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Act-In: An integrated view of memory mechanisms

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Act-In: An integrated view of memory mechanisms

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The present article proposes a new memory model called Act-In (Activation-Integration). Act-In extends the multiple trace memory models by placing them within the situated cognition perspective. Act-In considers that the activation and integration mechanisms play a key role in memory processes. These mechanisms are involved in both the construction of memory traces and the emergence of knowledge. The model is based on four main assumptions: (1) Memory traces reflect all the components of past experiences and, in particular, their sensory properties, actions performed on the objects in the environment and the emotional states of individuals. Memory traces are therefore distributed across multiple neuronal systems which code the multiple components of the experiences. (2) Knowledge is emergent and is the product of the coupling of the present experience with past experiences. (3) The brain is a categorisation system which develops by accumulating experiences and which, by default, produces categorical knowledge. (4) The emergence of specific knowledge (memories or episodic knowledge) requires very simple mechanisms which occur during learning and/or during retrieval. These assumptions are defended and discussed in the light of the work reported in the literature.

Keywords: Activation; Integration; Memory model; Memory traces.

Memory is a transversal function of the cognitive system. In all the situations we encounter, we rely on past experiences in order to deal with the present. Conversely, most cognitive activities give rise to a form of retention of information. The ways in which long-term memory influences (non-mnemonic) cognitive mechanisms are generally described as simple "top–down" influences. As a result of feedback, activations in long-term memory may therefore modify cognitive functioning that was initially independent of this memory. A variety of criteria are generally used to distinguish what are considered to represent memory activities. These criteria mostly take the form of: (1) the nature of the knowledge (or representations) that is thought to be involved, such as memories or conceptual knowledge; (2) the conscious or unconscious nature of encoding (incidental vs. intentional), retrieval (explicit vs. implicit) and even retrieved knowledge (e.g., Tulving's distinction between anoetic, noetic and autonoetic consciousness – Tulving, 1995). However, in all these memory activities, the retrieval mechanism is defined as an activation mechanism, i.e., activation of representations/knowledge stored in memory. What changes is thus primarily the nature of what is activated and the varieties of consciousness and levels of awareness of knowledge associated with this activation.

The liveliest debates reported in the literature primarily focused on the content of memory (or of

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memories). Levels of consciousness, just like the factors that influence encoding and retrieval, are often thought to be intrinsically linked to content. In the multi-system models (Sherry & Schacter, 1987; Squire, 2004; Tulving, 1995), even though the content varies depending on the memory system in question, there is always a correspondence between the content of the relevant memory system and, at the phenomenological level, the nature of the "retrieved" knowledge. One of the main goals of the present paper is to argue that knowledge is simply the result of the dynamic of memory functioning. In other words, different types of knowledge associated with different varieties of consciousness can emerge from identical content.

This idea of emergent knowledge is present in the so-called "single-system" models of memory as opposed to the multi-system memory models. Although, initially, authors suggested that the single system contained exemplars of semantic categories (see the exemplar models of categorisation, e.g., Estes, 1994; Medin & Schaffer, 1978), the idea of exemplars gradually gave way to the concept of traces of specific experiences (see the multiple trace models, e.g., Hintzman, 1986; Whittlesea, 1987). Within this framework, memory is primarily episodic in nature, even if the episodes are considerably more specific in nature in the multiple trace models than in the exemplar models. The retrieved knowledge is no longer exactly the same as knowledge that was activated. Instead, it emerges from the reactivation of the global content of memory. Of course, the result of this activation may be more or less similar to a specific trace. The episodic or semantic nature of the knowledge therefore depends entirely on the result of this activation mechanism, leading to a form of knowledge that is more or less specific to an earlier situation. As a consequence, the single-system models of memory attribute a central role to the link between the present and past experiences.

Our aim in this article is to propose a memory model, Act-In, which is consistent with the single-system models and which addresses three questions. The first relates to the nature of the experiential components that are actually encoded within memory traces. The second concerns the mechanisms that could explain how different forms of knowledge emerge from memory traces. Finally, the third question relates to the construction of the memory traces. The Act-In model extends and specifies the multiple trace models and transposes them to a perspective of situated cognition (e.g., Clancey, 1997; see also the theory of embodied cognition as described, for example, by Damasio, 1989; Edelman, 1987; Glenberg, 1997; Glenberg, Witt, & Metcalfe, 2013; see also Versace, Labeye, Badard, & Rose, 2009). The name of the model, Act-In, comes from the key role it attributes to the activation and integration mechanisms in memory processes. Later, we specify in greater detail these mechanisms, which are involved in both the construction of memory traces and knowledge emergence.

The general assumptions that underpin the Act-In model will be developed in the following section of the paper (Section 1) as the empirical evidence supporting these assumptions. We shall attempt to show that by restoring long-term memory to a central position in cognitive functioning, Act-In has the advantage of considering overall cognitive functioning in a highly integrated manner. This integrated conception of cognitive functioning will be illustrated by evoking the close association between the perceptual and memory mechanisms. Sections 2 and 3 will try to demonstrate that our model sheds new light (compared to existing models) on certain results reported in the literature, and more specifically in the literature on conceptual knowledge and discriminant activities. Finally, in the conclusion, we shall allude to the possible implications of Act-In for the field of neuropsychology and, more specifically, that of normal and pathological ageing. Indeed, any proposed model of memory is valid only if it can be applied in a variety of situations which reflect both normal and abnormal functioning.

1. ACT-IN MODEL

1.1. General assumptions underpinning Act-In

Before describing the mechanisms proposed by Act-In, it is important to note that the main objective of the present paper is to demonstrate that it is possible to account for a large body of empirical results based on a very limited number of memory mechanisms. Existing models of memory, by contrast, can account for some but not all of these empirical results. It is important to keep in mind that Act-In proposes a general operating principle that can be implemented in various architectures, with accompanying computational instantiations and simulations. It is not our aim

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here to propose a model in which the mechanisms proposed in order to account for the emergence of different forms of knowledge are instantiated. Moreover, the described mechanisms should be implemented in an architecture that respects the inherent constraints of the physical system in which they are implemented: the brain.

Act-In is based on four main assumptions: (1) Memory traces reflect all the components of past experiences and, in particular, their sensory properties as captured by our sensory receptors, actions performed on the objects in the environment and the emotional and motivational states of individuals which, to a large extent, determine their actions. Memory traces are therefore distributed across multiple neuronal systems which code the multiple components of the experiences. (2) Knowledge is emergent and is the product of the coupling of the present experience with past experiences. (3) The brain is a categorisation system which develops by accumulating experiences and which, by default, produces categorical knowledge. (4) The emergence of specific knowledge (memories or episodic knowledge) requires simple mechanisms which occur during learning and during retrieval (i.e., interactive activation and integration).

1.2. Sensory-based distributed memory traces

The first main assumption underpinning Act-In concerns the nature of the components encoded in the traces. This issue is closely related to the question of the form of knowledge in the brain and, consequently, to the question of the nature of knowledge that can emerge. The form of knowledge should somehow be related to the properties of the brain. One of the crucial properties of the brain that allows it to perform cognitive functioning is its plasticity, as demonstrated by a growing body of evidence (e.g., Frégnac, 1996). Moreover, it is broadly accepted that neuronal plasticity forms the basis for learning and memory (see, for example, Laroche, 2001, for supporting arguments). This plasticity makes it difficult to distinguish between areas which are specifically associated with memory and other "non-memory" areas, as illustrated by the extensive networks involved in memory functioning (for reviews, see Binder, Desai, Graves, & Conant, 2009; Desgranges, Baron, & Eustache, 1998; Ungerleider, 1995). The brain as a whole may be considered to be a system which retains the traces of an individual's experiences.

Many brain neuroimaging studies have confirmed the fact that knowledge emerges from the activation of neuronal systems that are typically associated with perceptuo-motor mechanisms (Jääskeläinen, Ahveninen, Belliveau, Raij, & Sams, 2007; Martin & Chao, 2001; Martin, Ungerleider, & Haxby, 2000; Slotnick, 2004; Weinberger, 2004). For example, in a Positron emission tomography study, Martin, Wiggs, Ungerleider, and Haxby (1996) showed that the identification of drawings of animals or tools is associated with the activation of many areas including areas associated with early visual perception in the case of the former and the premotor cortex in the case of the latter. Similar results have been reported in mental imagery tasks (visual and auditory, Wheeler, Peterson, & Buckner, 2000; olfactory, Bensafi, Sobel, & Khan, 2007; motor, Beisteiner, Hollinger, Lindinger, Lang, & Berthoz, 1995; Jeannerod, 1994; for a review see Farah, 1995), categorisation tasks (Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Martin et al., 1996; Proverbio, Del Zotto, & Zani, 2007), lexical decision tasks (Casasanto, Willems, & Hagoort, 2009), tasks requiring the judgement of sensory attributes (Kellenbach, Brett, & Patterson, 2001) and, finally, tasks requiring the verification of sensory properties associated with concepts (Goldberg, Perfetti, & Schneider, 2006).

