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Spontaneous Object Recognition in Animals: A Test of Episodic Memory

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1. Introduction

Episodic memory is characterized by Tulving (1983, 2002) as a discrete form of memory that involves mentally re-enacting previously experienced events. Traditionally, the investigation of episodic memory has been restricted to human subjects because the ability to mentally re-enact past experiences suggests that it requires self-consciousness and the ability to mentally travel forward and backward in time (Tulving, 1983, 2002). Because of the difficulty of demonstrating these abilities without the use of complex verbal language, many believed that episodic memory could not be studied in non-humans. However, through a series of elegant experiments, Clayton, Dickinson and their colleagues (e.g., Clayton & Dickinson, 1998) have developed a paradigm that allows researchers to model some aspects of episodic memory in non-humans. In particular, they focus on the abilities of food-caching birds to represent the “what/where/when” of an event into a single tripartite code. While this model has opened up the field of episodic memory to testing in non-humans, it is not easily applied to non-caching species. More recently, Eacott and Norman (2004) have developed a paradigm using object recognition that allows researchers to model episodic memory in a wider variety of non-human animals. Their paradigm involves altering the “what/where/when” code of Clayton and Dickinson to a tripartite code consisting of “what/where/which.”

In this chapter, we make the argument that this use of object recognition is a better paradigm for studying episodic memory in non-humans. We begin with a description of episodic memory and the paradigms used to study it in non-human animals. We then describe studies of object recognition in non-human animals and studies that use object recognition to test episodic-like memory in rodents and pigs. And finally, we discuss how this research complements the growing field of episodic-like memory in non-human animals.

2. Episodic memory

Episodic memory has been characterized as a discrete form of memory that involves mentally re-enacting previously experienced events (Tulving 1983, 2002). Specifically, this type of memory requires the integrated recall of the “what, where and when” circumstances

of an event, the ability to recognize subjective time, and autonoetic consciousness (knowledge of self; Tulving, 1983, 2002). The main distinction between episodic memory and other forms of recall involves the recreation of a personally experienced event. Simple retrieval of discrete facts (e.g., Marconi received a wireless transmission at Signal Hill in 1901), does not require the self-consciousness nor the ability to mentally travel forward and backward in time that are indicative of episodic memory (e.g., I was on Signal Hill yesterday and read a sign about Marconi). Despite the acceptance of episodic memory in humans, its presence in non-human animals is controversial.

In the absence of a measure of consciousness in non-human animals, it has not been possible to demonstrate episodic memory that is equivalent to humans. However, by studying food caching (Clayton & Dickinson, 1998), food finding (Babb & Crystal, 2006), fear conditioning (O'Brien & Sutherland, 2007), and object exploration (Eacott & Norman, 2004), researchers claim to have demonstrated a form of episodic memory in scrub jays (Clayton & Dickinson, 1998), pigeons (Zentall et al., 2001), mice (Dere et al., 2005), rats (Eacott & Norman, 2004; O'Brien & Sutherland, 2007), gorillas (Schwartz & Evans, 2001), rhesus monkeys (Hoffman et al., 2009), and chimpanzees/bonobos (Menzel, 1999; Martin-Ordas et al., 2010).

The interpretation of such studies is often controversial because there is no consensus regarding a definition of non-human episodic memory (Hampton & Schwartz, 2004). Schwartz, Hoffman and Evans (2005) outlined five operational definitions of non-human episodic memory including: (1) the demonstration of what/where/when memory (Clayton & Dickinson, 1998; Babb & Crystal, 2006), (2) the demonstration of what/where/which memory (Eacott & Norman, 2004), (3) the demonstration of spontaneous recall (Menzel, 1999), (4) the ability to recall an event when not expecting a test (Zentall et al., 2001), and (5) the ability to report on past events over a long term (Schwartz & Evans, 2001). Unfortunately, these definitions tend to be species-specific. For example, definitions of episodic memory based on research with food-caching birds (Clayton & Dickinson, 1998) often do not fare well when applied to non-caching species (Bird et al., 2003; Hampton et al., 2005). Consequently, alternative methods and definitions have been developed for rodents, primates, and non-caching birds.

