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Validating neural correlates of familiarity

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Familiarity is a pervasive memory phenomenon that occurs in its most basic form when someone recognizes a repeated stimulus without recollecting other aspects of the requisite prior learning episode. Theoretical controversy currently abounds with respect to both the cognitive and neural characteristics of familiarity. Here, we show that the extant data, particularly brain-potential data, are insufficient for validating putative neural correlates of familiarity, and we outline strategies for making progress on this problem. Conceptual priming is an implicit-memory phenomenon that often occurs together with familiarity; experiments that conflate the two phenomena can be misleading. Avoiding this conflation is required to understand familiarity and to determine the extent to which the neurocognitive processes that support priming also drive familiarity.

Introduction

Imagine the ease with which neural substrates of cognition could be dissected if relevant brain processes could be toggled on and off at the mere flip of an experimenter's switch. In reality, much greater effort is required to link patterns of brain activity to elemental units of cognition. Such a challenge in the field of memory research is especially thorny owing to the concurrent emergence during various types of memory testing of multiple expressions of memory (Box 1). These include explicit memory, which entails a conscious memory experience, and implicit memory, which can occur without any awareness of remembering.

The problem of linking brain activity to memory is perhaps most pronounced with respect to one expression of explicit memory known as familiarity. This impression of previous occurrence can be strong, as in déjà vu or butcher-on-the-bus experiences [1,2]. In both cases, we might claim that an object or event is familiar even though we cannot remember specific details regarding a previous encounter. Despite a recent explosion of research on familiarity, many questions remain unanswered about the underlying neurocognitive mechanisms. A controversial stance that strikes at the heart of the distinction between explicit memory and implicit memory is the proposal that the neurocognitive processes that support implicit memory also drive familiarity [3].

Neurophysiological evidence purported to pertain to familiarity has been widely cited for its presumptive relevance not only for understanding familiarity but also for understanding fundamental relationships among various memory phenomena. In particular, many investigators have claimed that FN400 potentials (also known as midfrontal old/new effects; Figure 1a) reflect familiarity (see Ref. [4], and Rugg and Curran [5] in this issue). Here, we argue that implicit memory must be examined more extensively before accepting this claim.

To reach a valid understanding of familiarity, we must actively consider both familiarity and conceptual priming, a type of implicit memory wherein conceptual information cued by a given stimulus is processed differentially as a function of a specific prior experience. Conceptual priming might be operating under typical circumstances of investigations of familiarity, although this possibility has often been underappreciated. In this regard, FN400 potentials might or might not be good markers of familiarity – they might partly or in their entirety reflect co-occurring mnemonic processes that are responsible for conceptual priming effects. Unfortunately, conceptual priming has yet to be extensively investigated in this field.

Here, we outline the literature on familiarity and event-related brain potentials (ERPs), and we describe the sort of evidence needed to adjudicate between the opposing views on the status of FN400 as a putative neural correlate of familiarity. The strategies we advocate hold promise for making progress in this area and also more generally for building neurocognitive explanations for a variety of memory phenomena.

Contemporaneous memory events in recognition tests

Recollection and familiarity are phenomenologically distinct expressions of explicit memory. They differ depending on whether retrieval is accompanied by simultaneous access to pertinent contextual or associative detail (recollection) or unsubstantiated by such detail (familiarity). Dual-process models hold that recollection and familiarity provide unique contributions to recognition [3] or that a unidimensional memory-strength variable is derived from graded recollection and familiarity signals [6]. Both recollection and familiarity are impaired in patients with amnesia, although the extent of familiarity impairment is somewhat controversial [7,8].

Priming effects, by contrast, do not entail any conscious experience either of memory access or of a learning episode (Box 1) and are usually intact in amnesia [9–11]. Conceptual priming, for example, can occur when a word or picture

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Box 1. Memory diversity

Memory is not a unitary behavioral capacity but instead refers to a large set of abilities (Figure I). Although numerous schemes have been used to classify memory phenomena, there is considerable consensus for singling out one type known as **declarative** or **explicit memory**. This form of memory is often accompanied by the awareness of remembering, for example, when people bring to mind an event from the past and figuratively re-live it.

In a recognition test, stimuli can be recognized in a very restricted manner when the subject experiences a sense of **familiarity** that is not accompanied by retrieval of specific aspects of the learning episode. Alternatively, recognition can take place together with a full-blown experience of **recollection**. Various behavioral measures have been used to distinguish between recollection and familiarity.

Many types of memory do not fit into the category of declarative memory. Among expressions of memory classified as non-declarative memory, **priming effects** are behavioral changes observed in

special tests that make no reference to previous learning episodes (implicit memory tests).

When a priming effect is produced, the awareness of memory retrieval is optional and sometimes even counterproductive. Priming effects can be categorized in several different ways, and might vary depending on the stimuli (e.g. words versus faces) and task (e.g. production versus verification).