In parallel with these observations, many behavioural studies have shown that even the most conceptual knowledge is based on the activation of multisensory and motor components. For ex-ample, studies of intermodal switching (Connell & Lynott, 2009; Pecher, Zanolie, & Zeelenberg, 2007; Pecher, Zeelenberg, & Barsalou, 2003, 2004; van Dantzig, Pecher, Zeelenberg, & Barsalou, 2008), or property verification, indicate that concepts are not amodal but are instead "simulated" in one or more sensory modalities. These simulations relate, for instance, to the shape of objects (Solomon & Barsalou, 2001; Zwaan & Yaxley, 2004), their size (Ferrier, Staudt, Reilhac, Jiménez, & Brouillet, 2007; Riou, Lesourd, Brunel, & Versace, 2011; Rubinsten & Henik, 2002; Solomon & Barsalou, 2004) or their spatial position (Oker, Versace, & Ortiz, 2009; Šetic & Domijan, 2007; Stanfield & Zwaan, 2001; Zwaan, Stanfield, & Yuxley, 2002; Zwaan & Yaxley, 2003). To illustrate these studies, we will evoke only the work of Zwaan, Stanfield, and Yuxley (2002). Participants have to read sentences which

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evoked an object or animal in a certain position, with the shape of the animal or object being different depending on the position (for example, an eagle in flight or perched on its nest). After each sentence, a drawing of an object or an animal was presented and the participants had to indicate whether or not this object/animal had been mentioned in the sentence (Experiment 1) or were simply asked to name the object/animal (Experiment 2). In both experiments, responses were faster when the shape of the object or animal was similar in the drawing and the sentence.

Many studies based on the priming paradigm have also demonstrated the modal nature of knowledge in memory. They show that the semantic processing of an object or the motor response to this object can be facilitated by the prior presentation of a stimulus that is associated in memory with the target or with the motor response. The prime and the target may share various components such as motor components (e.g., Brouillet, Heurley, Martin, & Brouillet, 2010; Ellis & Tucker, 2000; Glenberg & Kaschak, 2002; Helbig, Graf, & Kiefer, 2006; Labeye, Oker, Badard, & Versace, 2008; Myung, Blumstein, & Sedivy, 2006; Olivier, 2006; Zwaan, Madden, Yaxley, & Aveyard 2004), auditory components (e.g., Brunel, Labeye, Lesourd, & Versace, 2009; Brunel, Lesourd, Labeye, & Versace, 2010; Kaschak, Zwaan, Aveyard, & Yaxley, 2006; Vallet, Brunel, & Versace, 2010; Vallet, Riou, Versace, & Simard, 2011; Vallet, Simard, Versace, & Mazza, 2013) or gustatory components (Rey, Riou, Cherdieu, & Versace, 2013).

Overall, these data clearly demonstrate that the content of the memory trace is closely related to our former sensory–motor activities, whereas, in turn, these activities depend on the content of our memory traces. The traces are distributed across multiple neuronal systems which code the multiple components of the experiences.

1.3. Knowledge emergence: inter-trace activation and multi-component integration

Versace et al. (2009) proposed that exposure to the environment translates very rapidly into numerous neuronal structures that mainly encode sensory–motor dimensions by means of parallel activations. These initial activations then propagate very quickly to other components that are related to the other properties of the environment, the other sensory–motor components and the components associated with emotion. These multimodal activations are thought to become gradually integrated, thus permitting access to increasingly elaborate and increasingly unitary knowledge concerning the current environment. However, Versace and co-workers (2009) paid little attention to the question of the differentiation between the forms of knowledge that emerge from these activation and integration mechanisms. They assumed simply that “memories” and “concepts” are positioned on a continuum which reflects the “quantity” of reactivated traces: The reactivation of a very limited number of traces permits the emergence of specific knowledge (a memory) and, in contrast, the reactivation of a large number of traces leads to the emergence of abstracted knowledge. Since knowledge reflects the features common to the traces that are activated, the more traces there are, the lower the weight of the specific information carried by individual traces in the emerging knowledge. Emerging knowledge corresponds to states of the memory system, which may either be similar to a previous state (episodic knowledge) or represent a synthesis of a large number of previous states (conceptual knowledge).

To define more precisely the mechanisms that are thought to be involved in the emergence of knowledge, we make use of a matrix representation (see Figure 1) as proposed by Hintzman in Minerva II (1986). Each row in the matrix represents a trace and each column a component of the experience encoded by the trace. It should be noted that this matrix representation might be misleading with regard to the way traces are stored. In this view, traces seem to be specific to each experience and therefore independent of one another. Even though the multiple trace models, and Hintzman (1986) in particular, do not claim that traces can be retrieved in isolation (the content of the echo never reflects the content of a single prior trace), it seems difficult to argue in support of independent memory traces. In fact, there is no contradiction between the idea of a memory system which retains episodic traces and that of non-independent traces which are spatially and temporally distributed. As the same neuronal areas code multiple traces, adding a new trace amends the old traces. This means that memory traces are non-independent both spatially (they share the same neuronal structures) and temporally. Furthermore, this non-independence can be observed both proactively (the content of a trace depends on the content of previously activated

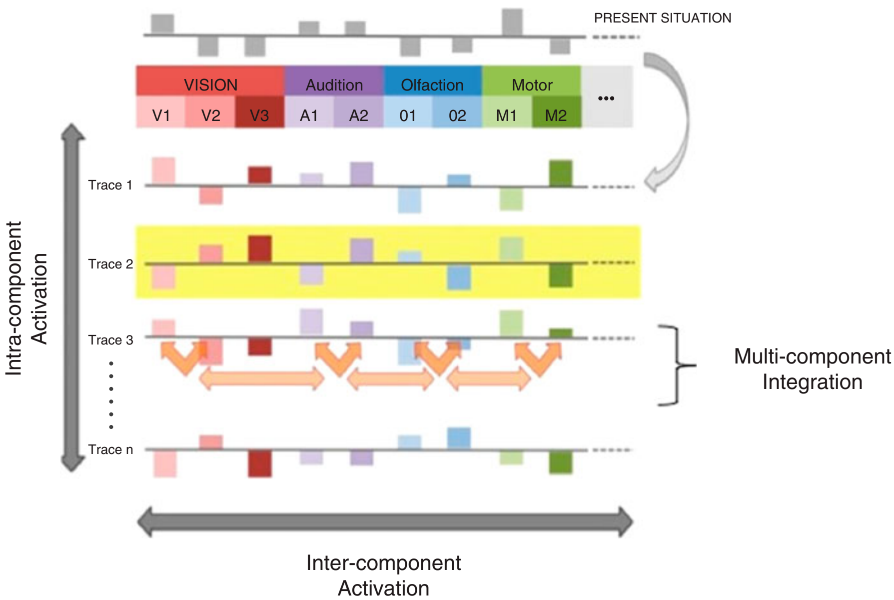

Figure 1. Schematic representation of Act-In based on the MINERVA II model (Hintzman, 1986). Each row represents an episode (an event) encoded as a memory trace. Each episode is composed of different, primarily sensory–motor, features. [To view this figure in colour, please visit the online version of this Journal.]

traces) and retroactively (the content of a trace modifies the content of previous traces). In fact, the traces represented in Figure 1 symbolise the specific states of the cognitive system. These states could be differentiated from one another even if the underlying traces are not independent.

The columns in the matrix represent the trace components which correspond to numerous neuronal structures that encode the sensory–motor properties of experiences. These components can belong to the same modality (e.g., colour and shape are both visual components), or to different modalities.

Our assumption is that, in any given situation, the nature of the knowledge that is likely to emerge depends on the dynamics of two mechanisms, *namely inter-trace activation and multi-component integration*. Inter-trace activation refers to the spread of activation to and between the different traces on the basis of the present experience (broadly defined by its content but also by the subject's activity, the subject's emotional state, etc.). For instance, seeing a picture of a dog activates all the memory traces corresponding to situations in which the individual has been confronted with similar visual stimuli (i.e., other dogs). Since inter-trace activation occurs at the level of each trace component, it should correspond to the spread of activation at the level of each neuronal structure that encodes sensory–motor properties of the experiences (intra-component spread of activation).

However, in our example, seeing a picture of a dog should also activate—at the level of each trace—all the other properties associated with the activated visual dimension, for instance, auditory, olfactory, tactile properties, etc. (e.g., barking sound, smell of the dog and dog hair). This activation, which occurs between the components of each individual trace, is referred to as inter-component activation. To summarise, inter-trace activation involves both intra- and inter-component activation, which operate in parallel. Inter-trace activation is the result of the cueing of traces of past experiences by the current experience (e.g., Nairne, 2006). It spreads on the basis of the properties that are directly activated by the current experience (and which are therefore perceptually present) as well as on the basis of properties that are activated via inter-component activations (which are not currently present). In sum, we propose that the activation mechanism depends on: (1) the strength of association between components within a memory trace; (2) the similarity between a cue (provided by the environment or self-initiated) and the memory traces; (3) the similarity between the memory traces (contrary to MINERVA 2, memory matrix could be organised regarding the instantiation of the memory traces).

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However, inter-trace activation is not sufficient to explain the emergence of knowledge. As Versace and co-workers (2009) have postulated, multi-component[1] integration is necessary if subjects are to be able to access elaborate and unitary knowledge, irrespective of the categorical or specific nature of the knowledge involved. In this view, integration could be assimilated as a simple sum of activation step during the memory activity (see Hintzman, 1986; Nosofsky, 1986). However, in opposition of classical global-matching memory model, we argue that integration must be: (1) an online mechanism; (2) dynamic and progressive; (3) non-linear. For instance, in Minerva 2, sum of activation occurred after that all similarity computations took place. Here we propose that sum of activation occurs in parallel with similarity computation and in a continuous way. Moreover, during integration mechanism, the system should construct and elaborate different forms of knowledge in a non-linear way.

The question remains how to account for the emergence of these different forms of knowledge.