3. What/where/when memory in western scrub jays

Clayton and Dickinson (1998) have been largely responsible for introducing and developing the concept of episodic memory in non-humans. They have demonstrated that Western scrub jays form integrated memories of what, where and when information in the context of caching and recovering food. Furthermore, they suggest that the types of caching behaviour shown by the scrub jays requires them to mentally travel forward and backward in time, which is a component of human episodic memory (Clayton et al., 2003a). However, because Clayton, Dickinson and their colleagues have not been able to demonstrate autonoetic consciousness (i.e., a sense of self) in scrub jays, they have stopped short of declaring that scrub jays have human-equivalent episodic memory. Instead, they have opted to conclude that scrub jays possess "episodic-like memory." This type of memory shares some characteristics with the definition of human episodic memory (Tulving, 1983), but avoids the currently impossible task of demonstrating consciousness without the use of verbal language (Clayton et al., 2003b).

Clayton and Dickinson (1998) took advantage of the scrub jays' natural food-storing behaviours and allowed each bird to cache both perishable, but preferred, worms and non-perishable peanuts in opposite sides of an ice-cube tray filled with sand. Initially, the scrub jays demonstrated the ability to recall the location ("where") in which they cached each type of food ("what"), and consequently retrieved the preferred food, worms, before peanuts. In subsequent trials, the researchers replaced freshly cached worms with decayed worms if worms were cached first (124 h before retrieval) and peanuts cached second (4 h before retrieval). In contrast, fresh worms were left in their cached locations if peanuts were cached first (124 h before retrieval) and worms cached second (4 h before retrieval). Remarkably, the scrub jays quickly learned to retrieve peanuts if worms were cached first (since decayed worms are unpalatable) and to retrieve worms if peanuts were cached first. A similar result, although less compelling, was found when jays were taught that worms were removed (pilfered) if they were cached 124 h before retrieval.

In numerous subsequent studies, Clayton and Dickinson further developed their case for episodic-like memory in scrub jays. Specifically, through allowing jays to cache peanuts and dog kibble and then recover these items on successive trials, they demonstrated that scrub jays update their memories about which cache sites contain food (Clayton & Dickinson, 1999). Furthermore, by making one food less preferable than another through pre-feeding, they found that jays successfully identified food caches that were both non-recovered and contained preferable food. Clayton and Dickinson (1999) argue that this ability indicates that scrub jays form episodic-like memories that integrate the type of food in a cache, the location of that cache, the last activity at that cache (recovery or caching) and how long ago food was stored. Clayton et al., (2005) have also shown that scrub jays use novel information about the decay of a food source to reverse their strategies for recovery, since jays cache more non-perishable food items if their caches are consistently degraded on recovery. Emery and Clayton (2001) found that scrub jays who have previously raided the food cache of a conspecific will re-cache food if they are observed during their own caching process. Recently, Cheke and Clayton (2011) examined caching in the Eurasian jay and demonstrated that birds distinguish between their current food preference (created by pre-feeding a specific food) and their future needs. This was evidenced by the birds overcoming motivation to cache currently desired food and instead caching currently non-preferred foods according to their future value. Taken together, these findings provide preliminary evidence that caching scrub and Eurasian jays make decisions based on past episodes and anticipated future needs. Because these results suggest that episodic-like memory includes aspects of the mental time travel involved in human episodic memory, further study in this area, including research on non-caching species, such as ant-following birds, is suggested (Clayton et al., 2003c; Logan et al., 2011).

4. What/where/when memory in other species

Many researchers have used the basic what/where/when criteria proposed by Clayton and Dickinson (1998) in their attempts to demonstrate episodic-like memory in species such as pigeons (Skov-Raquette et al., 2006), primates (Hoffman et al., 2009; Martin-Ordas et al., 2010), mice (Dere et al., 2005), and rats (Babb & Crystal, 2006; Fortin et al., 2002; Kart-Teke et al., 2006; O'Brien & Sullivan, 2007). The majority of studies have been conducted using mice and rats, which has led to the development of several different testing paradigms.

