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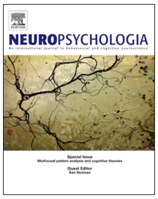

Reviews and perspectives

What is a memory schema? A historical perspective on current neuroscience literature

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ABSTRACT

The term "schema" has been used to describe vastly different knowledge structures within the memory neuroscience literature. Ambiguous terminology hinders cross-study comparisons and confounds interpretation of the suggested role of the ventromedial prefrontal cortex (vmPFC) in schema functions. Based on an extensive review of the psychological literature, we propose a framework for distinguishing memory schemas from other knowledge structures. The framework includes a definition of *schema* as possessing four necessary and sufficient features, and four additional features schemas are sensitive to, which are not required but do play a frequent and central role in schema functions. Necessary schema features are (1) an associative network structure, (2) basis on multiple episodes, (3) lack of unit detail, and (4) adaptability. Features schemas are sensitive to are (5) chronological relationships, (6) hierarchical organization, (7) cross-connectivity, and (8) embedded response options. Additionally, we suggest that vmPFC activity observed in studies of schemas corresponds with participants' coordination of existing schemas with ongoing task demands.

Contents

1. Introduction . . . 105
2. Emergence of the "schema": Historical milestones . . . 105
3. Defining features . . . 106
    3.1. Necessary features . . . 106
        3.1.1. Associative network structure . . . 106
        3.1.2. Basis on multiple episodes . . . 106
        3.1.3. Lack of unit detail . . . 106
        3.1.4. Adaptability . . . 108
    3.2. Features to which schemas are sensitive . . . 109
        3.2.1. Chronological relationships . . . 109
        3.2.2. Hierarchical organization . . . 109
        3.2.3. Cross-connectivity . . . 109
        3.2.4. Embedded response options . . . 109
4. Related cognitive structures . . . 110
    4.1. Narratives . . . 110
    4.2. Concepts and categories . . . 110
    4.3. Event gists . . . 110
    4.4. Statistical regularities . . . 110
5. Schemas and the ventromedial prefrontal cortex . . . 110
    5.1. Neuroscience studies on schemas . . . 111
6. Concluding remarks . . . 113
References . . . 113

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1. Introduction

It has long been observed that prior knowledge, and schema representations in particular, influence memory formation and retrieval (Anderson, 1984; Bartlett, 1932; Carmichael, Walter, & Hogan, 1932; Craik & Lockhart, 1972; Posner & Keele, 1968). Cognitive neuroscientists have investigated the influences of semantics and knowledge congruency on memory for almost two decades (e.g. Demb et al., 1995; Kapur et al., 1994; Wagner et al., 1998). However, only recently has there been investigation into the neural mechanisms of more complex knowledge structures such as schemas. Specifically, the ventromedial prefrontal cortex (vmPFC), and its interaction with the hippocampus and posterior neocortex, have been implicated in the facilitation of encoding of new information by prior schemas (Tse et al., 2011; Van Kesteren, Fernández, Norris, & Hermans, 2010a; Van Kesteren, Rijpkema, Ruiter, & Fernández, 2010b; Wang, Tse, & Morris, 2012).

This renewed interest in the psychological term "schema" has been characterized by heterogeneous usage of the term by cognitive neuroscientists. As applied in the field, schema appears to encompass an assortment of cognitive structures that facilitate encoding, which greatly vary in complexity, organization, and mechanisms. These include the first half of a coherent unique story (Van Kesteren et al., 2010a), multisensory representation of objects (Van Kesteren et al., 2010b), associative rules (Kumaran, Summerfield, Hassabis, & Maguire, 2009), implicit probabilistic statistical regularities (Durrant, Taylor, Cairney, & Lewis, 2011), and in the rat literature: odour-location associative maps (Tse et al., 2007, 2011; Wang et al., 2012). This diversity follows a historical precedent of applying the term loosely to manifold cognitive structures exerting influence over memory encoding and retrieval. Even Bartlett (1932) expressed significant reservations about the use of the term, proclaiming it poorly captured key characteristics of memory schemas as he viewed it, most notably their dynamic nature.

Investigation of the mechanisms by which prior knowledge influences memory formation is hindered by equating diverse cognitive constructs all under the same term. Specifically, the lack of clear definitions obscures the identification of the critical features that make schemas conducive to memory encoding and retrieval. This review will focus on these critical structural features of schemas and will not focus on the function of schemas, which has been addressed by others and does not appear to be subject to dispute (Anderson & Pichert, 1978; Anderson, 1984; Arkes & Freedman, 1984; Bartlett, 1932; Bransford & Johnson, 1972; Carmichael et al., 1932; Cooper, Shallice, & Farringdon, 1995; Head & Holmes, 1911; Kumaran et al., 2009; Piaget, 1926; Preston & Eichenbaum, 2013; Rumelhart, 1980; Shea, Krug, & Tobler, 2008; Tse et al., 2007; Van Kesteren, Rijpkema, Ruiter, & Fernández, 2013).

As a first step in an attempt to resolve the ambiguity of "schema" and facilitate cross-study communication about prior knowledge influence on memory encoding and retrieval, we review the psychological and educational literature on schemas. Based on this review we propose that schemas possess four necessary features: (1) an associative network structure, (2) basis on multiple episodes, (3) lack of unit detail, and (4) adaptability; and that they also have sensitivity to four additional features: (5) chronological relationships, (6) hierarchical organization, (7) cross-connectivity, and (8) embedded response options. We then map several of the different definitions of schema in recent neuroscience literature onto these features to illustrate their similarities and differences. This comparison, in conjunction with a discussion comparing task demands presumed to rely on schemas, illuminates how studies based on such disparate interpretations of schemas converge in finding an implication of the vmPFC in schema functions.