1.4. Categorical activities

1.4.1. The emergence of categorical knowledge. The way we apprehend the world and the behaviours that result from this depend on how we categorise the objects in our environment. The ability to determine very quickly whether an object is heavy or light, living or inert, dangerous or harmless is indispensable for the production of appropriate behaviours. The categorisation process is crucial for global cognition. Consequently, inter-trace activation and multi-component integration should enable individuals to produce behaviours that are both effective and appropriate in the situations in which they find themselves. Most of the time, knowledge and behaviour that are appropriate in a situation are those that have previously been associated with many earlier situations similar to the present situation. What is important is not the specificity of the current situation but instead its similarity to other previous situations.

According to Act-In, a high level of inter-trace spread of activation, particularly at the level of intra-component activations, coupled with the multi-component integration of properties that are therefore not specific to isolated traces, should permit the emergence of categorical knowledge: This knowledge reflects the components which are most frequently found in the activated traces and which are therefore characteristic of classes of objects (or experiences). In contrast, the emergence of specific knowledge should require only a limited inter-trace spread of activation, coupled with multi-component integration of properties that are specific to isolated traces.

The importance of multi-component integration during the emergence of categorical knowledge has been demonstrated in two studies performed in our team (Labeye & Versace, 2007; Labeye et al., 2008). Labeye and Versace (2007) used simple geometrical figures defined by three properties: their shape (circle or triangle), position (left or right) and colour (red, blue, green or yellow). The four stimuli (resulting from the combination of these 3 properties) were learned by the participants in a learning phase during which they had to memorise the associations between the properties. The test phase consisted of a priming paradigm in which the prime was a coloured screen and the target one of the geometrical figures presented in black and white, either to the left or the right of the fixation point. The participants had to decide whether the target figure appeared on the right-hand or left-hand side of the screen. The colour prime corresponded to (i.e., had, in the learning phase, been associated with) either the same shape as the target or the other shape (same shape *vs*. different shape), on the one hand, and to the same or opposite position as the target (same position *vs*. different position), on the other. For one group of subjects, the prime appeared for 100 ms and the target was presented immediately afterwards, thus resulting in a Stimulus Onset Asynchrony (SOA) of 100 ms. The authors assumed that a 100 ms SOA would be sufficient to permit the activation of the two components associated with the prime (its shape and position) but not their integration (inter-component activation, but not multi-component integration). The two components should therefore be activated independently. The authors predicted additive facilitatory effects of (1) congruency between the shape of the prime and that of the target and (2) congruency between the position of the prime and that of the target. For another group of subjects, the prime was presented for 500 ms, a duration that was expected to permit the integration of the prime components within a unitary trace (multi-component integration). A priming effect should

[1] Versace et al. (2009) use the term multimodal integration. We prefer to use multi-component integration, because integration is not limited to properties from different sensorimotor modalities.

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therefore be observed only if the integrated trace resulting from the presentation of the prime shared all of its elementary components with the target, i.e., only when the prime was associated with the same shape and position as the target. The results confirmed the authors' predictions.

These results show that the process of integration requires a certain minimum length of time. An examination of the literature reveals that, to date, the integration mechanism has primarily been studied in the fields of visual perception and attention. For instance, the feature-integration theory developed by Treisman and Gelade (1980) supposes that two stages are involved in the visual identification of an object, with the initial stage consisting of a very rapid and parallel analysis (or detection) of the elementary characteristics of the object, i.e., its shape, colour, orientation, size, etc. However, the objects do not yet exist as entities during this stage. Their identification and the extraction of knowledge relating to them are thought to require the integration of the elementary characteristics. This integration is only possible if attention is focused on a specific area of the visual field. This focusing of attention makes it possible to integrate all the elementary characteristics of the region in question.

However, Versace and co-workers (2009) have already pointed out a fundamental difference between Treisman's model and the integration mechanism proposed in Act-In. Within the framework of Act-In, the sensory features discussed by Treisman are considered to be memory features. Despite this difference, it can be seen that also in Treisman's model, integration is not immediate.

1.4.2. The brain is by default a categorisation system. We state above that one of the main assumptions of the Act-In model is that the brain is a categorisation system which develops by accumulating experiences and which produces categorical knowledge by default. Various types of argument can be proposed in support of this assumption. First, this idea is also prevalent in the neurosciences as well as behavioural works that have addressed the question of the formation of the memory system. As far as neuroscientific studies are concerned, beyond the above-mentioned plasticity of the system, another specificity of the nervous system is its connectivity. A large number of inter-neural connections permit the fast transmission of signals to areas distributed throughout the brain. These connections are formed gradually during the course of development. The cortex is in a state of permanent adaptation on the basis of the joint activity of all these neurons. It is the time-related correlations between the neuronal activities and between the neuron groups that makes it possible for these changes within the neuronal networks to occur (see Changeux, 1983; Damasio, 1989; Edelman, 1987). However, this connectivity is not uniform. There are more connections between localised sets of neurons than between the neuronal groups. This localised connectivity is responsible for what we refer to as intra-component activation. Consequently, although multi-component integration is essential for the emergence of elaborate and unitary knowledge, the categorical (non-specific) nature of this knowledge is due primarily to the extensive intra-component spread of activation.

Working from a cognitive viewpoint, many authors have attempted to describe the development of these categorisation systems (Goldstone, 2000; Goldstone & Barsalou, 1998; Schyns, Goldstone, & Thibaut, 1998). According to Barsalou (1999, 2005), the similarities between the various patterns of activation engendered by our different experiences result in the gradual acquisition of "representations" associated with all our sensory or motor modalities. Barsalou refers to these representations as perceptual symbols. According to this author, the progressive establishment of the categorisation mechanism involves a number of stages. First of all, being confronted with an object triggers the activation of feature detectors in the corresponding sensory areas (the activation of neurons that respond to edges, colours, orientations, but also to auditory, olfactory or motor properties). At the same time as the sensory–motor representations (or sensory–motor maps) are being activated, neurons in the associative areas register the configurations of sensory–motor features. Since different exemplars of the same category of objects (the same concept) activate similar sensory patterns, they should involve very similar populations of neurons. This neuronal reinforcement thus permits the construction (the abstraction) of modality-specific representations (perceptual symbols) and multimodal representations of the concept which involve both modality-specific and associative areas.

If we turn more specifically to the issue of trace formation, although the literature on memory almost systematically distinguishes between the encoding mechanisms and those involved in knowledge emergence, they are in fact difficult to dissociate. The propagation of inter-trace activation, coupled with multi-component integration, *simultaneously* permits both the emergence of knowledge and the modification of the content of memory. This means that the content of the traces reflects not only the present experience but also the earlier traces that are globally the most similar to the present experience. This once again suggests that the memory system is, above all, a categorisation system.

This idea can also be applied to procedural knowledge. It is through repetition that motor or cognitive skills are acquired. This acquisition is only possible if the repeated activity is appropriate for the task to be performed. Here again, the different repetitions of the activity reinforce the similarities between the various patterns of activation that are engendered. "Procedural" knowledge is adapted to a class of situations that share common characteristics. The situations for which this type of knowledge is appropriate (the situations that it "represents") are certainly less variable than in the case of "declarative" categorical knowledge.

Another illustration showing that the brain is, by default, a categorisation system is provided by neuropsychological data relating to the effect of ageing. Healthy elderly adults exhibit some episodic impairments which take the form of the recall of fewer items (Balota, Dolan, & Duchek, 2000) and less vivid memories (Friedman, de Chastelaine, Nessler, & Malcolm, 2010). At the same time, however, their semantic knowledge seems to remain intact and is perhaps even better than that of younger adults (Park & Gutchess, 2002), since they accumulate more knowledge with time. A second point, that has already been stressed by numerous psychologists, is that semantic knowledge appears to be more resistant than other cognitive functions to neuropsychological disorders (as predicted by the Serial–Parallel–Independent model, Tulving, 1995). This assumption finds support in the observation that only semantic dementia is characterised by semantic impairments (Hodges & Patterson, 2007) compared to other dementias such as Alzheimer's disease, episodic deficits (Carlesimo & Oscar-Berman, 1992), fronto-temporal dementia or the dysexecutive syndrome (Weder, Aziz, Wilkins, & Tampi, 2007). Finally, the robustness of semantic knowledge is confirmed by observations of traumatic brain injury patients whose semantic memory is found to recover better than their episodic memory (Himanen et al., 2006).

1.5. Discriminant activities

1.5.1. The emergence of specific knowledge. The question addressed here is how a system favouring the emergence of categorical knowledge can be effective in discriminant memory activities, which are activities that require the "retrieval" of specific knowledge. Discriminant activities should result from the activation of a limited number of traces of past situations. In other words, inter-trace activation should be constrained (more particularly, the intra-component activations) and inter-component integration should be restricted to components of specific traces. The effectiveness of discriminant activities thus depends, on one hand, on the potential for a trace to be specifically reactivated and, on the other, on the potential of the current situation to reactivate specific traces. The likelihood that a trace can be specifically reactivated depends on: (1) its distinctiveness and (2) the level of integration (or binding) of the components of the trace.

1.5.2. Trace distinctiveness. The literature on the distinctiveness effect indicates that this effect can generally only be observed with direct measures such as those used in free recall or recognition tasks (Geraci & Rajaram, 2004; Smith & Hunt, 2000; Von Restorff, 1933). Distinctiveness is often described as a qualitative property of a memory trace, because isolated information elicits better memory performance than non-isolated information (see Schmidt, 1991). However, recent work undertaken by our team has shown that the distinctiveness effect is also observed using both indirect (Brunel, Oker, Riou, & Versace, 2010; Oker & Versace, 2010; Oker et al., 2009) and direct (Brunel, Oker et al., 2010) measures of memory. These results suggest that the distinctiveness of the memory trace should vary along a continuum of similarity between memory traces (Cleeremans, 2008; Nosofsky & Zaki, 2003) and as a function of the task demands (i.e., indirect or direct, see Brunel, Oker et al., 2010). This continuum is possible, since knowledge emerges from the dynamic of the system that reflects a temporary state of the memory trace in a given task.