Babb and Crystal (2006) developed a radial maze task that required rats to remember the type of food contained in different maze arms at different times. They showed that rats were able to integrate what/where/when memories to obtain preferred foods, and that rats changed their preferences if these preferred foods were devalued. Fortin et al. (2002) developed a task in which rats were required to remember a series of odour cues to obtain food from sand-filled cups. The rats were able to remember the odour and whether it occurred before or after another odour in the sequence. However, Clayton et al., (2003a) argued that rats may have solved this task using internal interval timing, and that this task does not demonstrate integrated memory for "where." O'Brien and Sutherland (2007) took advantage of the observation that rats need exposure to a context to form context-shock associations (Faneslow, 1990) and that the associations formed can be based solely on the memory of the context (Rudy et al., 2002). They (O'Brien & Sutherland, 2007) exposed rats to two distinctive boxes, one in the morning and the other in the evening. After the exposure, rats were exposed to a third box that was an amalgam of the morning and evening box. They were shocked in this box in either the morning or the evening session. Tests of freezing at an intermediate time interval in either the morning or the evening box demonstrated freezing to the box congruent with the time of day the shock had been received. This finding indicated that the rats had formed a time-place memory and that this memory had been updated at the time the shock had been administered. A recent study with chimpanzees, bonobos and orangutans adapted the methods of Clayton and Dickinson (1998) and showed that apes integrate what/where/when memories to choose between frozen juice (the preferred food after a 5 min rest interval, but not after a 1h rest interval because it melts and becomes unavailable) and a grape (the preferred food after a 1h rest interval because the juice is unavailable) (Martin-Ordas et al., 2010).

Although not exhaustive, the above list illustrates the main testing strategies that have been used to demonstrate what/where/when memory in non-caching species. The absence of caching behaviour in many species is a serious hindrance to replicating the results found in scrub jays (Bird et al., 2003; Hampton et al., 2005). Although numerous clever methods have been developed to test the what/where/when criteria, many of these cannot avoid alternate, more parsimonious explanations for results. With the possible exception of O'Brien and Sutherland (2007), this is particularly true for the "when" component of episodic-like memory. Even studies that have gone so far as to show that memories are flexible (i.e., a rat's change in food preference shown by Babb & Crystal 2006) are confounded by the possibility of relative memory strengths and internal time intervals experienced by subjects.

The problematic nature of the "when" aspect of memory is also demonstrated by distinct but related research in daily Time-Place Learning. In daily Time-Place learning tasks, animals are trained that a food reward is available in one location in morning sessions and in another location in afternoon sessions (Thorpe & Wilkie, 2006). This task is different from episodic tasks in that the subjects require repeated training prior to restricting their searches to the appropriate locations at the correct times of day. To solve this task, an animal must learn to associate event/place/time or what/where/when information in a single code. Paralleling the results in the episodic-like literature, pigeons learn this task relatively easily (Saksida & Wilkie, 1994); however, both fish (e.g., Barreto et al., 2006) and rats (e.g., Thorpe et al., 2003) have much more difficulty acquiring the task. Research has shown, however,

that rats quickly learn to restrict their searches to the locations that provide food indicating that they have learned the bipartite what/where code (Thorpe, et al., 2003). It is also known that rats can learn when in the day that they will receive food – or the bipartite what/when code (Means et al., 2000; Thorpe et al., 2003). However, it is only under certain conditions that rats combine these three components into a tripartite what/where/when code and successfully solve the task. For example, in situations in which there is a high cost of making a mistake, either in effort or in time, rats are more likely to solve the task (Widman et al., 2000). Given these findings, animals may be able to learn temporal information, but it may not reflect the natural way events are encoded.