2. Emergence of the "schema": Historical milestones

Recent studies on schemas appear to have emerged from diverse interpretations of what is actually meant by the term "schema". This inconsistency was inevitable considering the many re-characterizations the term has undergone in its history. Researchers have long been aware of the problematic ambiguity inherent in its definition, but attempts at re-branding specific interpretations of "schema" with new terms have rarely persisted. While there is much debate over the structure of a schema and what qualifies as a schema, there actually appears to be little debate over the function of schemas. Schema literature consistently identifies the following functions: guiding behaviour (Bartlett, 1932; Cooper et al., 1995; Head & Holmes, 1911; Kumaran et al., 2009; Rumelhart, 1980; Shea et al., 2008); facilitating encoding of new information, including inferential elaboration (Anderson, 1984; Bartlett, 1932; Bransford & Johnson, 1972; Carmichael et al., 1932; Head & Holmes, 1911; Piaget, 1926; Preston & Eichenbaum, 2013; Rumelhart, 1980; Tse et al., 2007; Van Kesteren et al., 2013); and expediting retrieval processes (i.e. memory search and reconstruction) (Anderson & Pichert, 1978; Anderson, 1984; Arkes & Freedman, 1984; Bartlett, 1932; Rumelhart, 1980). To facilitate communication about schemas, it is crucial to identify which features in the varied depictions of schemas are implicated in these consistently observed functions. As context for this examination, first we present a brief overview of the development of the schema across several fields of psychology.

Modern psychology's first introduction of schemas as a cognitive structure is in the context of Head and Holmes' (1911) "postural recognition"—the consciousness of the position of a part of one's body. Postural recognition requires a measurement of postural change, which is only meaningful if compared to a standard or a "schema" against which all postural changes are measured. New sensory information, which is unique with each movement, should be congruent with the existing schema if this schema is represented properly. In describing the function of schemas, Head and Holmes (1911) suggested that these cognitive structures assist in the interpretation of new information. Specifically, they stated that schemas modify impressions produced by incoming sensory impulses such that the final sensations of position rise into consciousness charged with a relation to something that had happened before. This depiction of schemas was highly impactful because it highlighted the influence of prior information on perception.

Over a decade later, Piaget (1926) integrated schemas into the field of developmental psychology, noting that children rely more heavily upon schemas than do adults. He adopted the term to refer to a general cognitive structure that links multiple representations of a phenomenon. Unlike Head and Holmes' narrow application of schemas to somatosensory representations, Piaget generalized the notion to multiple cognitive domains. While he studied schemas primarily in the context of linguistics, he interpreted perceptual findings of Gestalt psychologists as resulting from schemas as well, and implied that the notion may have further applicability elsewhere. Similarly to Head and Holmes, Piaget indicated that the existence of a schema alters an individual's interpretation of new information.

Schemas were not treated explicitly as a memory structure until re-introduced by Bartlett (1932). While Bartlett proclaimed his strong dislike for the term "schema", he continued to use it due to its former characterization by Head and Holmes (1911). Bartlett's reservations about the term stemmed from its wide use at the time to refer to some persistent, but fragmentary "form of arrangement", where this interpretation neglects what Bartlett claimed to be the crucial aspect of schemas: that schemas are constantly developing. He was first to demonstrate the implications of schemas in retrieval processes, observing that remembering does not entail the reproduction of a situation, but rather its reconstruction at retrieval, where schemas facilitate this constructive process and may under certain conditions bias it.

Following its re-characterization by Bartlett, the notion of schemas was pushed forth again within the developmental literature (Piaget, 1952), where the adaptability of schemas were more formally described in line with Bartlett's ideas (see Section 3.1.4). Ideas about schemas were also refined in the perceptual literature where the extraction of commonalities among a set of patterns played a central role (Brown & Evans, 1969; Evans, 1967; Posner & Keele, 1968; Vernon, 1955). An interesting distinction was made by Schank and Abelson (1977) between "scripts" and "plans", both of which retain some characteristics of Bartlett's "schemas". A script depicted an appropriate sequence of events in a particular context (e.g. birthday party), while a plan depicted the possible actions to accomplish a goal. The introduction of scripts emphasized the importance of chronological order in certain knowledge structures (see Section 3.2.1), while the importance of plans is their provision of a link between these knowledge structures and prescribed contextually appropriate behaviour (see Section 3.2.4). Optimization of behaviour has been argued to be the evolutionary purpose of general knowledge structures such as scripts and schemas (Klein, Cosmides, Tooby, & Chance, 2002; Kroes & Fernández, 2012).

The burgeoning of research on semantic networks that occurred around this time (Rumelhart, Lindsay, & Norman, 1972; Kintsch, 1972; Collins & Quillian, 1969) was highlighted by Tulving (1972) in a seminal paper suggesting that to understand semantic memory, it must be contrasted to some other form of memory. This prompted his division of long-term memory into semantic and episodic classes. Episodic memory is memory for a specific autobiographical event, or episode, and so is quite distinct from schemas that are constantly developing over experiences through extraction of commonalities. By contrast, some of the highly structured networks of concepts described by Tulving as "semantic" memory align with schema definitions at that time—for instance: "a memory structure that is capable not only of memorizing facts, but also of solving problems, making logical deductions, and understanding ideas" (1972, pp. 383). Moreover, similarly to Bartlett, Tulving suggested new episodes are experienced and interpreted through the "prism" of existing semantic networks, and are encoded as a function of those interpretations.

Schema theory had a great influence on educational psychology, most notably introduced by Anderson (1984), who tailored the theory to explain reading comprehension. He highlighted six functions of schemas: (1) providing scaffolding for assimilating text information, (2) facilitating allocation of attention, (3) enabling inferential elaboration, (4) allowing orderly memory searches, (5) facilitating editing and summarizing of new information, and (6) permitting reconstruction of missing information from memory. Note that the six functions can be divided into those facilitating memory encoding (1, 2, 3, & 5) and those facilitating retrieval (4 & 6).

The cognitive science literature was also influenced by ideas about schemas, exploring how they facilitate the selection of actions, depicting schemas as each having associated goals and sub-goals (Norman & Shallice, 1986; Cooper et al. 1995). Additionally, schemas were central to models of artificial intelligence (Schank & Abelson, 1977; Schank, 1983). Computational modeling revealed four factors influencing activation of a schema: (1) excitement by a superordinate schema, (2) excitement by external cues, (3) inhibition by a competing schema, and (4) excitement by the schema itself. The modeling of schemas as competitive networks provided insight into the neural mechanisms of schema representation, and the means by which schemas can guide behaviour.

