

REMEMBERING PAST EVENTS IN CHIMPANZEES (PAN
TROGLODITES), BONOBOS (PAN PANISCUS) AND ORANGUTANS
(PONGO PYGMAEUS)

Amy V. M. Lewis

A Thesis Submitted for the Degree of PhD
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Remembering past events in chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and orangutans (*Pongo pygmaeus*).

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University of
St Andrews

This thesis is submitted in partial fulfilment for the degree of
PhD at the University of St Andrews

21 December 2017

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Abstract

Episodic memory is memory for personally experienced past events. Recently, there has been intense debate as to whether episodic memory is unique to humans, or whether it may extend to non-human animals. Although many insightful paradigms have shown elements of episodic memory in numerous species, research has been shrouded with difficulties, stemming from the extensive criteria and the phenomenological nature of such memories. This thesis, therefore, aims to move beyond a debate hindered by definition, and rather than searching for a definite answer to the question, focuses on comparing the similarities and differences between the way humans and animals (specifically, great apes) recall past events.

The thesis begins with an introduction to memory, before focusing on episodic memory and the episodic memory debate. In the following chapter, the subjects (great apes) and the general testing procedure are introduced. In Chapter 3, the distinctiveness effect is investigated in the recall of a past event. The distinctiveness effect refers to the enhanced memory for distinctive, as opposed to non-distinct information. The results suggest that the distinctiveness effect occurs in great apes' memory of past events, moreover, it occurs regardless of reinforcement, consistent with results found in humans. Chapter 4 explores involuntary memory in great apes; a form of memory that occurs frequently in humans and has been proposed to exist in animals, yet has been largely overlooked. Using a paradigm that draws upon elements of involuntary memory, apes show successful recall of a past event after long delays. Chapter 5 investigates the recall of social information from past events, an area which has received little attention. The results of this chapter indicate that apes fail to integrate social information (who) with what, suggesting that social information may not be

readily incorporated into the memory of past events; however, this is likely due to a lack of saliency. The final chapter discusses the findings of the three experimental chapters (3-5), before providing potential avenues for future research.

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Chapter 1 | General introduction

1.1 What is memory?

Memory is the retention of information over time. It enables us to remember what we did yesterday, to plan what we will do tomorrow, and to know that the sun will rise in the morning. Without memory, life would not be as we know it. Memory encompasses all types of information, from knowledge of the world, to personal experiences, habits and skills. It enables us to not only recall the past, but to influence future actions, to learn and to adapt (Nairne, 2010). The importance of memory is best illustrated by its absence; Clive Wearing (born 11th May, 1938) suffers from anterograde amnesia¹ (the inability to create new memories) and retrograde amnesia (the inability to recall past memories). He is in the constant state of believing he has recently recovered consciousness, yet he has been conscious since 1985. When he sees his wife enter a room, he greets her as though they have been apart for some time, despite having seen her only moments ago (Wilson & Wearing, 1995). This inability to form new memories means that his life is restricted to the here and now, and clearly demonstrates the importance of memory, but what exactly is memory?

Memory is the process of encoding, storing and retrieving information.

Encoding refers to the conversion of information into a construct that can be stored in the brain. Information can be encoded acoustically, visually, and semantically. For example, when learning a list of words one may encode them acoustically by saying them out-loud, visually by studying the lettering and font, or semantically by extracting

¹ Amnesia is the result of damage to the medial temporal lobe, which can be caused by disease, brain damage or psychological trauma (Baddeley, Kopelman, & Wilson, 2003).

the meaning of the words. In more complex material and real-life events, multiple pieces of information from all modalities can be encoded. Encoded information is then stored so that it can be accessed at a later time, this may be as brief as a few seconds, or as long as many years. This information can be stored in numerous ways, from factual information to detailed episodes.

Retrieval is the process of accessing stored information, and is what is commonly described as remembering. It is usually demonstrated through recognition and recall, but can also occur unconsciously (see declarative and non-declarative systems, p 12). Recognition is a response to sensory stimuli, and occurs when a stimulus in the environment matches information in memory (e.g., recognising a perpetrator in a police line-up), whereas recall involves the active search of stored information in memory (e.g., describing a perpetrator from memory). Recall can occur with a cue (cued recall) or without a cue; free recall and serial recall both occur without the presence of a cue. They differ in that serial recall involves recalling events or items in temporal order (e.g., recalling the order of words in a list), whereas free recall is not bound by order. Cued recall occurs when stimuli in the environment are related in some way to the stored (target) information (e.g., the word 'hot' may be given as a cue to recall the word 'sun'). As such, the difference between recognition and cued recall is not the presence or absence of cues, but rather the presence or absence of the target information; the former referring to recognition and the latter to cued recall.