Priming subtypes have also been described with respect to stimulus meaning (**perceptual priming** and **conceptual priming**). Perceptual priming might result from sensory processing independent of meaning. However, perception usually entails access to meaning, and priming can also result from alterations in meaning-based analyses – therefore priming might be perceptual, conceptual or both, in different circumstances. Priming can also result from new associations formed within an experiment. Further distinctions can be made according to the nature of these associations, which might cross stimulus domains or sensory modalities.
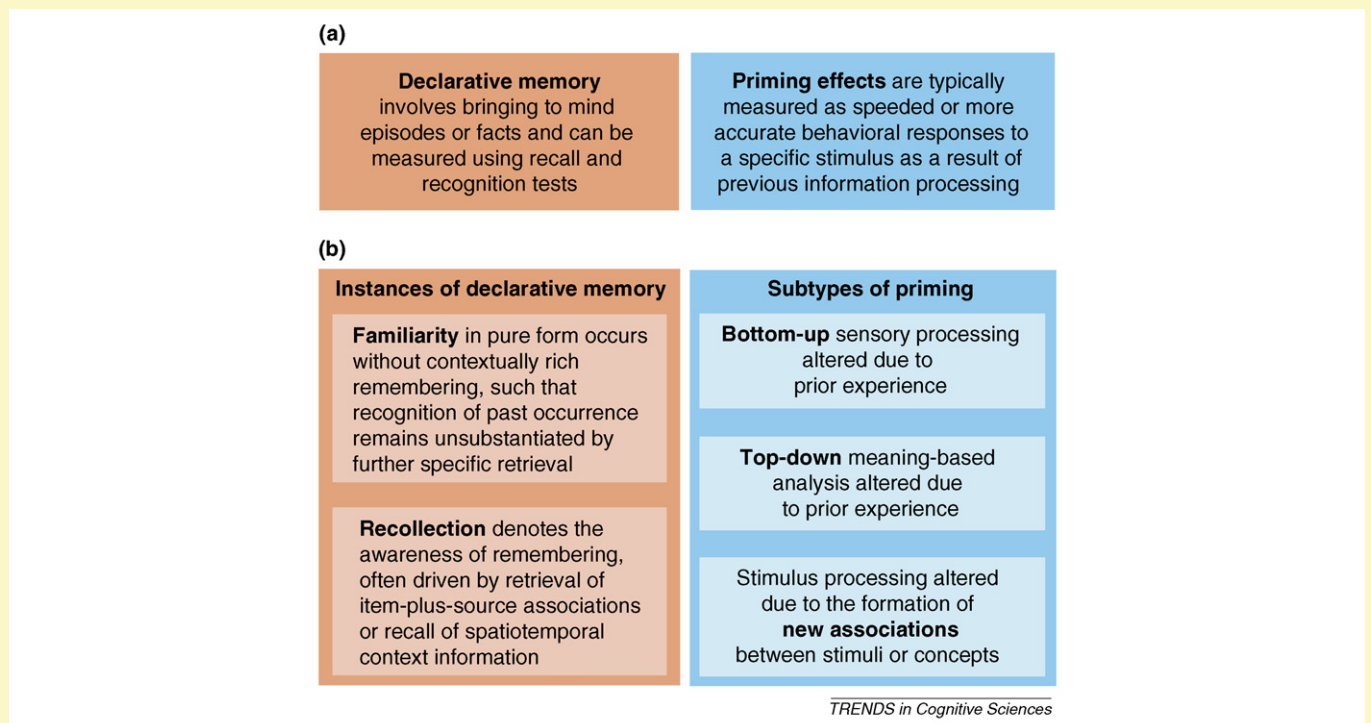
(a)

| **Declarative memory** involves bringing to mind episodes or facts and can be measured using recall and recognition tests | **Priming effects** are typically measured as speeded or more accurate behavioral responses to a specific stimulus as a result of previous information processing |

(b)

Instances of declarative memory

Familiarity in pure form occurs without contextually rich remembering, such that recognition of past occurrence remains unsubstantiated by further specific retrieval

Recollection denotes the awareness of remembering, often driven by retrieval of item-plus-source associations or recall of spatiotemporal context information

Subtypes of priming

Bottom-up sensory processing altered due to prior experience

Top-down meaning-based analysis altered due to prior experience

Stimulus processing altered due to the formation of **new associations** between stimuli or concepts

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Figure I. Memory definitions.

cues access to corresponding meaning that is consequently processed differently later. Conceptual priming can be distinguished from priming tied to the physical form of a stimulus (known as perceptual priming). Priming tests might be sensitive to both types of priming. Although the division between perceptual priming and conceptual priming is open to debate, considering the overlap between conventional notions of perceptual and conceptual processing, here we take conceptual priming to pertain to meaning that goes beyond the physical characteristics of a stimulus in a particular modality.