5. What/where/which episodic-like memory

In an attempt to avoid some of the confounds and problems involved in demonstrating “when” memory, Eacott and Norman (2004) used *context* to replace time as the “when” component of episodic-like memory, which broadens the definition of episodic-like memory to include integration of the “what, where, and *which*” details of an event. They argue that the function of the “when” aspect of episodic memory is simply to mark an event as being unique. Therefore, requiring animals to remember the discrete time at which an event occurred (e.g., 1 hour ago or 24 hours ago) is the same as having animals discriminate the context in which an event occurred (e.g., white-walled room vs. black-walled room; Eacott & Gaffan, 2005; Eacott & Norman 2004;). Either chronological time or context can serve as the reference point that identifies a specific event and allows it to be recalled. This idea is further supported by the fact that time does not appear to be an essential part of human episodic memory. Humans tend to use background cues that are present during an event, rather than time, to distinguish it from other similar events (Friedman, 1993).

6. Novel object recognition task

The paradigm used most often to assess what/where/which memory is the novel object recognition task. This clever but simple task takes advantage of a predisposition in many species to explore novel objects over familiar ones. Ennaceur and Delacour (1988) first reported the object recognition task, in which rats were exposed to objects during an acquisition trial and then tested on their ability to discriminate between familiar and novel objects, as a test of working memory. The object recognition test has been used to show that rats are sensitive to the location of objects (Dix & Aggleton, 1999; Ennaceur et al., 1997; Poucet, 1989), to the topological relationship between objects (Dix & Aggleton, 1999; Goodrich-Hunsaker et al., 2008; Harley et al., 2001; Lemon et al., 2009), to changes in the distance between objects (Goodrich-Hunsaker et al., 2008), to the context in which objects have been experienced (Dix & Aggleton, 1999; Eacott & Norman, 2004), and to changes in object compounds (Norman & Eacott, 2004).

In addition to the innovative what/where/which definition, Eacott and Norman’s (2004) unique method of testing episodic-like memory meets the requirements of spontaneous recall (Menzel, 1999) and recall during an unexpected test (Zentall et al., 2001). Eacott & Norman (2004) found that rats can integrate memories of a specific object (what), its spatial location (where) and the context in which it occurs (which) to discriminate the more novel of two object/location/context combinations. Rats explored the locations (left or right) of each

of the objects (A or B) in each of the two contexts (1 or 2). During the test, the rat was placed in one of the contexts with two copies of the same object (e.g., A and A), and the amount of time the rat spent exploring each object was recorded. Since identifying the more novel of two configurations requires the simultaneous recall of what, where and which (object/location/context) information, Eacott and her colleagues argued that novel object recognition tasks test episodic-like memory (Eacott et al., 2005; Kart-Teke et al., 2006). In fact, they argued that object recognition is superior to other methods because it requires very little training before subjects are tested, which reduces potential confounds caused by reinforced learning (Eacott & Norman, 2004). Furthermore, since exploring novelty is a natural response for many species, recall of the more novel object/location/context appears to be spontaneous, which meets Menzel's (1999) criterion for episodic-like memory. As well, explicit cues or rewards are not needed to prompt memories, which meets Zentall et al.'s (2001) criterion that episodic-like memory tests must be unexpected.

Similarly, others have shown that rats (Kart-Teke et al., 2006) and mice (Dere, et al., 2005) integrate what and where information with the order in which stimuli are presented. An object recognition task was used that required the animals to discriminate more novel objects based on a combination of the objects' locations and the order in which they were presented. The animals spent more time exploring a less recently presented object compared to a more recently presented object, which indicates that they had integrated "what and when" memory. The authors found that "what and when" memory was integrated with "where" because the animals responded differently to displacement of more recent and less recent objects. When presented with two more recently experienced objects, the animals spent more time with the object that had been displaced to an unfamiliar location as compared to the object in a familiar location. In contrast, when presented with two less recent objects, the animals spent more time with the object in the familiar location than with the object in an unfamiliar location. They concluded that these findings provided evidence for integration of what/where/when memories into a single tripartite code because they show that these three dimensions are not encoded, stored and retrieved independently (Dere, et al., 2005; Kart-Teke et al., 2006). As well, they argue that animals could not use relative memory strengths to discriminate whether an object was displaced because spatial information was obtained on a single trial.