Reviewing the emergence of the schema as a cognitive structure in the historical literature illustrates both the diversity of prior knowledge structures that have been considered as schemas and inversely, the consistency across models of the mnemonic functions carried out by these structures. To facilitate communication about schemas, we identify features which appear to be necessary for a knowledge structure to execute these functions. We also identify features that have often been recognized as characteristic and central to the functionality of a schema, but which are not necessary for a structure to be considered a schema. See Table 1 for a comparison of features that appear in an array of schema definitions and related cognitive structures.

3. Defining features

3.1. *Necessary features*

3.1.1. *Associative network structure*

While the term "schema" has adopted several distinct meanings in both past and present research, there appears to be consensus regarding some of the core features of the construct. For instance, most definitions of the term agree that schemas are composed of units and their interrelationships. A schema can thus be said to have an associative network structure.

Schema units have been referred to as elements (Anderson, 1984; Halford & Busby, 2007; Qiu, Li, Chen, & Zhang, 2008), events (Schank & Abelson, 1977), variables (Rumelhart & Ortony, 1976), schema nodes (Cooper et al., 1995), features (Van Kesteren et al., 2010b), paired-associates (Tse et al., 2007, 2011; Wang et al., 2012), and so on. Note that the interrelationships are often portrayed as more crucial than the units themselves (Anderson, 1984; Rumelhart, 1980).

An associative network structure is deemed a necessary feature as without units, a schema could not hold any information, and without their interrelations, that information would be isolated and its meaning vastly restricted. If the associative network structure of schemas was their only defining feature, then a pattern perceived only once could be included as a schema (e.g. Gestalt theory). Typically, however, schemas are depicted as being based upon multiple episodes that are variable but that share a basic structure. See Fig. 1 for a depiction of the associative network structure of a schema, amongst other necessary features.

3.1.2. *Basis on multiple episodes*

Schemas are general, higher-level constructs that encompass representations of the similarities or commonalities across events, rather than the specificity that make those events unique. This property was perhaps best articulated by Bartlett (1932), who said "the past acts as an organized mass rather than as a group of elements each of which retains its specific character." That schemas are composed of extracted commonalities across events relies on two necessary features: (1) basis on multiple episodes and (2) lack of unit detail.

It is important that schemas are based on multiple episodes as they could not facilitate encoding of new information or guide behaviour in a new situation if they were defined by specific episode information (Bartlett, 1932; Rumelhart & Ortony, 1976). When activated, extracted commonalities from multiple episodes form a cohesive collection of inferences about the possible occurrences of a set of events or objects within the context of the schema (Anderson, 1984; Bartlett, 1932; Rumelhart & Ortony, 1976; Schank, 1983).

3.1.3. *Lack of unit detail*

That schemas have a lack of unit detail follows directly from their basis on multiple episodes, since no two episodes are identical. In some models, schema units are referred to as "variables" in order to reflect their dynamic quality (Rumelhart & Ortony, 1976; Rumelhart, 1980). Rumelhart and Ortony (1976) claimed that each of a schema's units – or "variables" – has

Table 1
Dissection of features of semantic knowledge structures.

	COGNITIVE STRUCTURES[a]											
	Narrative	Plan	Category	Event gist	Statistical regularities	Schema[b] (edu.)	Script	Schema (dev.)	Schema (orig.)	Action schema	Schema (mem.)	Schema (mem. review)
FEATURES[c]												
Associative network structure	●		●	●	●	●	●	●	●	●	●	●
Lack of unit detail	/		/			●	●	●	●	●	●	●
Basis on multiple episodes			●	/	●		●	●		●	●	●
Adaptability	/	●	/			●	/	●	●		●	●
Chronological organization	●		/	●	+	+	●	+		+	+	+
Hierarchical organization			●							+		+
Cross-connectivity			+					+	+	+	+	+
Embedded response options		●							●	●		●
	Mar (2004)	Schank and Abelson (1977)	Collins and Quillian (1969), Patterson et al. (2007)	Nadel et al. (2000)	Durrant et al. (2011), Posner and Keele (1968), Tobia et al. (2012)	Anderson (1984)	Schank and Abelson (1977)	Piaget (1926, 1952)	Head and Holmes (1911)	Cooper et al. (1995), Goodman (1980), Humphreys and Forde (1998), Rumelhart and Ortony (1976)	Bartlett (1932)	Rumelhart and Ortony (1976)

[a] Note that the table is arranged in increasing number of features possessed.

[b] Multiple classic definitions of schemas have been included for comparison. Where relevant, the general school of thought or context of the definition has been included to differentiate the “schema” labels. "Edu" represents educational psychology; "dev." represents cognitive development; "orig." represents the original definition of the schema; "mem." represents memory; and "mem. review" represents a review on memory schemas.

[c] “●” Signifies a feature that is necessary to the definition of a cognitive structure; “+” signifies that the cognitive structure is sensitive to this feature, but that the feature is not necessary; “/” signifies that the cognitive structure necessarily does not include this feature by definition.