Recognition and recall both activate similar brain areas, but free recall is associated with greater levels of brain activity (Staresina & Davachi, 2006). This is likely due to less external support during free recall (i.e., retrieval is self-initiated).

When we retrieve a memory, we do not retrieve an exact replica of the original experience (as once thought by ancient Greek philosophers, such as Plato's (428/427 - 348/347 BC) description of memory as a 'wax tablet'), rather, our memories are reconstructed. This reconstructive process is often prone to distortion and error, influenced by personal knowledge and cultural beliefs. For instance, Bartlett (1932) found that English participants that read a native Indian story, "The War of the Ghosts", were able to remember the gist of the story, but omitted or changed parts that were not consistent with their own culture or beliefs. This included omissions of the ghosts, despite the title of the book. Moreover, early research with rats showed that memory traces are not isolated to a single region in the brain. Lashley (1963)² found that rats were able to remember how to complete a maze after sections of their brain had been removed, suggesting the memory trace was not located in a single area of the brain. Thus, although intuitively it's easy to envisage memory as a kind of storehouse that keeps identical copies of experiences in a single location, in reality, memory is a complex construct consisting of multiple processes and regions that interact with one another. The next section describes how the classification of memory developed over time, from the idea of a single system construct, to the multi-model system that is generally agreed upon today.

² Although Lashley was correct in his observation that memory is not confined to a single location, he incorrectly thought of memory as a unitary construct, that could be activated by multiple regions in the brain (i.e., he did not believe certain areas were specialised for certain functions).

1.2 Models of memory

Research into the multi-modal nature of memory did not truly commence until the mid 20th century, however, the concept of memory consisting of multiple systems originates back to the 17th century. William James (1842-1910) distinguished between primary and secondary memory, with primary memory reflecting the current contents of consciousness, and secondary memory reflecting “the knowledge of a former state of mind after it has already once dropped from consciousness” (James, 1890, p. 648). Additionally, habit was considered as a separate form of memory: “Indeed, this habit could not be called a remembrance, were it not that I remember that I have acquired it” (Bergson, 1910, p. 95).

It was not until later that experimental research (as opposed to theoretical conceptions) began to test the notion of multiple memory systems. Three areas of research were particularly influential in support of multiple memory systems: first, amnesiac patients do not suffer from a complete global impairment to memory, but show some spared memory functions, suggesting that memory can not be unitary. For instance, H.M suffered from amnesia after the bilateral removal of the hippocampus and surrounding region, yet his procedural memory remained intact, meaning he could learn new skills but could not explicitly remember learning them (Scoville & Milner, 1957). Second, healthy subjects show differential activation in brain regions in tasks designed to test different types of memory. For instance, left temporal and frontal cortices are recruited more during semantic retrieval, whereas the medial parietal region is activated most during episodic retrieval (Wiggs, Weisberg, & Martin, 1998). Third, experimental non-human animal (here after animal) studies show that lesions to specific brain areas result in a loss of specific, rather than global, memory. For

example, habit memory in rats is impaired with lesions to the caudate nucleus, whereas recognition memory is impaired with fimbria/hippocampal lesions (Packard, Hirsh, & White, 1989).

Such research converged on the finding that memory can not be composed of a single system, and spurred the development of multiple memory models. The next section provides a brief overview of (arguably) some of the most influential models of memory, and the memory systems that are generally agreed upon today (see Figure 1.1) For a more detailed overview of memory models, including models that cannot be covered here due to space restrictions, see Ericsson and Kintsch (1995), and Raaijmakers and Shiffrin (2002).