Central to our argument is the contention that the neural events supporting recollection, familiarity and both forms of priming can take place simultaneously during recognition testing, even if corresponding behavioral measures are not collected (Box 2). It has been widely acknowledged that some implicit memory tests can provide behavioral measures contaminated by explicit

memory processes. Here, we emphasize that neural measures obtained during a memory test are subject to a parallel problem that has been acknowledged much less often than behavioral contamination. In particular, neuroimaging measures collected during recognition tests might be contaminated by co-occurring implicit-memory phenomena.

Many experiments have contrasted old and new items in recognition tests to reveal putative ERP signatures of recognition that included positive parietal potentials from ~300–800 ms (greater for old than for new items). Logically, however, these potentials could reflect other mnemonic processes, such as priming, recognition confidence or novelty detection. Multiple experimental manipulations have been used to rule out these possibilities (see Figure 1 for examples), fostering the consensus that these late posterior ERPs can index retrieval processes that support recollection.
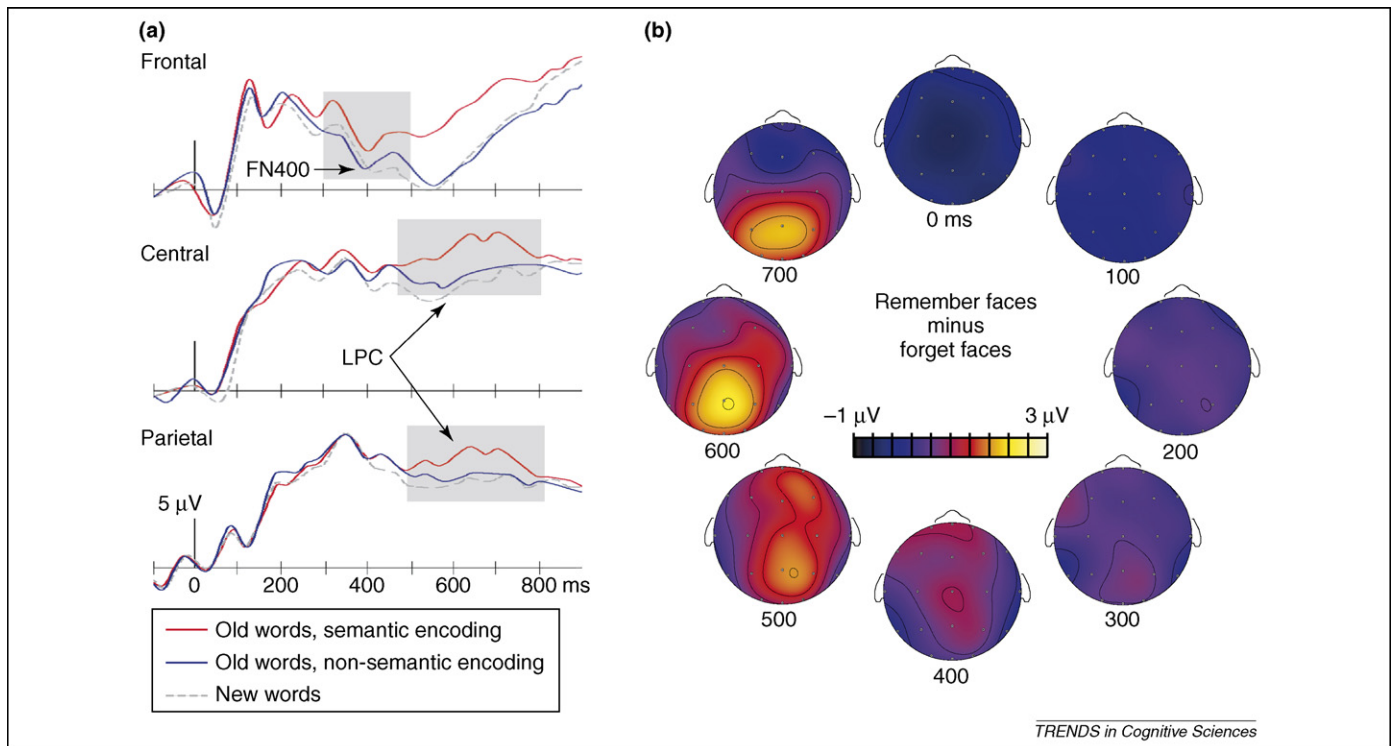
Figure 1. FN400 potentials and ERP correlates of recollection. **(a)** ERPs for old and new words in a memory paradigm [29]. The ERP method entails extracting time-locked potentials from scalp-recorded EEG records by averaging across various stimulus-, task- or response-defined conditions. Memory effects at retrieval typically involve more-positive ERPs for old items than for new items. Old/new ERP effects in this experiment can now be interpreted as encompassing FN400 potentials at frontal locations and a late positive complex (LPC) at posterior locations. Words were presented during an implicit memory test, including old words previously subjected to semantic encoding (visual imagery of corresponding objects) versus non-semantic encoding (emphasizing orthography). Semantic encoding led to relatively better recall and recognition, in addition to incidental recollection during the implicit memory test. Recollection was thus associated with ERP differences between these two conditions (red and blue traces) as magnitude of perceptual priming was matched. Conceptual priming was not assessed. Waveforms shown were from three midline scalp locations (Fz, Cz and Pz). **(b)** A parallel experimental strategy was used to obtain electrophysiological correlates of recollection cued by faces in a recognition test [30]. Some faces had been learned while subjects intentionally associated them with biographical information; other faces were viewed for the same duration while subjects tried to forget them. Episodic recognition of these faces was superior in the former condition, which was presumed to engage recollection given that subjects accurately recalled the associated biographical information. By contrast, the two conditions led to the same magnitude of perceptual priming in a perceptual-identification test with visually degraded facial images. The ERP contrast between these two conditions (remember faces versus forget faces) in an explicit memory test thereby provided neural correlates of recollection, shown here as topographic maps for consecutive 100-ms intervals starting at face onset (0 ms). Each map depicts difference amplitudes on the scalp as if viewed from above with the nose at the top. Posterior ERP differences apparent from 400–800 ms were thus associated with recollection independent of perceptual priming. Adapted, with permission, from Refs [29,30].