The use of object recognition/preference to study episodic memory has also been extended to the study of recall of information without the stimuli being re-presented in the test phase (Eacott et al., 2005). Rats were trained to explore an E-shaped maze with two objects, followed by exposure to a different E-shaped maze with the same objects in opposite locations. After the two exposures, the rats were placed in a different context with one of the objects for a habituation session. When the rats were placed back into one of the E-shaped mazes, they tended to go to the non-habituated object, which was not visible from the middle stem of the E. In order to explore the more novel (non-habituated) object, the rats must remember which of the two objects (what) is in each arm (where) in which context. This recollection task, like the caching task used with scrub jays, 'asks' rats about objects that they cannot see and is more akin to the types of recall used in human measures of episodic memory.

7. Episodic-like memory in pigs

Eacott and Norman's (2004) successful demonstration of what/where/which memory in rats has led to an interest in applying this definition and method to other species. Similar to

rats, pigs naturally tend to explore novel aspects of their environment (Wood-Gush & Vestergaard, 1991). Pigs also have good spatial memory abilities and they are able to learn tasks quickly (e.g., Croney, 1999; Held et al., 2002; Held et al., 2005; Puppe et al., 2007; reviewed in Gieling et al., 2011). As well, wild and feral pigs have a life history in which memory is valuable; particularly because they live socially, have large foraging ranges, and have foraging habits/movement patterns/nesting sites that change with season and food availability (Graves, 1984). Since domestic pigs have retained many natural behaviours despite the domestication process, particularly in foraging (Gustafsson et al., 1999), it is reasonable to speculate that domestic pigs retain the memory abilities possessed by their wild ancestors. These factors indicate that episodic-like memory in pigs may be more developed than in some other species.

The physiological similarity between humans and pigs is likely responsible for the recent increased popularity of pigs as biomedical models of human disease and cognition (for reviews, see Gieling et al., 2011; Kornum & Knudsen, 2011; Lind et al., 2007). Accordingly, pigs may also provide a more effective comparison than other species between human episodic memory and episodic-like memory in animals. Specifically, the pig brain is more similar to the human brain in structure (gyration), myelination and electrical activity than are the brains of rodents and other small laboratory animals (Dickerson & Dobbing, 1966; Pond et al., 2000). Also similar to humans, the pig brain develops perinatally, with a growth spurt extending from mid-gestation to about 40 days after birth (Dickerson & Dobbing, 1966; Dobbing & Sands, 1973; Pond et al., 2000). Such similar physiological brain development may be particularly valuable in studies of changes in memory with age.

Prior to our work (Kouwenberg et al., 2009), the existence of episodic-like memory in pigs remained virtually unexplored. However, there were several studies that demonstrated pigs can perform spontaneous object recognition, using modifications of the Ennaceur and Delacour (1988) protocol (Gifford et al., 2007; Kornum et al., 2007; Moustgaard et al., 2002). We explored episodic-like memory in pigs by examining their ability to discriminate between objects according to the location and context in which they occurred (Figures 1 and 2). On each trial, a pig was confined to a holding pen for 2 min prior to a 10 min exposure to one context containing two objects (e.g., Context 1 with Object A on the right and Object B on the left). After an additional 5 min in the holding pen, the pig was given a 10 min exposure to another context containing the same objects but in opposite locations (i.e., Context 2 with Object A now on the left and Object B on the right). The test trial was administered after another 5 min in the holding pen, and consisted of a 10 min exposure to one of the contexts with two identical objects (e.g., Context 2 with two copies of Object A). If the pigs remembered the location and context in which each object occurred during the two exposure phases, they should allocate their exploration time differentially, based on the familiarity of the object/location/context configurations during the test phase.