This view has been confirmed by Brunel, Oker et al. (2010) who manipulated and tested different levels of trace isolation: A "global" level of isolation between items that related to the overarching features involved in the memory trace ("living" words vs. "non-living" words), and a

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"partial" level of isolation ("sound" words vs. "silent" words), in which the difference between memory traces related only to one feature, i.e., a sound component which was either encoded or not encoded in the memory trace. Distinctiveness effects were observed in a series of memory tasks of increasing complexity, namely a lexical decision task, a recognition task and a free recall task.

The results showed that whatever the level of isolation, lexical decision was faster for old isolated items than for old non-isolated items and that old isolated items were recognised faster than old non-isolated items. Therefore, trace distinctiveness seems to increase perceptual fluency, because judgements (lexical decision, recognition decision) on distinctive items were faster. Isolation changed the global level of memory access by affecting the context of the memory traces, with the result that isolated memory traces were accessed faster during retrieval operations. Moreover, the authors observed that manipulating the level of trace distinctiveness selectively influenced the conscious recollection of items. In the case of global isolation, distinctive traces were sufficiently distinct to reach the level of consciousness. As expected, distinctiveness effects were observed in terms of the degree of confidence expressed by the participants (isolated items were associated with a higher degree of confidence than non-isolated items) and the free recall percentage (isolated items were associated with a higher probability of recall than non-isolated items). However, these observations were restricted solely to the globally isolated items.

The authors concluded that trace distinctiveness improved subsequent access to the trace, whereas the level of trace distinctiveness also determined the possibility of conscious or explicit retrieval. Discriminant activities are defined as activities involving the retrieval of specific traces. However, trace specificity is itself very often dependent on the situational information and the temporo-spatial context associated with the trace in memory. Indeed, whereas the properties of objects remain relatively stable between situations, the situational and temporo-spatial contexts vary greatly from one experience to another. Most of the time, the context specifies the episode as the encoding specificity principle illustrates (Tulving & Thomson, 1973). The difficulty of what is referred to as episodic retrieval thus often lies in the problem of "putting the information back into context". There is considerable data showing that episodic retrieval is more effective in the case of information associated with particularly salient contexts (for a review, see Davis & Thomson, 1988, or, for a discussion of emotional contexts, see Bower, 1994, or Blaney, 1986).

These data indicate that the efficiency with which specific (episodic) knowledge emerges depends on the specificity of this information as well as on the general context associated with the trace. We stated above that the specificity of the target information depends in particular on the strength of the link between its different components. Similarly, context specificity is of value only if there is a strong link between the contextual and the target information within the trace. This is why we assume that the second important factor influencing the probability that a trace will be specifically reactivated is the level of integration (or binding) of its components.

1.5.3. The level of integration of the trace. Act-In assumes that the emergence of specific knowledge requires multi-component integration at the level of the individual trace during encoding, i.e., the components have to be integrated within the same trace. This integration could be described as intra-trace integration. Our main assumption is that the effectiveness of the re-emergence of specific traces depends on the level of integration of the features within the trace. The notion of level of integration refers to the strength of the link between the components of the trace. The more integrated the features are, the more likely it is that the trace as a whole will be dissociated from other traces and can therefore be specifically retrieved. Many factors may increase the level of intra-trace integration, such as the nature of the processing involved during encoding as well as the presence of multimodal information and the subject's emotional state. These factors will be discussed in more detail in § 4, which is devoted to the literature on discriminant activities.

According to Versace and co-workers (2009), "the term integration should be used when the addition of elementary components results in a new entity in which the elementary components are no longer differentiated" (p. 532). They illustrated their definition with reference to the McGurk effect (e.g., McGurk & MacDonald, 1976). The sound "ba" is perceived as "da" when it is associated with lip-reading of the sound "ga". The question is to determine whether the different parts of the integrated objects remain accessible. An important distinction should be made between the integral and separable components (Garner, 1974). In the presence of integral components, it is quite difficult to attend to one component without

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attending to the others. In contrast, in the case of separable components, it should be possible for the components integrated in the trace to be activated separately, even if interactive activation permits a measure of re-integration of the components during retrieval. In fact, different forms of integration should be differentiated depending on the nature of the components that are involved as well as on whether the components belong to the same or to different modalities.

Although the dynamics of integration probably depends on the nature of the components that are involved, one important characteristic of this mechanism is that it is not immediate (see the study by Labeye & Versace, 2007 referred to in § 2.4.1., as well as Treisman's studies, e.g., Treisman & Gelade, 1980). The hypothesis that a certain minimum length of time is required in order for an integrated trace to be constructed has been tested by Versace (1998) and Versace and Nevers (2003) in word-level studies. For instance, Versace and Nevers (2003) used a priming paradigm in a target task, namely a lexical decision task that could not be performed solely on the basis of the orthographic and phonological properties of the target. Consequently, long-term priming effects could result only from the construction of memory traces that integrated these perceptual levels. The authors hypothesised that when masked primes are presented for a brief period, priming arises from a pre-lexical activation of the orthographic and/or phonological components. That is why the influence of lexical frequency on priming has been observed only when the conditions of presentation of the prime have permitted the integration of the activated elementary components and, consequently, the identification of the prime (e.g., Forster & Davis, 1984; McKone, 1995). Their results showed that in the case of primes presented for 50 ms, repetition priming did not vary with the frequency of the targets and decreased as the interval between the prime and the target (Interstimulus Interval (ISI)) increased, before disappearing at an ISI of 3000 ms, irrespective of the frequency of the words. In the case of primes presented for 700 ms, repetition priming was systematically greater with rare words than with frequent words and remained significant at an ISI of 3000 ms. This confirms the fact that when the time available to process the primes is very limited, priming effects arise due to the early activation of the infra-lexical level, since no effect of frequency on priming was observed. In contrast, when the time available to process the primes increases, the integration of the perceptual components seems to permit the emergence of frequency effects on priming and priming seems to persist in the long term.

To conclude, these results clearly show that when subjects are confronted with multi-sensory experiences, they form memory traces which reflect the content of these experiences (or, in more general terms, the situation), and that the repetition of the associations between the components of the trace facilitates the subsequent emergence, at a conscious level, of forms of multimodal unitary knowledge.

1.5.4. The potential of the current situation to reactivate specific traces. It is clear that if the potential for a trace to be specifically reactivated is an important factor in the retrieval of specific information, the efficiency of this retrieval should also depend on the potential of the current situation to reactivate specific traces. Since one of the functions of memory is to combine the current experience with past experiences (Glenberg, 1997), the characteristics of the current situation determine the re-evocation of traces. As stated above, inter-trace activation spreads on the basis of the properties that are directly activated by the current experience. Specific knowledge can only emerge if the elements of the current situation lead to a very limited level of inter-trace propagation. Thus, the presence of strong cues in the current situation might reduce the number of activated traces. These cues include the sensory properties of the objects (visual, auditory, olfactory, etc.), as well as the properties associated with the gestures involved in the use of these objects (see the notion of affordance as proposed by Gibson, 1977). However, this activation also depends more broadly on the situation confronting the individual (situational context, intentions/motivations, emotional state) as well as his/her activity.

In most cases, information linked to the situation confronting the individual (situational, representational, emotional context) will provide cues that lead to the reactivation of specific traces (as point out by Tulving & Thomson, 1973). Based on the encoding specificity principle, i.e., the idea that the context at the time of encoding determines the content of the memory trace, the effectiveness of a retrieval cue should depend on the similarity between the information supplied by this cue and the specific representation that results from encoding. This assumption has given rise to a large body of work on contextual effects on memory (for a review, see, for instance, Davis & Thomson, 1988).

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Within the multi-system approach, these context effects are thought to be specific to episodic memory, thus explaining why they are primarily observed in direct memory tests. According to Act-In, context effects should be observed as of the time when a specific item of knowledge is useful for the subject's activity, that is to say, in both direct and indirect tests of memory.

This is precisely what was found by Oker and Versace (2010). The main objective of these authors was to assess whether the distinctiveness effect can be observed in implicit memory tasks and to test how the specificity of an item can be varied by manipulating the contextual information associated with it during encoding. In an encoding phase and a test phase, participants had to categorise target words as referring to either artefacts or natural items. Each target word was associated with a context which consisted of a coloured frame in which the word was presented. In order to manipulate the distinctiveness of the contextual information, three quarters of the words were encoded with the same contextual information (frequent context), whereas the other quarter was encoded with different contextual information (rare context). In the test phase, the context effect was tested by presenting words with a context either of the same colour as in the encoding phase, or of the other colour. The authors predicted that if the distinctiveness effect is due to the contextual information, then a change in contextual information between the encoding phase and the test phase should be more detrimental for items encoded with a rare (or specific) context than for items encoded with a frequent context. The results confirmed this prediction since words that had been presented in the rare condition during encoding were categorised more rapidly when presented in the same context at test than when they were presented in the other context. In contrast, no significant context effect appeared for words that had been initially presented in the frequent context condition.