Empirical links between FN400 potentials and familiarity, however, are less clear, and much of the evidence is indirect. The typical reasoning can be summarized as follows: FN400 potentials are insensitive to some experimental manipulations that enhance recollection, and are often associated with familiarity experiences during recognition tests. Essentially, FN400 potentials have been attributed to familiarity through a process of elimination – they are neural markers of memory that do not index recollection, and so seemingly must index familiarity.

This interpretation is problematic because these potentials could instead index an unknown combination of familiarity and other co-occurring memory phenomena. Indeed, the prospect of contamination by conceptual priming is highly likely given that familiarity and conceptual priming overlap considerably in their sensitivity to experimental manipulations [3,12], and so might operate similarly in many experiments. The possibility that familiarity responses are driven by processes underlying perceptual or conceptual priming has been intensely debated in recent years. To make progress in this regard, we therefore argue that it would be a mistake to assume either that familiarity is inherently a result of priming or that familiarity is always orthogonal to priming, as is common in the

FN400 literature. Rather, we need to make efforts to conduct separate neural analyses of familiarity and priming without conflating the two [13–17].

Evidence that FN400 reflects conceptual priming is also mostly indirect and currently rather sparse. An association was first suggested by the finding that word repetition produced normal modulations in potentials similar to FN400 in patients with amnesia [18]. These N400 potentials were equally large at frontal and parietal locations (as in many studies linking N400 to semantic integration [19]). By contrast, only later positive potentials showed correlations with explicit memory. Although the frontal extent of N400 was not directly associated with measures of conceptual priming, a connection was conceivable [18] given that patients with amnesia can exhibit intact conceptual priming despite their impoverished explicit memory [16].

Evidence taken as support for the 'familiarity-equals-FN400' hypothesis
The notion that FN400 potentials index familiarity has frequently been invoked by citing the distinct neural correlates obtained through a manipulation of word plurality [20]. Words were presented with a different plurality at
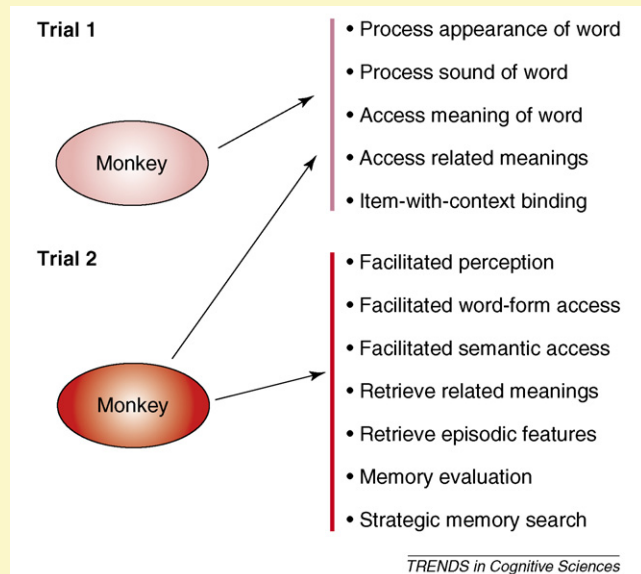
initial encoding and memory testing, or with a consistent plurality. The former were thought to be recognized with less recollection, whereas estimates of familiarity were comparable in the two conditions. In common with previous findings, late-positive ERPs were greater for consistent-plurality compared with inconsistent-plurality words. FN400s, however, were not affected by plurality reversal, and so were taken to reflect familiarity.