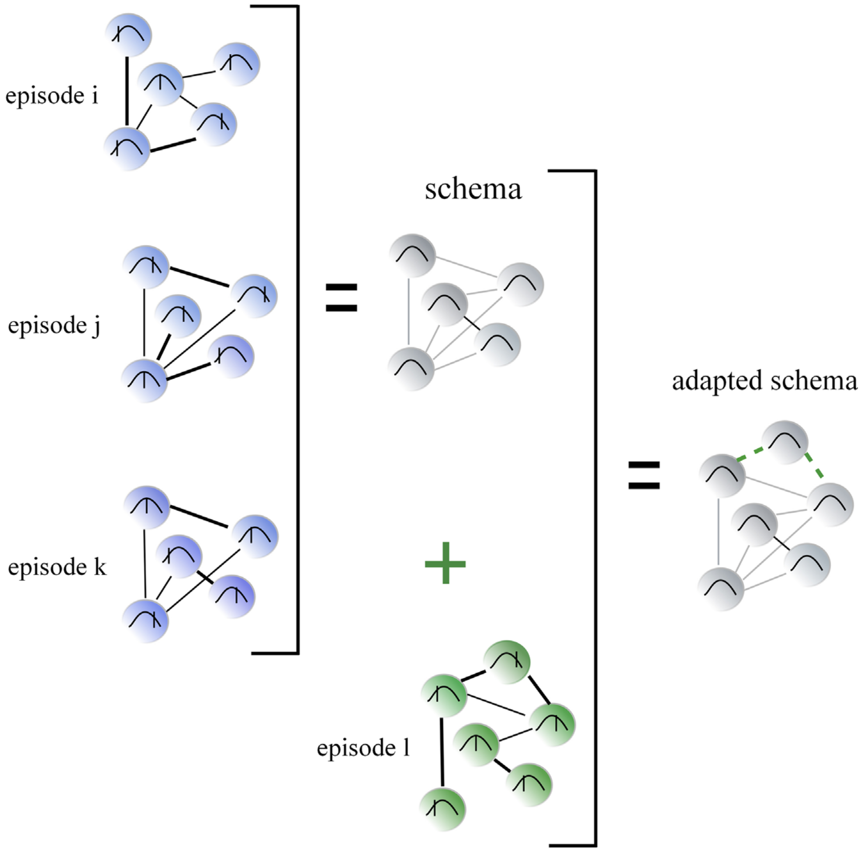

Fig. 1. Necessary features of schema structure. Gray networks in the figure represent the schema as a latent neurocognitive structure of strongly interconnected nodes that could potentially be re-activated together. Colourful networks are either novel episodes or specific instantiations of the schema during a particular context of experience. The schema's *associative network structure (feature 1)* is depicted through circles, which represent schema units, and lines connecting those circles, which represent their associations. Differences in line connections and thickness indicate variability across episodes. The schema's *basis on multiple episodes (feature 2)* is illustrated through episodes i-k. Each episode differs in specificity, but all conform to the same general structure, which can be extracted as the schema. The schema's *lack of unit detail (feature 3)* is indicated by the normal distribution curve within each schema unit, which has the potential to take different values. For specific episodes or schema instantiations i–k, each unit takes a particular value on that curve. Lastly, the schema's *adaptability (feature 4)* is indicated by the inclusion of new information from episode l as green dotted lines in the adapted schema.

constraints, which are regarded as distributions rather than inviolable limits. It is the flexibility of variable constraints that differentiates schemas from definitions, as it allows them to tolerate and accommodate more significant deviations from what is normally true. Schemas must be general such that they can organize new information and provide additional meaning, but still hold space for details of particular new episodes.

3.1.4. Adaptability

The final necessary feature of schemas is their adaptability. Head and Holmes (1911) described schemas as constantly developing, affected by every incoming sensory experience. Bartlett (1932) emphasized this aspect of Head and Holmes' definition as its crucial feature, and Piaget (1952) expanded upon the adaptability of schemas by identifying two means by which schemas could be altered: (1) assimilation, and (2) accommodation. “Assimilation” referred to incorporating environmental elements into a schema without challenging the existing relationships within the schema. “Accommodation” referred to modifying a schema under pressures by new environmental elements.

Adaptability appears to be the feature that catalyzed the emergence of schemas into the field of neuroscience. Tse et al. (2007) discovered that new information becomes more rapidly hippocampal-independent when assimilated into an existing schema, and this prompted investigation into the neural mechanisms supporting the addition of new information into prior schemas (Tse et al., 2011; Van Kesteren et al., 2010a; Wang et al., 2012). Accommodation, however, has not yet been investigated and may be more difficult to track as it involves gradual changes of extensive knowledge structures, which are difficult to capture.

Adaptability is a necessary feature of schemas because it enables them to store vast amounts of information derived from many experiences and update that information in an environmentally sensitive manner. In order for schemas to allow efficient information processing and selection of contextually optimal behaviour, they must be flexible to support acquisition of new information associated with similar past settings, along with outcomes of behaviour in these situations. If schemas were not adaptive, meaning that new information could not be integrated into an existing schema (e.g. assimilation) nor potentially alter a schema (e.g. accommodation), then they would contain specific information rather than extracted commonalities. Subsequently, their applicability to new similar contexts and information would be eliminated, and they could play no role in facilitating encoding and in guiding behaviour. Fig. 1 depicts how new information from “episode l” can be assimilated into an existing schema, resulting in adaptation of that schema.

One schema-like structure that only partially conforms to the notion of adaptability is the “script” (Schank & Abelson, 1977). Scripts are cognitive structures that organize representations of event-based situations and support their comprehension. In their strongest sense they reflect very rigid rituals that allow perfect prediction of the sequence of steps and therefore are not easily subjected to change and do not provide an efficient apparatus for handling novel situations. However, these are relatively rare and most scripts allow a degree of flexibility and also possess other features of schemas—an associative network structure, basis on multiple episodes, and lack of unit detail. Schank and Abelson's "plans" are better able to adapt to novel situations.

3.2. *Features to which schemas are sensitive*

3.2.1. *Chronological relationships*

Due to their event-based nature, a necessary property of scripts is that their contributing units are organized in chronological order (Schank & Abelson, 1977). We suggest that schemas more broadly defined, present with *sensitivity to chronology*, meaning that chronological ordering could be entrenched in the relationships between schema units, but primarily in cases where the schema has a significant event-based content. Notably, the extent to which chronological units can be interchanged has a substantial effect on the adaptability or flexibility of a schema. Importantly, while not all schemas possess chronological relationships between units, when they are present, chronology of units (like other types of unit relationships) becomes crucial to schema functions. For example, chronological organization can guide behaviour based on what is expected to occur next, or facilitate inferences about something that likely just occurred.

