-exposure stage was removed), which increased the amount of perceptual processing necessary during the match stage of the task. Note that the only difference between the tasks was whether or not, during the match stage, the object itself was presented (Feature–Image) or the label associated with the target object (Feature–Label).

growing body of research is attempting to uncover the characteristics of that relation.

Indirect evidence for a tendency towards serial re-enactment of encoding order was obtained by Thomas et al. [48], who demonstrated a response time advantage for forward (congruent) recall over backward (incongruent) recall. These results are consistent with a retrieval mechanism that recovers items in the order in which they were encoded. In the forward condition, items could be reported immediately once they were retrieved. In the

backward recall condition, the response times suggested that repeated forward looping through the list (or at least parts of the list) was needed before recall could be completed.

It is well known that the features of a visual object or scene are not all perceived at the same time (e.g. [49]). Although feature processing times are inherently stochastic, salient features tend to be processed faster than less salient features (e.g. [50,51]). Kent and Lamberts [18–20] examined the stochastic properties of the time course of



**Figure 3.** Data from a Feature–Image matching task (left graph) and a Feature–Label matching task (right graph) (Experiment 2, sequential matching tasks from Ref. [19]; see Box 3). The plots represent proportion correct as a function of response time (signal onset time + lag, in milliseconds) for the three stimulus features of the sail boat stimuli (see Figure 2). Accuracy increased with an increase in processing time. The clear differences between the features present at shorter processing durations, disappear at longer processing times. Crucially, the horizontal ordering of the features is the same in both the Feature–Image and Feature–Label matching tasks, indicating a relationship between the speed with which features are encoded and the speed with which feature information is retrieved.

feature retrieval in relation to the time course of feature perception. Using various speeded perceptual and memory tasks (Box 3 and Figure 2), they demonstrated that there was a close relation between perception rates and retrieval rates of object features [19,20] (see also [52]). The nature of this relation depended crucially upon the memory demands of the task [18,20]. When the retention demands were low (such that the encoded information could be kept in a readily accessible short-term store), there were no differences in retrieval rates between features. When the retention demands exceeded the capacity of immediate visual memory, however, significant differences in retrieval rates emerged. Although retrieval was slower than perception, features that tended to be perceived quickly also tended to be retrieved quickly [19,20] (Figure 3). These results do not imply that the time course of retrieval is completely determined by the time course of encoding (as would have been assumed in deterministic reinstatement models), but they do indicate that there is a strong stochastic relation between encoding and retrieval processes.

### Concluding remarks

In summary, three rapidly developing research strands support the idea that retrieval involves mental simulation of the original encoding event: (i) specific cortical areas involved in perception overlap with areas activated at retrieval of the same perceptual material; (ii) re-enactment of encoding processes is functional for retrieval; and (iii) the time courses of perception and retrieval are closely related. Studies looking more closely at the time courses of retrieval and encoding will help specify the exact nature of simulator-based retrieval (see Box 4). Current evidence suggests that retrieval is one of many possible cognitive mechanisms that could rely on mental simulation [24]. Regardless of whether mental simulations underlie retrieval in all cases, it is essential that memory theorists and perception theorists alike realize the importance of the encoding–retrieval relationship when designing experiments and building models of cognition.

#### Box 4. Questions for future research

- Do all retrieval tasks involve simulation, or do some tasks rely on non-simulation-based retrieval? If so, what factors determine whether a simulation is necessary?
- How do cueing and priming work within a simulator-based retrieval system? For example, how does semantic overlap affect cue effectiveness, especially when the items involved are perceptually different?
- How do processes such as working memory, attention and rehearsal relate to simulations? Are they inherently interconnected, or are they separate systems?
- How flexible are simulations? Can episodes be simulated at any arbitrary point, or must they start and end at set points?
- To what extent are simulations veridical to encoding episodes? Why and how do errors occur in simulation?
- Do perception-based simulations give rise to nonperceptual forms of representations? If so, how?
- Does the nature of simulation change over time, either developmentally or over repeated simulations of the same representation?

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