Although conceptual priming was not measured in this study, plurality reversal should exert minimal influence on the magnitude of conceptual priming because reading the same word – whether singular or plural – is likely to activate equivalent conceptual networks. Indeed, altering surface characteristics of words, a manipulation akin to plurality reversal, reduces recognition but not priming [21]. This kind of FN400 pattern [20] is thus equally amenable to familiarity or conceptual-priming interpretations.

The majority of reports claiming to link familiarity and FN400s are subject to similar interpretive limitations. The literature is summarized in Table 1. Manipulations that influence both familiarity and conceptual priming in the same way are insufficient for adjudicating between the two positions. Only a few studies employed manipulations with differential effects on familiarity and conceptual priming. Overall, results do not support the familiarity account over the conceptual-priming account. Although a few findings favor one or the other position, conclusive support for either interpretation is lacking.

One recent study purported to directly support the 'familiarity-equals-FN400' hypothesis [22] likewise fails in this regard. Phenomenological recollective assessments

were conjoined with familiarity-confidence ratings (with four response options if recollection was absent: confident old, unconfident old, unconfident new and confident new). FN400 amplitude varied with familiarity confidence. However, old and new items were collapsed to form ERPs for each familiarity-confidence level; lower familiarity implied a lower proportion of old relative to new items. The observed FN400 effect could thus have arisen merely from the different proportion of old and new items at each level. Although the authors attempted to take this into account in another analysis, this follow-up analysis was unconvincing owing to its reduced statistical power and a bias to produce reduced old/new effects because most trials were selected from the two low-confidence conditions (~72% of those trials selected). Furthermore, a fundamental limitation of this study is the absence of measures of conceptual priming. The authors' assumption that conceptual priming was orthogonal to familiarity confidence is unwarranted. It is possible that the same factors responsible for variations in familiarity confidence across trials – although not identified in this study – could have also led to parallel variations in conceptual fluency. Thus, evidence for attributing FN400 to familiarity in this study is no stronger than the evidence for attributing FN400 to conceptual priming. Similar concerns also apply to an fMRI experiment using the same design [23].

In another study ostensibly supporting the 'familiarity-equals-FN400' hypothesis, criteria for making 'old' responses in a recognition test were manipulated [24]. In the conservative-criterion condition, recognition hits were presumably based on stronger familiarity, on the whole, than in the liberal-criterion condition; FN400s for correct-old and correct-new items were more positive with the conservative criterion. Results were thus taken to indicate that FN400s reflected familiarity. Yet, an alternative interpretation is that encoding that produced strong explicit memory also produced enhanced conceptual priming, such that the conservative criterion led to stronger explicit and implicit memory in each condition, on average. Furthermore, even new words could be subject to differential conceptual fluency, if recent processing of related concepts unevenly activates words in this condition. False alarms might be more likely for precisely the words for which associated meaning was most strongly (but indirectly) activated. By this account, the conservative/liberal contrast did not dissociate the two types of memory (and the same argument applies to the use of inclusion tasks to influence response criteria, e.g. [25]). Again, we question the assumption that familiarity and conceptual priming are orthogonal, especially when behavioral results concern only explicit memory, as in these studies.

How should we arbitrate between conceptual priming and familiarity?

We assert that it is necessary to collect behavioral measures of both conceptual priming and familiarity to determine their respective contributions to neuroimaging measures. This step is a prerequisite for determining whether FN400 potentials are more tightly linked to familiarity or to conceptual priming, given the viability

Table 1. The FN400 literature includes results that support the familiarity account (blue) and results that support the conceptual priming account (green), although most findings are ambiguous with respect to these two accounts (red)[a]