Anderson (1984) studied the chronological aspect of schemas, demonstrating that it is more important in some schemas than in others. An example provided by Anderson is that one cannot as easily recall the order in which food items appear in a story about a grocery store as one can recall the order in which food items appear in a story about a restaurant. This finding is explained by the greater importance of chronology in a restaurant visit than in grocery-shopping. Bartlett (1932) also wrote that there is often a chronological order to schemas, but that this order can at times be broken up. He explained that in rupturing the chronology associating schema units, actions are prevented from always being determined by the immediately preceding event, suggesting that adaptive chronology is an important aspect of the adaptability feature of some schemas.

3.2.2. *Hierarchical organization*

Some models portray schemas as having hierarchical organization, meaning that they are configured of sub-schemas. Rumelhart and Ortony (1976) suggested that hierarchical organization allowed for top-down and bottom-up activation of cognitive structures. Top-down – or "concept-driven" – activation refers to when a schema activates a sub-schema, while bottom-up – or "data-driven" – activation refers to when a sub-schema activates the various schemas it is nested within. Cooper et al. (1995) adopted the hierarchical nature of schemas into simulations of automatic action selection and specified that attention can be aimed either at high-level schemas or at a sequence of lower-level schemas.

Having hierarchical organization does not necessitate that all schemas have constituent schemas and belong to larger encompassing schemas, but that the capacity for hierarchy is inherent in the way that schema units are connected. Rumelhart and Ortony (1976) speak of this recursive nature as a possibility but not as a necessity for something to be considered as a schema. In agreement with this idea, we propose that hierarchical organization is not a necessary feature, but rather a feature that schemas are sensitive to. Having a hierarchical organization allows for the storage of more complex information; however, there is no evidence to suggest that schema functions could not be executed without this type of structure.

3.2.3. *Cross-connectivity*

Cross-connectivity refers to overlapping units between schemas. This feature exists in the original depiction of schemas by Head and Holmes (1911). In order to identify the exact location of a particular body part, the schema representing the relationships between the parts of one's own body would need to reference a new schema which could identify where in space this body part lies (Head & Holmes, 1911). Bartlett (1932) also implied that schemas could communicate in some way to one another; however, it was Rumelhart and Ortony (1976) who directly laid out the relationship between the hierarchical organization and cross-connectivity of schemas, explaining that a sub-schema could be part of multiple larger schemas, thus connecting them. There is no reason to suspect that the cross-connectivity of schemas is necessary for their functionality, but rather that it is a likely property of schemas based on the fact that the same concepts and sub-schemas may hold different meanings in different contexts. It is thus deemed a feature to which schemas are sensitive.

A consequence of schema cross-connectivity is that schemas can be in competition. According to Cooper et al. (1995), if several higher-level schemas share a sub-schema associated with the goal in question, then these schemas are said to compete. A schema is selected based on its activation exceeding its selection threshold (pre-defined in their simulations) and being greater than the activation of its competitors. Schank and Abelson (1977) also provided examples where scripts are in competition. They described these as unusual situations in which some aspects of a situation correspond to one script and other aspects correspond to a different script. They explained that such situations are extremely difficult to interpret without additional information to support resolution of the conflict.

3.2.4. *Embedded response options*

In some cases, schemas are interpreted to only be knowledge structures, while in others they also possess links between this knowledge and contextually appropriate behaviours. This latter position was perhaps most eloquently described by Rumelhart (1980) who likened schemas to packets of knowledge, wherein embedded in these packets is, in addition to the knowledge itself, information about how this knowledge is to be used. This position was supported by Cooper et al. (1995), who stated that schemas each have an associated goal and means of achieving that goal. Consequently, they interpreted schemas as responsible for the production of well-learned action sequences, such as preparing coffee.

While many models include a relationship between schemas and behaviour, it is at times unclear as to whether response options are viewed as an inherent part of the schema itself. For instance, Bartlett acknowledged that behaviour is manufactured out of those schemas relevant to the moment and their interrelations; however he did not specify the means by which that behaviour was "manufactured".

In other cases, it is clear that certain schemas contain response options, but these are designated as a particular type of schema, meaning that this characteristic is not a defining feature of schemas. This subset is typically referred to as "action schemas" (Goodman, 1980; Humphreys & Forde, 1998; Rumelhart & Ortony, 1976), and are similar to "plans" (Schank & Abelson, 1977).

In our framework, embedded response options is deemed a sensitive feature, rather than a necessary one as it is crucial for situations where a schema serves to guide behaviour; however, it seems possible that not all schemas have this function. For example, a schema for a certain film genre would not require there to be associated response options, as no behaviour is required of the individual watching a given film. However, this schema would require the necessary structural features outlined above to ease interpretation of the film, and facilitate encoding and retrieval processes.

4. Related cognitive structures

The discussion on schemas thus far has touched on a few related knowledge structures, such as action schemas, plans, and scripts; however, other organized, meta-cognitive structures relevant to memory should be noted as well. Table 1 compares existing definitions of schemas and a variety of other knowledge structures across the features identified above. A brief discussion on these structures follows.

4.1. Narratives

A review on the neuropsychology of narratives (Mar, 2004) defined narratives as a series of actions and events that unfold over time, according to causal principles. As such, to be considered a narrative, both an associative network structure and chronological organization are necessary. Unlike schemas, however, in which units are lacking in detail, narratives are specific in that each unit, or event, occurs in a particular way. Similarly, narratives are fixed, rather than adaptable. Further distinguishing them from schemas, narratives can be encoded in one episode, rather than being composed from commonalities extracted from multiple episodes.

4.2. Concepts and categories

Several influential models of conceptual knowledge (e.g. Collins & Quillian, 1969; Patterson, Nestor, & Rogers, 2007), have in common the proposition that categories have an associative network structure where each unit, or “node”, represents a concept, which is in turn linked to a set of defining features. A concept or category's defining features determine its membership in a broader category. Unlike schemas, the unit features are fixed, non-adaptable definitions, although categories may contain exceptions that do not possess one or more defining features. Categories are hierarchical by definition with a capacity for cross-connectivity. Units necessarily cannot hold chronological relationships.