Pigs spent more time with the less familiar object/location/context during the test phases of the episodic-like memory trials, indicating that they were able to simultaneously recall memories of what (object), where (location) and which (context). Since the separate aspects (object, location, and context) of each object/location/context configuration are equally familiar, it is only the combination of all three aspects that makes one configuration less familiar than another. Therefore, the pigs' significant preference for the *less* familiar configuration cannot be attributed to object preference alone, location preference alone, or

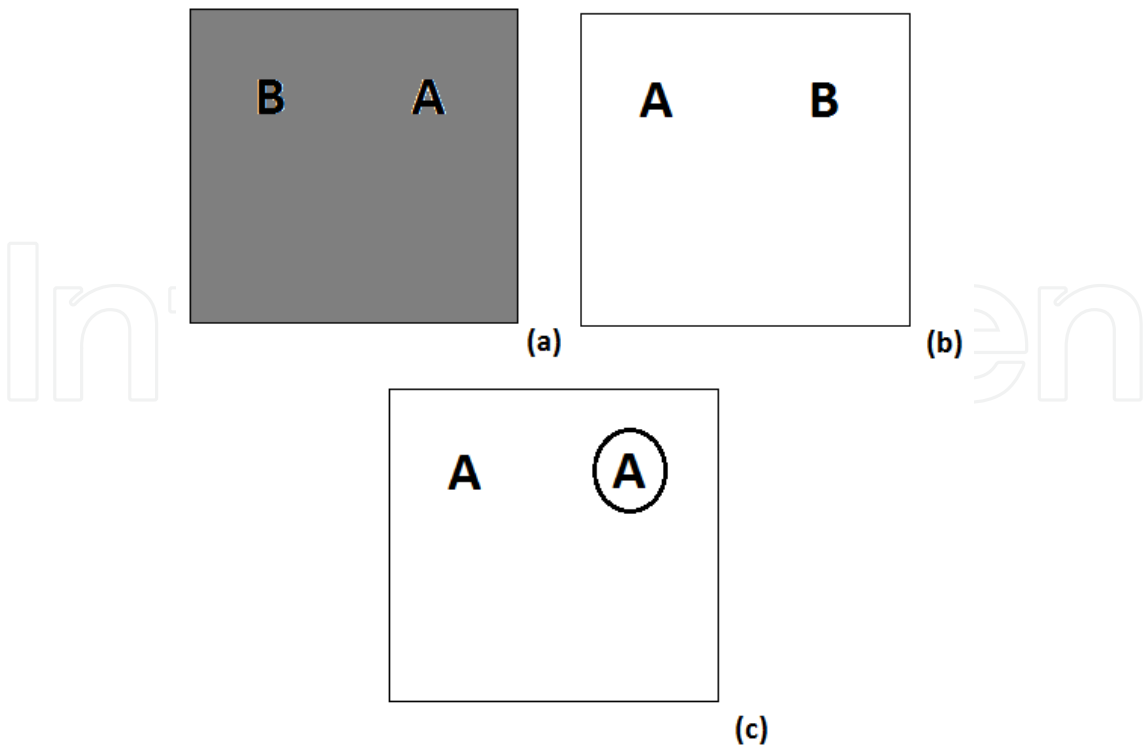


Fig. 1. A diagram of the episodic-like memory trial used in our study. An example of a possible configuration for the first exposure phase (a), second exposure phase (b), and test phase (c). Shading indicates a different floor colour (i.e., different context). The black circle indicates the novel object/location/context in the test phase of this trial.



Fig. 2. A pig interacting with an object during episodic-like memory test.

context preference alone. Objects in the test phase were identical, pigs had been equally exposed to both locations before the test phase, and pigs had been equally exposed to both contexts before the test phase. Furthermore, the preference for the less familiar object/location/context could not be attributed to object and location alone because objects and locations were counterbalanced for each pig. Thus, each pig received an episodic-like memory trial with two objects "A" in the test phase and a trial with two objects "B" in the test phase. If pigs were ignoring context and making decisions based solely on object and location, half of the time pigs would spend more time with the left-hand object and the other half of the time the pig would spend more time with the right-hand object. This would have resulted in no significant overall preference for either object/location/context. Our data indicate that this is not the case, leading to the conclusion that pigs formed integrated memories of what/where/which information. Whether pigs can also do the recollection task used by Eacott et al. (2005) remains to be determined.