To conclude, it is important to note that the content of the current situation is not only important for the retrieval of specific knowledge. It is also relevant for categorical knowledge and, more generally, for overall cognitive functioning. Knowledge is simply the result of the dynamic of cognitive functioning, which is entirely dependent on the current situation (environment, subject's activity, emotional state, etc.). It is the situation that produces the knowledge.

1.6. An integrated view of cognition

The conception of memory proposed by Act-In is able to respond to many of the criticisms levelled at both the multi-system models (for a discussion, see Versace et al. 2009) and the single-system models. With regard to the single-system models of memory, and Minerva 2 in particular, we stated before that although Act-In is fully consistent with these models, it also attempts to clarify three points: (1) the nature of the experiential components that are actually encoded within memory traces; (2) the mechanisms that might explain how different forms of knowledge emerge from memory traces; and (3) the construction of the memory traces and the importance of the level of integration between the components of the trace.

Based on the literature as well as on the studies performed in our team, we assume that memory traces reflect all the components of past experiences and, in particular, their sensory properties as captured by our sensory receptors, as well as the actions performed on the objects in the environment and the emotional and motivational states of individuals. We also postulate that knowledge is emergent and is the product of the coupling of present experience with past experiences. The emergence of categorical knowledge is assumed to require a high level of inter-trace activation coupled with the multi-component integration of properties that are not specific to isolated traces. In contrast, the emergence of specific knowledge is assumed to require a limited inter-trace spread of activation, coupled with the multi-component integration of properties that are specific to isolated traces. Finally, concerning the construction of the memory traces, we assume that the re-emergence of specific traces depends on the level of integration of the features within the trace: The more integrated the features are, the more likely it is that the trace as a whole will be dissociated from other traces and will therefore be specifically retrieved.

Act-In specifies in detail the content of the traces and the mechanisms involved in the emergence of knowledge. However, perhaps, the greatest advantage of Act-In lies in the fact that it considers overall cognitive functioning in a highly integrated manner. As Versace et al. (2009) concluded: "knowledge, the resulting states of consciousness, the evolution of these states of consciousness, and the ensuing behaviour can all be described in terms of the

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successive states of a multimodal memory system". This integrated conception of cognitive functioning is particularly evident in the close association between the perceptual and memory mechanisms.

Perceptual and memory processes are often studied separately, and the description of the interactions between these mechanisms is highly dependent on the approach to memory adopted by each individual author. In the literature, the interactions between perception and memory have long been explained in terms of top–down processes. This tendency is due to the long-held dominant conception of an abstractionist memory that is independent of the sensory systems. Moreover, perception is considered to be strictly hierarchical and sequential (e.g., Biederman, 1987; Marr, 1982), with the result that memory is viewed as the final processing step that follows on from the perceptual stage. This step consists of a sort of comparison between the object derived from perception and a representational store present in memory.

However, in these strictly top–down models, the mechanism responsible for the comparison between the result of perception and the representational store in memory has never been clearly defined. That is why more recent models of perception accept the existence of top–down effects (Bar, 2004; Bar et al., 2006) which facilitate this correspondence. Nevertheless, the results of research in the field of categorical perception, while confirming the close links between perception and memory (Goldstone & Hendrickson, 2010), also suggest that these links can no longer be described in terms of reciprocal interactions. For example, Goldstone (1995) has shown that the perceived sensory differences between objects are accentuated when these objects belong to different semantic categories. Two objects of the same colour, one of which belongs to a category which tends to be red and the other to a category which tends to be purple, are not always judged to be the same colour (see also, Niedenthal & Kitayama, 1994; von Hippel, Hawkins, & Narayan, 1994). Similarly, Hansen, Olkklonen, Walter, and Gegnfurtner (2006) have shown that an object's typical colour (memory) has an influence on its perceived colour.

This effect of category similarity has also been observed in studies of attentional processes. The visual search for a target surrounded by distracters is more effective when the distracters are perceptually similar to each other than when they are perceptually different (Humphreys & Müller, 1993; Treisman, 1988). Duncan and Humphrey (1989) consider that this effect is due to a perceptual grouping that makes it possible to exclude the distracters as a group. However, the same type of effect has been obtained by varying the homogeneity of the distracters at the memory level rather than the perceptual level (e.g., Goldstone & Hendrickson, 2010).

Following in the same line of research, our team recently revealed an effect of the difference in typical size between a target and distracters in a visual search task based on a perceptual difference (Riou et al., 2011). The participants took less time to detect a difference in perceptual size when the difference in typical size between the target and the distracters was congruent with the perceived size difference than when it was not.

The studies that we have mentioned above suggest that perceptual and categorical (i.e., memory-related) mechanisms operate simultaneously. However, the crucial question is to determine whether the results reflect reciprocal interactions between perceptual and memory processes (top–down mechanisms) that are underpinned by independent cognitive and neuronal systems, or whether they point to the existence of shared systems or systems which, at the very least, possess significant overlaps. Demonstrating the simultaneity of the perceptual and memory mechanisms does not necessarily imply that there are shared neuronal systems and shared forms of "representations". Conversely, however, the involvement of shared forms of "representations" and systems implies that the mechanisms operate simultaneously and that influences between perception and memory are symmetrical. We have reported many brain neuroimaging studies that demonstrate this involvement above.

It is worth noting that although many of the works referred to above have been interpreted as indicating the presence of distinct but interacting mechanisms, we have seen that a growing number of authors now consider that perceptual and conceptual mechanisms are at least partially based on the same systems. If we agree, as Act-In suggests, that knowledge is constructed and (re-)emerges through the activation of neuronal systems that are typically associated with sensory–motor mechanisms, then the content and functioning of memory are intrinsically linked to our past and present sensory–motor activities and, conversely, our sensory–motor activities are completely dependent on the memory traces of past sensory–motor experiences.

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Finally, Act-In proposes a radical change in the explanation of the links between memory and perception (see Figure 2). This is referred to as a horizontal view (in contrast to the traditional vertical and hierarchical views) according to which both perception and memory result from the activation of components of multimodal traces of the same type. When the activity relates directly to the perceptually present components, these are perceptual mechanisms and, in contrast, when the activity relates to perceptually absent components (which are nevertheless activated by and depend on the components that are present), these are memory mechanisms. During the perception of the sensory–motor characteristics present in the environment, the other components of the memory traces that are not perceptually present are activated and influence the perceptual mechanisms. In contrast, if we consider that memory activities systematically involve the sensorimotor components of traces of past experiences, it is clear that the reactivation of these components is dependent on the perceptual content of the current situation and the individual's sensory–motor activity. It is therefore clear that it is difficult to dissociate memory mechanisms from perceptual mechanisms other than on the basis of the presence (perceptual processing) or absence (memory processing) of the characteristics of the objects to which the processing is applied.

In accordance with this assumption, in a recent study, Rey, Riou, and Versace (in press) used an adaptation of the Ebbinghaus illusion paradigm in two experiments in order to demonstrate that similar effects can be observed whether the size difference between the inner circles and the inducers is manipulated perceptually (the size difference is perceptually present, Experiment 1) or only reactivated in memory (it is perceptually absent, Experiment 2). In Experiment 2, the size of the inducers was not manipulated perceptually but was reactivated in memory through the use of different colours which had been associated with different sizes during a learning phase. In Experiment 1, the perceptual size of the inducers created a bias in the perception of the size of the inner circles. In Experiment 2, the same effect was obtained, despite the fact that the perceptual size of the inducers was identical. It was therefore the colour of the inducers that reactivated the different sizes in which they been displayed during the learning phase. Thus, not only the emergence of knowledge, but also behaviour in general, depends on the interactions between the present and activated components of traces.

We have seen that Act-In considers overall cognitive functioning in a highly integrated manner. Cognitive functioning involves categorical and discriminant activities, and many studies over the years have attempted to describe their main properties. The remainder of this paper will therefore focus on categorical and discriminant activities and attempt to show how the Act-In model sheds new light on classical results reported in the literature.

2. THE LITERATURE ON CONCEPTUAL KNOWLEDGE

The purpose of this section is to discuss the work on the idea of concept. We first discuss the classical studies on the typicality effect and on the level of generality of concepts. We then discuss the numerous studies that have specifically examined category-specific disorders.

2.1. The typicality effect

One of the results that is most frequently discussed in the literature on categorisation is the typicality or prototype effect. A prototype is an exemplar that differs from the others due to the fact that it is much more salient, such as a sparrow compared to a penguin in the case of birds. This differentiation is primarily due to the presence of more frequent or classical properties shared by other exemplars of the same category (for instance, a classroom chair compared to a designer chair). Typicality effect can be observed in the form of a higher level of availability in memory, as demonstrated by property verification tasks and, to an even greater extent, classification tasks (Cabeza, Bruce, Kato, & Oda, 1999). According to the so-called prototype models, a category is created from prototypical exemplars. Classification is then performed by comparing the exemplar to be categorised to the prototype (Homa, Goldhardt, Burruel-Homa, & Smith, 1993). In contrast, the so-called exemplar models consider that each exemplar is stored individually and that classification proceeds via a comparison of the exemplar to be classified with all the other stored exemplars (Zaki, Nosofsky, Stanton, & Cohen, 2003). The evidence from a growing number of studies seems to provide support for the exemplar models to the

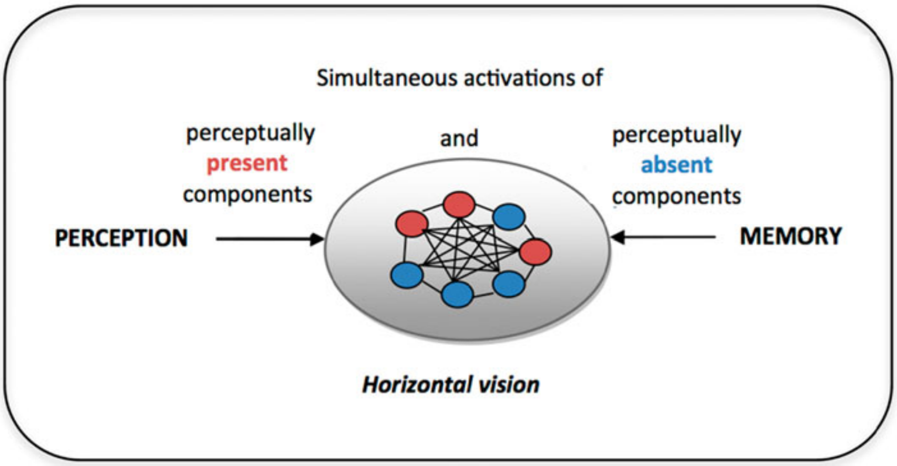

Figure 2. A "horizontal" view of the relations between memory and perception. [To view this figure in colour, please visit the online version of this Journal.]