4.3. Event gists

Event gist, while not explicitly defined, appears to refer to a general sequence of events that occurred on one occasion (Nadel, Samsonovich, Ryan, & Moscovitch, 2000; Winocur & Moscovitch, 2011). Thorndyke (1977) defined gist as high level story elements that are central and critical to the coherence of the overall plot as opposed to low-level details whose omission would not alter the overall plot. As such, event gist would be defined as containing multiple units and their interrelationships, which would be chronologically organized. Event gists can be lacking in detail, similarly to schemas, but this is not a necessary condition. Moreover, unlike schemas, gist refers to a specific event and is not based on multiple episodes.

4.4. Statistical regularities

Behavioural tasks where participants are required to extract statistical regularities involve the presentation of multiple units (e.g. tones, dots) and their interrelationships (e.g. frequency differences, spatial orientation) (Durrant et al., 2011; Posner & Keele, 1968; Tobia, Iacovella, Davis, & Hasson, 2012). Several tone sequences or visual patterns are presented, where tones of a particular frequency difference to the previous tone have a high probability of occurring (Durrant et al., 2011; Tobia et al., 2012), or visual patterns with units differing in location by a certain distance (Posner & Keele, 1968). By this definition, statistical regularities are similar to schemas in that they possess an associative network structure, are based on multiple episodes, and are sensitive to chronological organization. It is unclear as to whether they are adaptive and flexible, as this kind of learning often involves non-declarative, procedural learning (Squire, 1992). It also appears that the nodes themselves are detailed units that allow for little variance or distribution of identity.

5. Schemas and the ventromedial prefrontal cortex

Although schema definitions in the neuroscience literature vary considerably, studies consistently demonstrate the importance of the vmPFC in schema functions (Kumaran et al., 2009; Qiu et al., 2008; Tse et al., 2011; Van Kesteren et al., 2010a,b, 2013). These studies are presented in Table 2 and will also be discussed in terms of our proposal. First, we turn to two reviews that provide frameworks to account for the interplay between the hippocampus and medial prefrontal cortex in memory. While our proposal is not inconsistent with neurocognitive mechanisms suggested by these frameworks, it challenges their definition of schemas.

A review by Van Kesteren, Ruiter, Fernández, and Henson (2012) proposes a neuroscientific concept of schema as a network of neocortical representations that are strongly interconnected and that when activated affects processing of new information. However, we believe this definition is too broad and may overextend the concept's denotation; as the authors rightly note, overextension is partly to blame for the loss of interest in the schema as a concept within psychology in the 1980s. As this neuroscientific definition only considers the first of the four necessary features we propose, it equally applies to narratives, conceptual categories, event gists, statistical regularities, and scripts.

Similarly, our proposal provides important constraints to a recent review by Preston and Eichenbaum (2013). These authors also focus only on the network structure of schema and consider any network of overlapping representations to be a schema, defining it by its functions of memory integration, network adaptation, support of inferences, and generalizability. In addition to the possibility of overextension, both definitions risk circularity when used in the context of memory research. Specifically, it would be circular to operationally define a schema as an associative structure that affects memory when investigating the effects of schemas on memory. These issues do not mean that previous research is flawed, but rather that better definitions are needed in order to move forward.

Specifically, we agree with Preston and Eichenbaum (2013) that transitive inference paradigms can be explained in a schema framework, but believe a detailed, positive definition of schema might better capture how transitive inference informs schema theory. Inferential elaboration is an undisputed function of schemas, and possession of the four necessary schema features enables this function. However, the elementary transitive inference paradigm described in the review by Preston and Eichenbaum likens a set of specific associations (A–B and B–C) to a schema. These associations possess the first criterion of an associated network structure, albeit on a minuscule scale. This structure also partially meets the second criterion, as it was learned across multiple episodes (several trials for A–B and several trials for B–C), but with no variability across episodes. It also has the potential for adaptation, the fourth criterion, as demonstrated during the transitive inference stage (inference of A–C relationship). However, in its current form, it does not meet the third criterion of lack of

Table 2
Features of “schema” characterizations in primary neuroscience literature.

	Kumaran et al. (2009)	McKenzie et al. (2013)	Qiu et al. (2008)	Tse et al. (2007, 2011), Wang et al. (2012)	Van Dongen et al. (2011)	Van Kesteren et al. (2013)	Van Kesteren et al. (2010a)	Van Kesteren et al. (2010b)
FEATURES	**COGNITIVE STRUCTURES**							
Associative network structure	○	○	○	○	○	○	○	○
Lack unit detail	○	○	○	○	○	○		○
Basis on multiple episodes	○	○	○	○	○	○		○
Adaptability	○	○		○		○	○	
Chronological organization		○					○	
Hierarchical organization								
Cross-connectivity	○							
Embedded response options	○	○		○				
	NEURAL CORRELATES OF FUNCTION							
FUNCTION TESTED								
Learning individual associations	PHPC cortex			HPC; mPFC immediate early gene upregulation				
“Schema” development	HPC-vmPFC[a]							
Influence of “schema” on decision-making	HPC, vmPFC		mPFC					
Learning new “schema”-consistent associations	HPC	HPC		HPC, mPFC	fusiform-mPFC in sleep	mPFC	vmPFC; weak HPC-vmPFC	
Learning new information that disambiguates weak prior information							strong HPC-vmPFC	
Retrieval of “schema”-consistent associations				mPFC				mPFC-SS network[b]

[a] A “-” between region names signifies functional connectivity between those regions.
[b] These schemas pertained to visual-tactile congruency based on prior semantic information.

unit detail. Thus, the paradigm offers a great potential for understanding schemas as it contains the building blocks of schemas and there are obvious ways in which these building blocks could be manipulated to probe the contributions of different schema features to memory. However, in its current stripped down form we believe it would be inaccurate to call these specific A–B–C associations a “schema”.