8. Conclusion

The above findings indicate that the formation of a tripartite code of either "what/where/when" or "what/where/which" seems to be within the compass of animals when species-typical preferences are taken into account. While the what/where/when model of Clayton and Dickinson (1998) is an elegant demonstration of episodic-like memory, its usefulness may be restricted due to the limited number of animals that cache food. While some researchers, notably Babb and Crystal (2006), have attempted to modify this task with rodents it requires a significant amount of pre-training because it does not use behaviours that naturally exist within the repertoire of some species. The recent findings from object exploration indicate that this may be a powerful way to study the formation of a tripartite code in animals. The paradigm allows for the testing of a tripartite code of what/where/which but not what/where/when memory (Eacott & Norman, 2004). It takes advantage of the tendency to explore novel objects, seen in many species, to demonstrate spontaneous recall (Menzel, 1999). It tests an animal's recall of an event when the test is not expected (Zentall et al., 2001) and may even allow for a test of past events over a long period of time (Schwartz & Evans, 2001) although no such long term tests have yet been carried out.

While a model of episodic memory based on object recognition is applicable to a greater variety of animals than a model based on food caching behaviour, we acknowledge that many of the criticisms that have been lodged against the what/where/when model (e.g., Suddendorf & Busby, 2003) also apply to the what/where/which model. For example, evidence for future planning and mental time travel would greatly improve both models of episodic-like memory. Clayton et al., (2003a) have recognized that their basic what/where/when criteria no longer adequately define the evolving concept of episodic-like memory. In response, they have refined their definition of episodic-like memory to include three particular behavioural criteria. Specifically, they state that a solid demonstration of episodic-like memory requires *content* (what/where/when details of a specific past event), *structure* (integration of the what/where/when details into a consolidated memory), and *flexibility* (ability to change how information gained from an episodic-like memory is used). Eacott et al. (2005) have argued that these three criteria are also met in their modified task examining recall of objects.

If we are willing to accept that the what/where/which model of episodic memory is a *model* of human episodic memory, and therefore, concede that it does not encompass the human characteristics of consciousness and mental time travel, then we can use this model to investigate the tripartite what/where/which code. One of the main strengths of this model is that it allows for episodic-like memory to be studied in a wide range of species. Comparative work should focus on the ability of other animals, including pigs, to recall information without the stimuli being re-presented on test (similar to that of Eacott et al., 2005) and to determine if this ability is long-lasting.

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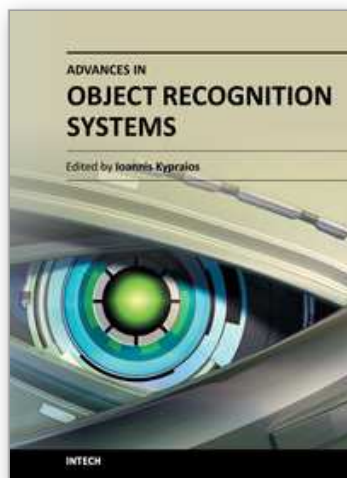
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An invariant object recognition system needs to be able to recognise the object under any usual a priori defined distortions such as translation, scaling and in-plane and out-of-plane rotation. Ideally, the system should be able to recognise (detect and classify) any complex scene of objects even within background clutter noise. In this book, we present recent advances towards achieving fully-robust object recognition. The relation and importance of object recognition in the cognitive processes of humans and animals is described as well as how human- and animal-like cognitive processes can be used for the design of biologically-inspired object recognition systems. Colour processing is discussed in the development of fully-robust object recognition systems. Examples of two main categories of object recognition systems, the optical correlators and pure artificial neural network architectures, are given. Finally, two examples of object recognition's applications are described in details. With the recent technological advancements object recognition becomes widely popular with existing applications in medicine for the study of human learning and memory, space science and remote sensing for image analysis, mobile computing and augmented reality, semiconductors industry, robotics and autonomous mobile navigation, public safety and urban management solutions and many more others. This book is a "must-read" for everyone with a core or wider interest in this "hot" area of cutting-edge research.

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