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detriment of the prototype models (Goldstone & Kersten, 2003).

As a multiple trace model, Act-In represents an extension of the exemplar-based approaches. Whereas it is now accepted that concepts are defined by sets of features, we also know that certain features are characteristic of almost all the exemplars of a category (see the defining and essential features described by Smith, Shoben, & Rips, 1974); however, others are typical of a category but are not necessarily shared by all the members of the category (the characteristic or accidental features described by Smith et al., 1974). Consequently, all the exemplars of a category are not equivalent. Some are more representative of the category than others. Whereas all the members of a category possess defining features, only the most typical among them possess the characteristic features or, at least, the majority of these features. The most typical exemplars are considered as prototypes of their categories (e.g., Rosch, 1978; Rosch & Mervis, 1975). As we argue above, inter-trace activation allows the emergence of knowledge that reflects the components which are most frequently found in the activated traces and which are therefore characteristic of classes of objects. This means that inter-trace activation accounts for the emergence of prototypical knowledge.

2.2. The level of generality of concepts

Concepts do not differ solely in terms of their typicality. They are also distinguished by their level of inclusion or generality. For instance, the concept "animal" is more inclusive (i.e., it contains many more elements) than the concept "fish" and is therefore located at a higher level of generality. It is conventional to differentiate three levels of inclusion: The superordinate level (e.g., animal), the basic level (e.g., dog) and the subordinate level (e.g., poodle). The basic level is considered to be the level that is most important in cognitive terms (see Rips & Medin, 2005 for a discussion). For instance, Rosch, Mervis, Gray, Johnson, and Boyes-Braem (1976) showed that basic level categories are preferred by adults when naming objects, are learned first by children and are associated with the fastest categorisation reaction times. Rosch et al. (1976) also demonstrated that basic objects are the most inclusive categories whose members: (1) possess significant numbers of attributes in common, (2) have motor programmes which are similar to one another, (3) have similar shapes and (4) can be identified from the averaged shapes of members of the class.

However, as Thibaut (1999) points out, the advantage of the basic level is probably linked to the properties of the concepts that exist at this level. Basic level concepts are both homogeneous (i.e., they share a large number of features) and distinctive (i.e., they possess many features which distinguish them from other concepts). On the contrary, the categories at the subordinate level do not tend to be highly contrasted (e.g., a sparrow and a canary have many features in common), and the concepts at the superordinate level are not very homogeneous (e.g., birds and fish do not share many features). Basic level concepts provide the best compromise between maximising

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within-category similarity and minimising between-category similarity (Rips & Medin, 2005).

Instead of differentiating between concepts on the basis of their level of inclusion or generality, a better approach would therefore be to differentiate between them on the basis of the homogeneity and specificity of the features associated with them. The progressive access to the different levels of generality can be fully explained in terms of the dynamic of inter-trace activation. Given that inter-trace activation first reflects the components which are most frequently found in the activated traces, it should permit the rapid emergence of basic level concepts. Basic level concepts are nothing more than the most prototypical perceptual "representations" (see the perceptual symbols described by Barsalou, 1999, 2005). Taking these basic level concepts as a starting point, it is then possible to access more specific knowledge (subordinate level concept) by taking into account more specific perceptual properties, thus, in turn, restricting inter-trace activation. However, it is also possible to access more general knowledge (at the superordinate level) through the increased inter-trace spread of activation and, more particularly, inter-component spread of activation. Let us take the example of a banana (a basic concept according to Hoffmann, 1982, for instance, but at the same time also a subordinate concept). This is characterised by shape, colour, taste, smell and consistency, as well as by motor properties relating to the way it is held, etc. The concept of fruit (superordinate concept) is associated with a greater variety of shapes, smells, flavours and colours. What groups the various types of fruit together is primarily the fact that they come from plants; are usually edible; and are associated with visual, olfactory, tactile, gustatory experiences and so on. The same applies to the concept of food. Here again, food can be characterised on the basis of an extremely varied range of features. What is specific to all the elements in this category is the fact that they serve to nourish us. They are associated with "food-related" experiences and consequently all the sensorimotor features which may characterise these experiences.

Consequently, the variations in the time taken to access concepts as a function of their level of generality or the number of exemplars characterising them (e.g., Collins & Quillian, 1969; Landauer & Freedman, 1968) reflect the greater or lesser extent of intra-component and inter-component activation necessary in order for this knowledge to emerge.

2.3. Category-specific disorders

Categorical activities are very important not only in normal cognition, but also in abnormal cognition, as illustrated by patients with category-specific disorders (for a review, see Capitani, Laiacona, Mahon, & Caramazza, 2003). A category-specific disorder consists of a processing deficit that is more marked for one knowledge category (or a small number of sub-categories) than for other categories that are better processed (Caramazza & Mahon, 2006). The most regularly reported dissociation is an impairment on living objects, typically animals, compared to non-living objects, typically tools. The reverse dissociation has also been reported but remains rare (Basso, Capitani, & Laiacona, 1988). Category-specific disorders such as the above-mentioned double dissociation question the way memory models address the organisation of knowledge.

Double dissociations between semantic categories could first suggest that different stores or systems underlie these categories as proposed in the domain-specific knowledge approach (Caramazza & Shelton, 1998). This theory is primarily based on neuroimaging studies that have demonstrated that distinct areas of the brain are activated as a function of the processed categories (Marques, Canessa, Siri, Catricalà, & Cappa, 2008). This suggests the existence of specific and relatively independent knowledge stores which are underpinned by specific brain regions. Knowledge relating to living objects is thought to be underpinned by the anterior temporal lobes, whereas knowledge relating to non-living objects is thought to depend on more posterior regions of the same lobe. This hypothesis raises the problem that the stores themselves would increase in size with every newly observed dissociation. Moreover, this theory assumes that there is an amodal semantic hub that is underpinned by the anterior temporal lobes (Rogers et al., 2006). This hub would serve to extract the meaning and shared properties of objects on the basis of abstract units (concepts). However, this supposed hub has been criticised on numerous occasions (Simmons & Martin, 2009) and amodal knowledge goes against assumptions underlying Act-In.

A second hypothesis proposed to explain the category-deficit disorders and which fits more readily within the framework of a sensory-dependent approach is based on the relationship between features and categories. According to the "sensory/functional theory" (SFT) (Warrington & Shallice,

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1984), living objects are primarily defined in terms of their sensory properties, whereas non-living objects are primarily defined in terms of their functional properties (what they were created in order to do). The exemplars of these categories also differ more specifically at the level of certain of these properties, i.e., sensory properties in the case of animals and functional properties in that of objects. For instance, a lion is distinguished from other animals by its appearance and its roar, whereas a desk primarily differs from a table in terms of its function (which allows people to work, arrange documents, etc.). Within this approach, a deficit in the processing of living objects would be associated with a deficit in the processing of sensory knowledge such as a deficit relating to the visual properties associated with the item. In contrast, a deficit in the processing of non-living objects would be due to a deficit in the functional knowledge relating to these objects. SFT assumes that knowledge is organised into semantic sub-systems which reflect the sensory or functional modality to which the knowledge relates. However, this theory comes up against considerable limitations in the form of the observation that some patients present more subtle dissociations between categories such as between fruits and animals (e.g., Caramazza & Shelton, 1998) or in the fact that some patients with impairments on living objects exhibit no impairment of the sensory knowledge associated with these objects (Sartori, Gnoato, Mariani, Prioni, & Lombardi, 2007).

Beyond the limits of SFT, the idea that the categories could be differentiated on the basis of the mean of their relative features is clearly consistent with Act-In and related memory models. For instance, the OUCH model, standing for Organized Unitary Content Hypothesis (Caramazza, Hillis, Rapp, & Romani, 1990), considers that knowledge is organised based on the frequency of co-occurrence of items or properties. Consequently, conceptual properties which regularly co-occur are stored close to one another in a semantic space, in a way that leads to the creation of categories, as also defined in the CSA hypothesis (Conceptual Structure Account; Tyler, Moss, Durrant-Peatfield, & Levy, 2000). The CSA hypothesis goes further by defining different types of relations between certain groups of objects and specific properties. Knowledge of "living objects" would be characterised by a greater level of intra-category structural similarity than is the case of inanimate objects. The characteristic "has a mouth" is almost always associated with the characteristic "has eyes". "Living" objects therefore have relatively constant structural properties. In contrast, the correlation between their structural properties (such as their shape) and their functional properties is thought to be quite weak, unlike non-living objects: An animal's shape does not make it possible to predict the animal's behaviour (carnivorous, timid, etc.). In contrast, non-living objects seem to be characterised by a low level of intra-category structural similarity but by strong links between shape and function (for example, a chair is for sitting in). These different types of link between structural and functional properties would therefore explain why category-specific deficits may or may not be observed depending on whether the processing impairment is located at the structural level or the level of the relation between shape and function.