Variable	Effect on familiarity	Effect on conceptual priming	Effect on FN400 difference	Reason for FN400 functional interpretations
Perceptual transition	Minimal reduction	Minimal reduction	None [20,31,32] Reduction [33,34]	FN400s for original and perceptually altered stimuli were similar in some studies; in others there were differences. Although effects on familiarity and conceptual priming might depend on the circumstances, the two types of memory tend to show similar responses to perceptual manipulations (e.g. changing word plurality, mirror reversal of pictures and auditory-to-visual shifts), owing to facilitated implicit or explicit access to conceptual representations.
Depth of encoding	Minimal increase	Minimal increase	None [35,36] Increase [29,37,38]	FN400s for deep and shallow encoding were sometimes similar and sometimes increased for deep encoding. Depth of encoding does not exert differential effects on the two types of memory.
Quantity of recollected information	None	None	None [20,39,40]	FN400s were unrelated to source retrieval, and source retrieval takes place irrespective of familiarity or conceptual priming strength.
Divided attention during encoding	Reduction	Possible reduction	None [41] Reduction [41]	Similar FN400s after full or divided attention during encoding (experiment 1) or FN400s reduced after divided attention (experiment 2). Divided attention at encoding reduces behavioral estimates of familiarity and conceptual priming, but effects on conceptual priming are contentious. Whether divided attention exerts differential effects is thus unclear.
Drug-induced memory impairment	Minimal reduction	Minimal reduction or none	None [42]	FN400s were not influenced by benzodiazepines. Administration of benzodiazepines during encoding reduces familiarity, whereas effects on conceptual priming are inconsistent. These FN400 results thus do not fit well with either hypothesis.
Retrieval intention	Increase	None	None [43,44] Increase [34,46,47]	Similar FN400s were noted when retrieval was intentional or incidental in some studies, but FN400 effects were reduced or absent for incidental retrieval in others. Retrieval intention usually enhances familiarity (but see Ref. [45]), whereas conceptual priming is theoretically unaffected (though behavioral data on this are lacking and perhaps problematic to obtain).
Organic amnesia	Reduction	None	None [18]	Changes in N400 due to word repetition were similar in amnesic and control subjects. Results favor a conceptual priming account of FN400, given that the anterior portion of N400 potentials in this study were subject to normal repetition effects and that amnesia disrupts familiarity but not conceptual priming [16].
Directed forgetting	Reduction	Possible reduction	Reduction [38]	Smaller FN400 old/new effect for forget words than for remember words were seen. However, evidence of specific effects of directed forgetting on conceptual priming and familiarity is mixed and might depend on the extent to which the directed-forgetting manipulation influences semantic processing, so generalizations are unclear.
Recognition confidence	Increase	Possible Increase	Increase [22,41]	Larger FN400s were seen for high- compared with low-confidence recognition. Whereas familiarity increases with response confidence, it is plausible that conceptual priming concomitantly increases in some circumstances, so it is unclear whether recognition confidence produces differential effects on the two types of memory.
Aging	Possible reduction	Possible reduction	Reduction [39]	Reliable FN400s in control subjects but only a trend in the elderly. Familiarity is commonly thought to decline with age, whereas conceptual priming might or might not [48,49], so it is unclear whether healthy aging produces differential effects.

[a]A representative sample of relevant studies from the ERP literature was included. Most studies did not provide behavioral measures of familiarity, and none provided behavioral measures of conceptual priming. Memory effects shown are estimated on the basis of theoretical accounts of familiarity and conceptual priming, or in some cases on separate behavioral experiments. Despite the fact that these studies have been repeatedly used in the literature to support the 'FN400-equals-familiarity' account, interpretations are unconvincing with respect to associating FN400 with either familiarity or conceptual priming because of the absence of behavioral indices of the two types of memory under circumstances matching those in which FN400 potentials were recorded.

of both possibilities at present. It is also necessary to find circumstances wherein the two memory phenomena are not highly correlated with each other across trials. Neural measures differentially associated with familiarity versus conceptual priming can then be identified.