5.1. Neuroscience studies on schemas

Schema definitions in the neuroscience literature can be directly compared based on presence or absence of each of the features listed above (see Table 2). Such a comparison concretely illustrates the diversity of the types of knowledge structures being interpreted as “schemas”. Despite these differences in interpretation of schemas, and also despite differences in the schema functions tested (e.g. facilitating encoding, guiding behaviour, schema development), the implication of the vmPFC in completing these tasks is relatively consistent across the studies.

We propose two reasons to account for these collective findings.

First, we posit that the tasks employed in each of these studies do require the engagement of schemas that possess the necessary schema features we have outlined. However, these schemas are in some cases not the same as the knowledge structures that the authors have identified as “schemas”. This idea will be illustrated below. Secondly, the vmPFC may be engaged in the one aspect of the tasks that is shared. All the tasks require that participants monitor relevance of ongoing schema activation to task demands and coordinate activation of schema representations in the neocortex accordingly.

Here we will illustrate how each of the studies demonstrating vmPFC involvement in schema functions highlighted in Table 2 fit with our proposition. For a more complete comparison of the neuroscience literature on schemas, we also include a rat electrophysiological study of schema functions that did not measure vmPFC activity (McKenzie, Robinson, Herrera, Churchill, & Eichenbaum, 2013).

To begin, Kumaran et al. (2009) considered “conceptual knowledge” to be associative patterns, where across multiple episodes, participants extracted how shape-location and shape-shape conjunctions predict outcomes. These patterns shared units and thus were cross-connected. This depiction possessed all four necessary schema features. When participants were presented with partial patterns upon which to base their predictions, they were able to generalize their prior knowledge to the new situation to inform their decision. The hippocampus and vmPFC were both involved in this process of guiding decisions based on conceptual knowledge. By our interpretation, in this part of the task, the partial patterns cued activation of the appropriate schema, and potentially the inhibition of competing irrelevant schemas, which would account for the vmPFC involvement. Note that in this case, competing schemas were those which share with the relevant schema certain units of the partial pattern presented.

In an electroencephalography (EEG) study by Qiu et al. (2008), participants were required to learn a rule based on an example string of units (letters) and logically deduce how the relationship in the example can be applied to a set of new units. The relationship between units in the example was interpreted as the “schema” which was applied to the new units. Units in the example always had one of three different types of interrelations, and so in this sense, these three “schemas” could have been extracted based on commonalities of multiple episodes. In this case, performance on very early trials would not have activated a schema. Instead the problem could have been solved by applying an analogy between the sample and the target. On later trials, however, it is possible that performance depended on extracted commonalities across trials, which corresponded to schemas. The schemas were not adapted in this study so it is not known to what extent they were flexible. Qiu et al. (2008) found that at the time point associated with mapping the schema to the target problem to solve it, there was a greater late negative component in the left mPFC (Brodmann area 10). This finding pertained to when the example corresponded with a pattern that is new, rather than a pattern following traditional alphabetical ordering. The additional mPFC activity in this condition can be interpreted either as the process of formation of a new pattern, or as reflecting competition between a strongly represented pattern and a novel one.

In a landmark series of experiments (Tse et al., 2007, 2011; Wang et al., 2012) the definition of schema possessed the four necessary schema features. In this case, schemas were considered to be associative maps, where schema units were flavour-location paired-associates and their interrelationships were their relative allocentric spatial locations within an event arena. These schemas were experimentally manipulated to adapt new information. Tse et al. (2011) found that encoding new associations was facilitated by the presence of a congruent schema, where this facilitation crucially depended on the mPFC. Wang et al. (2012) found that retrieval of schema information is dependent on glutaminergic transmission in the mPFC, specifically on that mediated by AMPA receptors. They showed that assimilating new information into an existing schema is also dependent on AMPA-mediated transmission in the mPFC, as well as glutaminergic transmission at NMDA receptors. These data were interpreted as reflecting the central and crucial role of mPFC in assimilating new information into an existing schema. One possibility is that the mechanism mediating this assimilation is the activation of relevant schemas by the novel cues. Disrupting mPFC function may prevent new cues from activating the congruent schema and impair schema-facilitated rapid encoding.

Van Dongen, Takashima, Barth, and Fernández (2011) tested the neural mechanisms involved in sleep-dependent consolidation of face-location associations, where there was no organizing rule underlying the associations. One finding was fusiform-mPFC functional connectivity enhancement during stage 2 sleep, which was positively correlated with retention of associations learned prior to sleep. One of the authors' interpretations of this finding was that participants' task knowledge, extracted across a training session from several days prior as well as the test session, could be a schema. They thus speculated it is possible that this task schema facilitated initial sleep-dependent consolidation after learning, which may have been mediated by the mPFC. In this case, the schema would possess an associative network structure, basis on multiple episodes, and lack of unit detail. Although there is no evidence of its adaptability, this task schema bears a structure which could potentially lend itself to this. It seems possible that the observed fusiform-mPFC connectivity was underlying activation of the relevant schema, which would be required for schema-facilitated encoding.

Three studies by Van Kesteren et al. (2010a,b, 2013) attempted to directly address the role of schemas in memory acquisition. In one of these studies (2013), participants identified the congruency of object-scene pairs with their own prior knowledge while undergoing functional magnetic resonance imaging (fMRI). “Schemas” in this study are referred to as the prior knowledge that is used to make congruency judgments. These schemas, as defined by the authors, do meet our above criteria. For example, one of the object-scene pairings was an umbrella and a tennis court. Congruency judgments would be based on prior representations of a tennis match extracted over one's lifetime experiences with tennis. These cognitive representations are composed of multiple related units, and would have the capacity for being adapted. The key finding of the study was that encoding-related activity in the mPFC increased linearly with increasing congruency, while encoding-related activity in the medial temporal lobes increased with decreasing congruency. The mPFC activity at encoding corresponds with activating relevant schema representations in the neocortex in order to inform congruency judgements.