Act-In is therefore able to explain the category-specific disorders. Act-In, like the CSA theory, supposes that when individuals interact with the environment, they extract the properties relating to each item in it. This probabilistic learning also leads to certain objects which frequently share the same properties being grouped together. Categories are therefore created through the individual's experience as a function of the features shared by these objects. This approach considers that there is a vast network which is distributed throughout the entire brain and which underpins properties rather than categories per se, with visual aspects being underpinned by the occipital lobe, for instance (Taylor, Moss, & Tyler, 2007). Finally, within this framework, category-specific impairments would be due to a degradation of the properties that differentiate the exemplars of a category. In the case of animals, for instance, a degradation of the properties that allow distinguishing between the overlapping visual properties might explain the category-deficit in disfavour of animals (see Vallet, Simard, Fortin, Versace, & Mazza, 2011). This hypothesis is supported by the finding that the perirhinal cortex is involved in high-level multi-sensory integration (Taylor, Moss, Stamatakis, & Tyler, 2006).

3. THE LITERATURE ON DISCRIMINANT ACTIVITIES

Discriminant activities could be described as the probability of retrieving a particular memory trace in the context of a memory activity. This kind of activity is generally assessed on the basis of "explicit"/"episodic"/"conscious" memory testing

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procedures (Reder, Park, & Kieffaber, 2009), that is to say, direct tasks (Johnson & Hasher, 1987). Direct tasks have been described as tasks involving a specific event from the subject's personal history (e.g., free recall, cued recall, recognition), whereas indirect tasks measure the effects of prior exposure to a given material on the processing of a subsequent motor or cognitive task in the absence of any explicit reference to earlier events (e.g., lexical decision, trigram completion, etc.).

How can a given trace be specifically reactivated? We have already said that, according to Act-In, the answer is: (1) when it is distinctive from other traces, (2) when the link between its features is so strong that the activation of one of the features of the trace automatically results in the reactivation of the other features and (3) when the current situation has specific characteristics that act as strong cues for the specific reactivation of traces which possess these same characteristics. Later, we refer to results typically reported in the literature with reference, in particular, to the effect of: (1) the nature of the processing involved during encoding, (2) the presence of multimodal information and (3) the subject's emotional state. We do not undertake a presentation of the state of the literature relating to each of these domains but instead simply illustrate the fact that the Act-In framework makes it possible to explain a very large number of observations.

3.1. Encoding manipulations

It has been repeatedly demonstrated that encoding manipulations produce strong effects on performance in direct tests but do not affect repetition effects in indirect tests (for a review, see Richardson-Klavehn & Bjork, 1988). The most frequently performed manipulations have consisted of modifying the level of processing (semantic vs. perceptual) or increasing elaborative processing at study time (e.g., Craik & Lockhart, 1972; Craik & Tulving, 1975; Jacoby & Dallas, 1981). Generally speaking, it is very clear that encouraging semantic processing at encoding time primarily improves performance on explicit memory tests. Some authors (e.g., Roediger & Blaxton, 1987) have even replaced the dissociation between the explicit and implicit memories by an opposition between data-driven processing and conceptually driven processing. According to these authors, most indirect tests can be classified as data-driven, because the subject is required to act in response to perceptual information provided by the experimenter (e.g., fragment completion, perceptual identification). In contrast, direct tests usually involve a significant amount of conceptually driven processing, because the subject must mentally reconstruct the study episode (e.g., in free recall).

Within the framework of Act-In, these results can be explained in terms of the fact that encouraging semantic processing means both increasing the number of components involved in the trace (increasing the multidimensional nature or richness of the information, to use more familiar terminology) and strengthening the link between these components, that is to say, the level of integration of the features of the trace.

3.2. Multimodal encoding

Many studies have examined how multimodal encoding may be able to improve memory efficiency compared to unimodal encoding. For instance, according to the dual coding theory (e.g., Paivio, 1986), concrete words are more likely to evoke a mental image than abstract words. At the same time, when subjects have to memorise words, recall is better for concrete words (high imageability) than for abstract words (low imageability). To interpret these results, some authors have hypothesised that concrete words undergo dual encoding (imaging and verbal) which facilitates recall compared to abstract words which have only been subjected to verbal encoding. However, this type of result is not specific to verbal material. Thus, Thompson and Paivio (1994) manipulated the nature of the encoding by presenting pictures alone, sounds alone or sounds and pictures simultaneously. In a second, free-recall phase, they were able to demonstrate the advantage of the bimodal presentation over the unimodal presentations and interpreted their results within the framework of the dual-coding theory.

In a more recent EEG-based study, Murray et al. (2004) used a continuous recognition paradigm in which the authors manipulated the initial presentation condition of pictures. When they were displayed for the first time, the pictures could be presented alone or could be accompanied by the naturally associated sound. The pictures depicted animals or objects and were presented together with the sound naturally produced by them. On a subsequent presentation, the participants had to say whether or not each of the

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pictures was being presented to them for the first time. The results showed that the pictures were recognised better at the time of the second presentation when they had initially been presented with a sound than when they had been presented in the visual modality only. Furthermore, the amplitude of the evoked potentials was greater for the items that were initially presented in the multimodal condition than for the items initially presented in the unimodal condition.

This study shows that a single multisensory presentation is sufficient to improve the recognition performance. However, it does not permit any firm conclusion regarding the specificity of multisensory encoding. Other research conducted by the same team (Lehmann & Murray, 2005) has contributed to our understanding of this issue. Using the same paradigm as in 2004, Lehmann and Murray (2005) compared a condition in which the initial presentation of the picture was associated with a white noise (1000 Hz) and a condition in which the initial presentation was unimodal. The results showed that the correct response percentages were higher when the pictures were presented only visually than when they were associated with a white noise. It is therefore not the multisensory nature of the encoding in itself that explains the improvement in performance but instead the specificity of the multisensory components involved during encoding. A simple sound that is not related to the picture produces interference (see also the above-mentioned results reported by Vallet et al., 2010; Vallet, Hudon et al., 2013).

In a second set of experiments, the authors manipulated the semantic nature of the multisensory associations. In a congruent condition, the first presentation of the picture was associated with a natural sound, whereas in a non-congruent condition, it was associated with another sound (picture of a dog + sound of a cat mewing). Finally, in the last condition, the initial presentation was visual only. Performances were better in the congruent condition than in the other two conditions. Consequently, the multimodal encoding of an item is beneficial only if the sensory features involved are components that are linked to (integrated in) the memory traces corresponding to this item. Thus, multimodality is beneficial, because by increasing the "richness" of the trace and facilitating the "simulation" of the items, it also facilitates the integration of multimodal traces.

3.3. Role of emotion

A considerable body of evidence exists showing that the content of the memory trace is closely related to our earlier sensory-motor activities. It is also clear that the experiences underlying trace construction are also associated with specific emotional states. The emotional nature of experiences must therefore also be encoded at the level of the memory traces. However, as emphasised by Versace and co-workers (2009), we can consider (see Damasio, 1994) that emotions correspond to pleasant or unpleasant sensations that are associated with specific corporal states characterised by a number of different parameters (heartbeat, feeling of pain, heat, etc.). Consequently, it is possible to consider that emotion is itself an elementary component of memory traces in the same way as the other sensory–motor components whereas simultaneously being closely associated with subjects' corporal states (see, the "somatic markers" of Damasio, 1994). If this is the case, emotion would correspond more to an emergent state of the reactivation of traces of past experiences and this state would be strongly linked to all the components in the trace. Emotion would therefore make a trace more accessible in two ways: on the one hand, because by representing particularly salient information that facilitates the re-emergence of the corresponding trace (e.g., Bower, 1994) and, on the other, by acting as a common denominator for all the components in the trace.

In the latter case, emotion would make it possible to strengthen the link between, or the level of integration of, the various elements in an experience. Neuroscientific studies have produced arguments in favour of this hypothesis. Neuroanatomical observations reveal that specific structures such as the prefrontal cortex and the hippocampal region play an important role in the integration mechanism (Bechara et al., 1995; Bechara, Tranel, Damasio, & Damasio, 1996; Goldman-Ravic, Scalaidhe, & Chafee, 2000; Stuss & Alexander, 1999; Ungerleider, 1995). The prefrontal cortex occupies a particularly important location due to its numerous connections with many different regions of the brain (e.g., the convergence zones described by Damasio, 1989, 1994). As far as the hippocampus is concerned, Opitz (2010) suggests that this structure might represent the substrate for the "*relational binding*" of the cortical representations of the items,

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actions, etc. and the spatio-temporal context which gives the experience its unique character. These binding activities can be described in terms of relational operations which link together and organise the individual elements of the experience. However, numerous studies have also demonstrated that the nervous structures involved in integration are also involved in the emotional mechanisms (for a discussion, see Versace et al., 2009).