Voss and Paller [17] recently employed a novel behavioral paradigm to obtain ERP correlates of memory for famous faces. During equivalent viewing of two sets of faces, the potential for conceptual priming was enhanced selectively for one set by presenting corresponding biographical information. Subsequently, subjects discriminated famous faces from non-famous faces. Fame decisions were faster and more accurate for primed compared with unprimed famous faces, providing a behavioral measure of conceptual priming. ERP results linked conceptual priming with FN400 (Figure 2). ERP correlates of explicit memory for famous
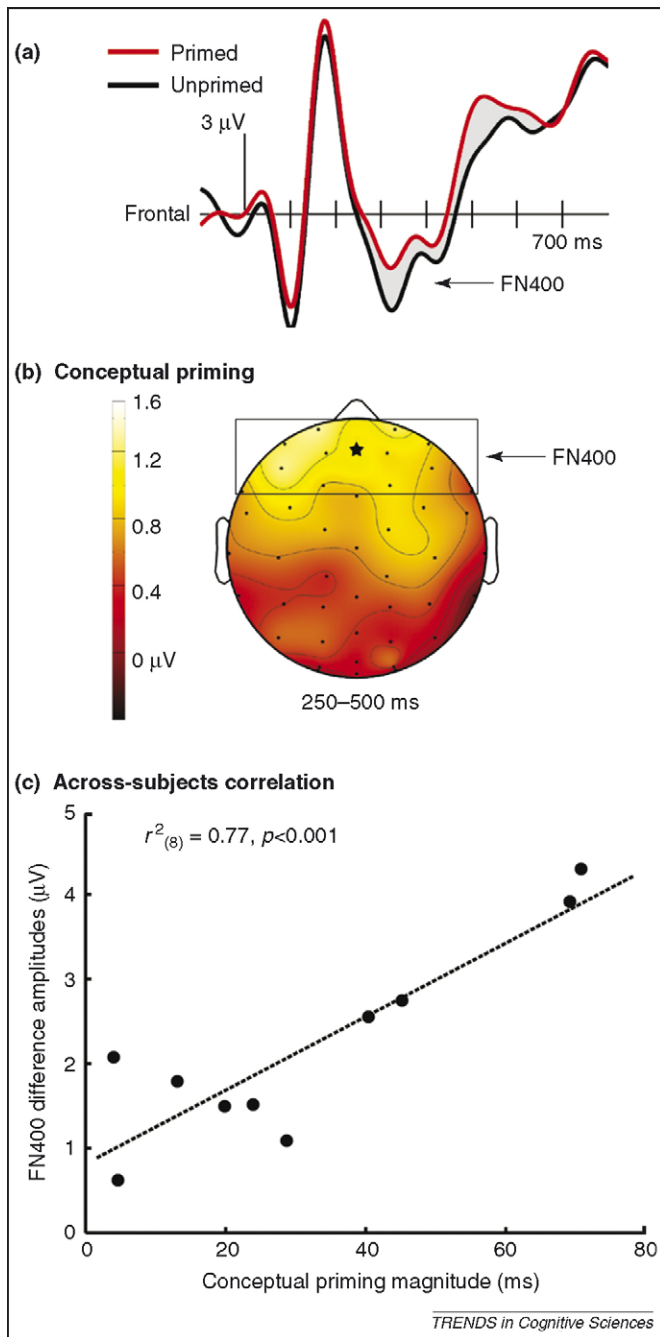
Figure 2. Conceptual priming for famous faces elicited an FN400 effect [17]. **(a)** This ERP effect was observed by contrasting conceptually primed and unprimed faces that were all subjected to the same visual exposure, which should produce the same degree of perceptual priming [30]. **(b)** The distribution of the ERP difference on the scalp, as viewed from above, was maximal at anterior locations. The effect was clear at mid-frontal scalp locations where FN400s are typically described (including Fz, the frontal location marked with a star and used for the waveforms in a). **(c)** Behavioral measures of conceptual-priming magnitude were strongly correlated across subjects with FN400 difference amplitudes. By contrast, conceptual priming was not correlated with late posterior potentials also identified during the performance of the same task. Instead, late posterior potentials were correlated with a behavioral measure of explicit memory obtained later in the experiment. Thus, FN400 potentials directly track conceptual priming for famous faces, and this relationship can be dissociated from neural correlates of explicit memory. Adapted, with permission, from Ref. [17].

faces comprised late, posterior-centered potentials resembling those identified with familiarity for non-famous faces in other experiments [2,26]. Across experiments, behavioral measures of both types of memory thus enabled neural

correlates of conceptual priming to be dissociated from those of familiarity. This method exemplifies the approach we advocate to arbitrate between the two alternatives, and it provided direct evidence that FN400s can selectively index conceptual priming.

Novel human faces activate much less conceptual information than famous faces, and the finding that introspectively rated familiarity for faces elicited later posterior potentials, not FN400s, was taken by Yovel and Paller [2] to fit with the hypothesis that these potentials instead reflect conceptual priming. In subsequent studies with novel faces, however, FN400 effects were sometimes present [27] and sometimes absent [26]. An interpretation of these conflicting results is that a heterogeneous set of face stimuli [27] provides richer facial meaning of a conceptual nature (e.g. associations to concepts of class, race or personality), thus engaging more conceptual activation for repeated faces and greater FN400 effects. In other words, FN400 effects with novel faces might be absent only when the potential for conceptual priming is minimal. Testing this idea requires that behavioral measures of conceptual priming be included.

Although faces were used in the aforementioned studies [2,17,26,27], similar approaches could be used with many types of verbal and non-verbal stimuli to assess whether generalizations should or should not be made across stimulus categories. Indeed, another tactic for studying neural correlates of familiarity uses stimuli low in inherent meaning, such as minimalist artwork, pseudowords or squiggles (Box 3). For example, by dissociating explicit memory and conceptual priming for squiggles behaviorally, Voss and Paller [28] showed that distinct ERPs were associated with the two types of memory – posterior ERPs with explicit memory and FN400 potentials with conceptual priming. An additional approach would be to isolate ERP correlates of conceptual priming produced in the absence of explicit memory, as might happen with subliminal word presentations, drug-induced amnesia or in patients with an amnesia dense enough to rule out subtle contributions from explicit memory.

Valid neural correlates of familiarity can be attained
Although the extant data are insufficient for validating neural correlates of familiarity, this situation is likely to improve. Future studies should strive to account for conceptual priming and familiarity by quantifying memory performance for both phenomena.