In the Van Kesteren et al. (2010a) study, participants viewed the first half of a film either chronologically ordered or chronologically scrambled. The following day they viewed the second half of the movie in chronological order. The first part of the film was depicted as a schema into which new information, from the second half of the film, was assimilated. Schema units were thus defined as events that occur within a film viewed once and their interrelationships were defined in part by chronology. These schemas were depicted as adaptive because new information could be integrated into them. Unlike the previous study, they do not meet our definition of schemas as they are not based on multiple episodes, and consequently the units do not lack detail. Instead they are more like a narrative or a gist, depending on the amount of information still available to subjects when the new information is presented to them. When participants viewed the first half of a video ordered chronologically, there was increased vmPFC intersubject synchronization and decreased hippocampal-vmPFC interregional connectivity during encoding of information in the second half of the video. The group that viewed the first half of the video as chronologically scrambled showed the reverse pattern. We propose that the schemas implicated in this task are not necessarily the first halves of the videos per se. Instead, coherent storylines correspond to participants' existing knowledge structures, which were employed to interpret and encode the information in the videos. In the chronological condition, when encoding new information provided in the second half of the video, vmPFC activity may underlie monitoring of the consistency of new information with the schemas identified as relevant when viewing the first half of the video.

In the Van Kesterenet al. (2010b) study, schema units seemed to be defined as typical features of an object (e.g. material of a coat). This would not adhere to our requirement of possessing a network structure if the relationships were solely between units and the “schema” itself (e.g. relationship between “coat” and “leather”), rather than interrelationships amongst the units. Adaptability of the schemas would be restricted without these relationships, and the structures could be better likened to categories. The key finding of the study was that retrieval of associations between fabric, a visual motif, and a word was correlated with enhanced functional connectivity between the mPFC and left somatosensory cortex if those associations were congruent with prior knowledge, or an existing “schema”. Here, the somatosensory cortex is assumed to underlie a portion of the schema representation while the mPFC is proposed to underlie activation of a schema based on cues given on a particular trial, which in the case of congruent associations could facilitate retrieval.

Finally, a recent study monitored the firing of hippocampal CA1 neurons as rats learned new goal locations in an environment in which they had already learned multiple light-cued goal locations (McKenzie et al., 2013). In this study, the term “schema” referred to a collection of goal locations, the behaviour required to achieve a goal at those locations (e.g. waiting for a few seconds within a certain distance of the goal location), and the associated cues or preceding behaviours signifying reward availability at each location. This “schema” has an associative network structure as it contains multiple units (i.e. cues, locations, behaviours) and both the interrelations within a cue-location-behaviour triad and the spatial interrelations between locations. The cue-location-behaviour interrelations are extracted from the commonalities across multiple locations. The structure is adaptable as subjects were able to assimilate new information following initial acquisition. As already indicated, response options were embedded within the schema. Furthermore, there was a sensitivity to chronology as some of the locations were cued by a behaviour at a previous location, implying a temporal relationship between them (i.e. after visiting location 1, a reward becomes available at location 2, then location 3). The key finding of the study was that when assimilating new information into a schema, there was initially heightened common hippocampal activity across behaviour at the new and original goal locations, although they became decorrelated over time. Of course these findings cannot speak to the role of the vmPFC in schema functions as activity in this region was not measured. Based on the human literature and other paradigms involving schema learning in rats, we would predict prelimbic mPFC to become more engaged over time, in parallel to hippocampal decorrelation.

The proposed role of the vmPFC in schema representation is also congruent with human lesion studies. One of the most prominent memory-related consequences of lesions to the vmPFC is spontaneous confabulation (Gilboa & Moscovitch, 2002). Confabulation is a memory disorder characterized by erroneous memories without awareness of their falsehood (Moscovitch, 1989), and damage to the vmPFC is sufficient to cause confabulation (Gilboa & Moscovitch, 2002). Several models for confabulation posit that it impairs reconstructive processes during retrieval (Burgess & Shallice, 1996; Fotopoulou, 2008; Gilboa et al., 2006; Wagner et al., 1998). Memory reconstruction requires an organizing structure, such as a schema, to assemble details into a coherent memory and it has been suggested that the content of confabulation could be influenced by strong pre-existing schemas (Burgess & Shallice, 1996) particularly when these are related to a strong self-schema (Gilboa, 2010, 2004). Indeed, confabulations are sometimes constructed based on frequently encountered or generic situations in patients' lives (Burgess & McNeil, 1999), as well as on generic self-schemas (Metcalf, Langdon, & Coltheart, 2010). In the context of our proposal, damage to the vmPFC may elicit confabulation by impairing an individual's capacity to monitor and control activation of inappropriate schemas, which in turn serve as a template for memory reconstruction.

6. Concluding remarks

Recent studies on neural underpinnings of schemas emerged from diverse interpretations of what is meant by the term “schema”. This dilemma was inevitable considering the many re-characterizations the term has undergone in its history. A schema is a memory structure capable of representing extremely complex constructs employing this information to influence encoding and retrieval of episodic memory, and guide elaborate, context-specific patterns of behaviour. We propose based on the history of the term and current neurobiological research that this structure would require an associative network structure, basis on multiple episodes, lack of unit detail, and adaptability. It would also have a capacity for chronological relationships, hierarchical organization, cross-connectivity, and embedded response options.

Several studies demonstrate an implication of the vmPFC in schema functions (Kumaran et al., 2009; Qiu et al., 2008; Tse et al., 2011; Van Dongen et al., 2011; Van Kesteren et al., 2010a,b, 2013; Wang et al., 2012) and we propose that the vmPFC activity is associated with monitoring relevance of ongoing schema activation to task demands and coordinating activation of schema representations in the posterior neocortex accordingly (Gilboa, Alain, He, Stuss, & Moscovitch, 2009). A combined lesion-electrophysiological study lends initial support to this hypothesis, as lesions to vmPFC interfere with a very early posterior neocortical electrophysiological signature (N170) of self-related remote memory for faces (Gilboa et al., 2009).

Along with a direct test of the hypothesized function of the vmPFC, future directions should include an evaluation of the necessity of our proposed schema features for a knowledge structure to be able to guide behaviour, facilitate encoding, and enhance retrieval processes.

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