However, only a small number of behavioural studies to date have specifically tested the role of emotion in integration. In one of these, Versace and Rose (2007) conducted an experiment in which the participants initially had to judge the degree of association between pictures of objects or animals and sounds presented simultaneously with them. Each picture/sound pair was preceded by an image with a negative valence or by a neutral picture. In the second phase, the same object or animal pictures were presented to the participants, either associated with the same sound as in the first phase (sound congruent with picture) or associated with a sound different from that used in the first phase (non-congruent sound). In this second phase, the picture/sound pairs were always presented alone (without emotional induction). The participants had to indicate whether the picture and the word were congruent or not.

The results revealed an interaction between encoding condition (negative vs. neutral) and sound type (old/congruent vs. new/non-congruent): When an old picture was presented with the same sound as in the encoding phase, reaction times were shorter in the negative than in the neutral encoding condition. On the contrary, when an old picture was associated with a new sound, it tended to be processed more slowly when it had been encoded in the negative condition than in the neutral condition. These results clearly showed that the encoding condition affected the strength of the link between the picture and the sound, and not only the strength of the memory trace of the picture and the sound. When this link was broken in the test phase, the responses slowed dramatically only in the negative encoding condition.

Thus, even though there are arguments in support of the role of emotion in the integration of the elementary components of traces, further studies are still required in order to confirm that this is indeed the case.

4. CONCLUSION

To summarise, Act-In is a functional model of memory which has its roots in the multiple trace models and assumes that memory contains traces which reflect all the sensory, motor, and emotional components of past experiences. As in the multiple trace memory models, the knowledge present in memory is no longer considered to constitute representations, some of which are abstracted from their encoding context, and therefore from the sensory systems which permitted their emergence, whereas others are not. Instead, all knowledge is considered to be grounded in its respective properties. This embodied view of cognition is necessarily and ontologically opposed to so-called structuralist approach which defines different forms of representations in order to explain the various manifestations of memory (semantic, episodic, etc.).

In Act-In, just as in the multiple trace memory models, knowledge is assumed to emerge from the activation, by the present experience, of multiple memory traces of past experiences. The main objective of Act-In is therefore to specify the mechanisms that are thought to lead to the emergence of different forms of knowledge, and in particular episodic and semantic (or categorical) knowledge. We assume that the nature of the knowledge that is likely to emerge depends on the dynamic of two mechanisms, namely inter-trace activation and multi-component integration. Inter-trace activation refers to the spread of activation to and between the different traces. It implies both intra- and inter-component activations, which operate in parallel. Multi-component integration is necessary in order to access elaborate and unitary knowledge. A high level of inter-trace spread of activation, particularly at the level of intra-component activations and coupled with the multi-component integration of properties shared by a large number of traces, permits the emergence of categorical knowledge. In contrast, a limited inter-trace spread of activation, coupled with the multi-component integration of properties that are specific to isolated traces, is required for the emergence of specific knowledge.

However, as we already pointed out in the introduction, our aim in this paper was to propose a general operating principle that can be implemented in various architectures. Therefore, the next step will be now to propose computational

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instantiations and/or simulations of the mechanisms proposed in Act-In, leading to falsifiable predictions.

Beyond the many experimental arguments presented in this paper in support of the hypotheses put forward in Act-In, the strength of a model also lies in its ability to explain and predict cognitive dysfunctions. In the field of memory, this means that the model must also be able to account for memory disorders. The value of studying neuropsychological memory disorders within the framework of Act-In and the functionalist models in general is all the greater, given that dissociations in memory profiles are one of the key arguments in favour of the existence of multiple memory systems. In effect, if a patient exhibits episodic memory disorders even though his or her semantic knowledge remains intact, whereas another patient presents the opposite profile, then it would seem logical, at least on an initial appraisal, to suppose that different memory systems underpin these different forms of memory (for a discussion, see Dunn, 2003; Dunn & Kirsner, 1988). These profiles can be observed, for instance, in the case of patients suffering from Alzheimer's disease (episodic disorders) and those suffering from semantic dementia (semantic disorders). It is therefore essential that the functionalist models are able to propose credible interpretations and predictions of memory dysfunctioning.

It should be noted that only a small number of studies have genuinely tested neuropsychological disorders within the theoretical framework of functionalist theories. For example, Nosofsky and Zaki (1998) showed that the double dissociation between categorisation and recognition can be explained perfectly adequately by non-abstractionist theories of memory. Of even greater interest is the fact that these same authors (Zaki, Nosofsky, & Jessup, 2003) have shown that when the categorisation task is made more difficult, patients with amnesia exhibit a categorisation deficit in addition to their recognition deficit. The authors concluded that the difficulty of the task (referred to as sensitivity) explains the apparent double dissociations between semantic tasks (categorisation) and episodic tasks (recognition). This problem of task demands was also emphasised by van der Linden as early as 1991 (van der Linden & Bruyer, 1991). These authors suggested that the results of comparing healthy subjects and amnesic patients may be due simply to the availability of the memory trace. For instance, amnesic patients have been found to perform as well as controls (cued recall, recognition, confidence in their recall) when they were tested one hour after learning and the controls a week later (Shimamura & Squire, 1988, see also Jamieson, Holmes, & Mewhort, 2010). This design created a "low learning" condition for the controls, with the result that memory strength may have been comparable in the two groups.

Another way of addressing episodic disorders in the functional approaches to memory is to focus on the role of the hippocampus. This brain structure is known to play a crucial role in episodic memory (e.g., Tulving, 1995). It is also of great importance for spatial processing (e.g., Eichenbaum, Dudchenko, Wood, Shapiro, & Tanila, 1999). A number of authors have therefore suggested that episodic disorders may also be explained in terms of a deficit in the processing of the spatio-temporal context (Bird & Burgess, 2008). In support of this idea, it has recently been shown that the retrieval of episodic memories is influenced by the subjects' ability to represent themselves in space (egocentric updating) (Gomez, Rousset, & Baciu, 2008).

The disconnection between the hippocampus and the other brain structures might also play a role in impairments to episodic memory (Stoub, Stebbins, Leurgans, Bennett, & Shah, 2006). Furthermore, Alzheimer's disease can be characterised as a disconnection syndrome (Delbeuck, van der Linden, & Collette, 2003). In other words, Alzheimer's disease patients would seem to suffer from a neurological disorder which impacts most greatly on communication between the regions of the brain. This would result in a cognitive deficit that is more severe in situations requiring a transfer of information between different brain regions (e.g., Delbeuck et al., 2003; Stam, Jones, Nolte, Breakspear, & Scheltens, 2007; Vallet, Hudon, Simard, & Versace, 2013). This communication deficit could be partly due to episodic memory problems.

For their part, semantic disorders are frequently studied within the framework of semantic dementia. Indeed, this pathology is contrasted with Alzheimer's disease in order to provide support for the idea that multiple memory systems exist (Graham, 1999). However, a growing number of studies are now providing evidence of the relevance of connectionist or multiple trace models in accounting for semantic deficits (Moscovitch & Nadel, 1999; Murre, Graham, & Hodges, 2001).

More generally, it would appear that the non-abstractionist approaches to memory are able to provide a more parsimonious account of semantic

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deficits. Thus, Carbonnel (2000) has produced a critical summary in which classical interpretations are compared to non-abstractionist interpretations of various case studies involving semantic disorders. This indicates that semantic disorders are generally observed on specific categories or as a function of specific input modes (e.g., visual modality). According to the non-abstractionist approaches, semantic disorders can be explained in terms of the degradation of a certain type of property. As we have stated above, a deficit in the processing of living objects could be due to a deficit in the processing of visual properties. This hypothesis, initially put forward within the SFT (Warrington & Shallice, 1984), has recently been revisited as a possible explanation for the semantic disorders observed in semantic dementia (see Barense, Rogers, Bussey, Saksida, & Graham, 2010; Vallet, Simard et al., 2011).

Even though we have, to date, collected only little experimental data to corroborate our hypotheses concerning memory deficits, it should nevertheless be possible to account for these deficits on the basis of the mechanisms referred to in Act-In. As far as the emergence of semantic knowledge is concerned, we have said that this depends on a high level of inter-trace activation, particularly at the level of intra-component activations. Impaired inter-trace activation can therefore explain a deficit in the emergence of semantic knowledge. A modality-specific (e.g., visual) impairment is therefore perfectly able to account for semantic disorders on specific categories of items for which the modality in question is particularly important (e.g., animals, see Taylor et al., 2007), that is to say, for which the modality contributes significantly to inter-trace activation.

In contrast, Act-In explains deficits in the retrieval of specific episodic knowledge in terms of the reduced effectiveness of inter-component activation at the level of a given trace, as well as in terms of a deficit in multi-component integration. Consequently, the hypothesis that a communication deficit might in part be able to explain episodic retrieval disorders is entirely consistent with the idea that the effectiveness of the emergence of this form of knowledge is primarily due to the role played by multimodal activation and integration.

To conclude, the proposals for the development of Act-In at the neuropsychological level are still at a relatively exploratory stage and a considerable amount of research remains to be undertaken. Nevertheless, this memory model is of interest for two reasons. First of all because it allows us to formulate extremely precise hypotheses concerning both the efficiency of memory and its dysfunctions. These hypotheses are not only credible but are also often more parsimonious than those defined in the structuralist approaches. They also have the advantage of making it possible to refute or invalidate the model. Starting from a very limited number of memory mechanisms, it is possible to account for a large number of empirical result. Existing models of memory, by contrast, can account for some but not all of these empirical results. Finally, Act-In has the advantage of proposing a highly integrated view of cognitive functioning as a whole. Within such an approach, it is neither necessary nor possible to dissociate the perceptual mechanisms, the memory mechanisms, the mechanisms associated with mental imagery or even the attentional mechanisms.

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