Are conceptual priming and familiarity causally linked [3] or, as evidence from amnesia suggests [16], is familiarity a weak form of memory largely independent from priming? Identifying valid and distinct neural correlates of familiarity and conceptual priming might ultimately permit a systematic evaluation of these possibilities and of the notion that everyday memory experiences reflect interactions between familiarity and conceptual priming. Neural correlates of memory will help to solve these puzzles only if cross-contamination does not effectively conflate the two types of memory.

Our warning call to avoid mistakenly associating a specific neural measure with the memory experience of familiarity can be extended to any neuroimaging

Box 3. Disentangling meaningfulness and memorability using squiggles

Stimuli low in inherent meaning have been used during recognition testing on the assumption that such stimuli cannot support conceptual priming and thus can be used to isolate uncontaminated neural correlates of familiarity [44,50]. However, some of these stimuli can be idiosyncratically perceived as meaningful (such as imagining that a cloud resembles an animal or a Rorschach splotch a couple embracing). When subjects are asked to remember such stimuli, we claim that this is exactly the mnemonic strategy they tend to invoke. Squiggles (as in the examples in Figure Ia) can engender conceptual priming to the extent that the subject infers meaning when viewing the squiggle [28,50]. Accordingly, we recently found that these stimuli varied in subjective meaningfulness such that the potential for conceptual priming could be assessed and dissociated from familiarity strength [28]. Conceptual priming was shown by speeded meaningfulness ratings for repeated stimuli, but only for stimuli rated high in meaning (Figure Ib). Further results from control conditions showed that the response facilitation was not due to perceptual priming, response priming or explicit retrieval. We also found that this conceptual priming for squiggles occurred in conjunction with FN400 effects [28]. Similar experimental strategies could be fruitfully applied with other sorts of minimally meaningful stimuli. To the extent that the dimensions of familiarity and conceptual priming are orthogonal in such experiments, neural measures can separately be attributed to familiarity or conceptual priming.
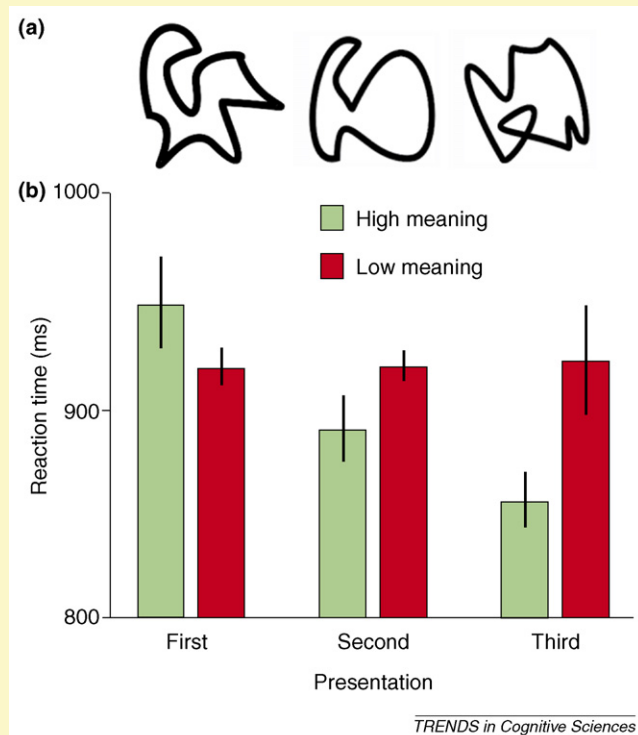

Figure I. Minimalistic 'squiggle' stimuli **(a)** have been used in various implicit and explicit memory tests [28,50]. The graph **(b)** shows results from an implicit memory test [28] in which subjects used a four-point scale to rate stimulus meaningfulness: 1 = looks like a nameable object, face or animal; 2 = looks like a more abstract nameable object, face or animal; 3 = does not look like anything nameable but is in some way meaningful; 4 = a random collection of lines that is in no way meaningful. Ratings were idiosyncratic in that most stimuli were meaningful for some subjects but not for other subjects. In one experiment, squiggles were presented in a continuous-repetition design with a lag of 5-15 trials from first to second presentation. Conceptual priming was observed as a response–time decrease with repetition for stimuli endorsed at the highest two ratings (high meaning) but not for those endorsed at the lowest two ratings (low meaning). Results from an experiment using an explicit memory test for squiggles showed that familiarity-based recognition was associated with positive ERPs that were more posterior and later than those associated with conceptual priming [28].

experiment in which the neurocognitive processes contributing to performance on a particular task are under-specified by corresponding behavioral measures. Neuroimaging provides an unparalleled window into brain events that support cognition, but the theoretical usefulness of these data depends on an accurate mapping of cognitive phenomena to neural measures.

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