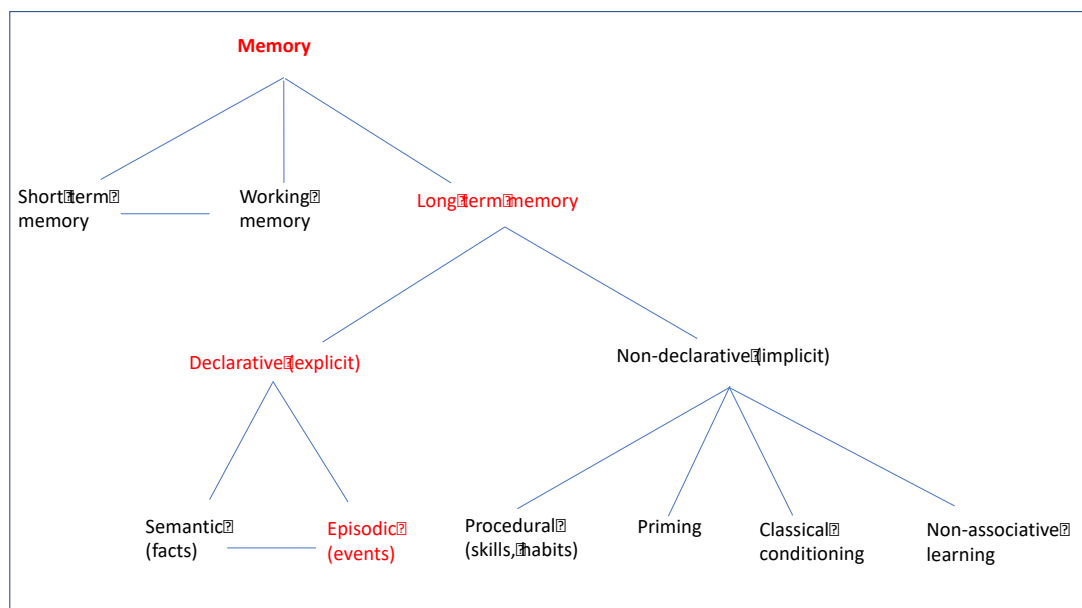


Figure 1.1 An overview of the memory systems that are generally agreed upon today, adapted from Squire (2004). Text in red indicates the focus of this thesis. Note that the short-term/working memory systems have been simplified in this illustration, as they are not the focus of this thesis; however, details of these systems can be found below.

1.2.1 Multi-store model

Atkinson and Shiffrin (1968)'s seminal paper on the multi-store model proposes that memory consists of three stores: sensory memory, short-term memory and long-term memory. The three components are dependent upon one another (i.e., without short-term memory information cannot be transferred to long-term memory), consequently, this model regards memory as a series of stages on a continuum, rather than separate independent systems. In the sensory store, information is perceived by our senses and held momentarily (for a matter of milliseconds) until it is processed into short-term memory. If the information is not processed, then it is lost at this stage. Information in short-term memory lasts for only a matter of seconds (Peterson & Peterson, 1959), at which point it is forgotten unless transferred to long-term memory. In order for information to be transferred from short-term memory to long-term memory, it must be rehearsed by repeating the information (maintenance rehearsal).

The capacity of short-term memory has been found to be seven items (± 2) (Miller, 1956); however, this can be increased through strategies such as chunking (Bower, 1970; Miller, 1956). In contrast, the capacity and duration of information stored in long-term memory has the potential to be unlimited, so long as it's accessible (Tulving, 1974); although see Roediger, Weinstein, and Garwal (2010) for other theories that suggest information can be completely lost from storage. Regardless of whether information is forgotten due to loss or inaccessibility of the memory trace, forgetting should not be regarded as a failure of memory, but rather as an adaptive function that enables us to retrieve the most relevant information (Bjork & Bjork, 1988).

The multi-store model is able to account for certain phenomena, such as why we remember the first (primacy) and last (recency) items on a list better than the middle items (Atkinson, 1970). However, a large amount of research has cast doubt on the simplicity of this model. For instance, the case study of K.F (Warrington & Shallice, 1969) showed that short-term memory can be impaired in one sense (e.g., auditory), but not another (e.g., visual), suggesting that short-term memory is not a unitary store. Moreover, K.F's long-term memory remained intact, whilst short-term memory was completely lost. Such a finding is incompatible with this model, as the transfer of information to long-term memory is possible only via short-term memory (Shallice & Warrington, 1970). Additionally, merely rehearsing information by repetition does not always lead to long-term memory. For example, repeatedly reading an essay leads to poorer recall after long delays compared to being tested on the material during learning (Roediger & Butler, 2011; Roediger & Karpicke, 2006). Indeed, this testing effect shows that by practicing the skills during learning that are later required during retrieval, long-term memory performance can be enhanced. Despite the shortcomings of this model, it has nonetheless been highly influential in the development of subsequent multi-system models.

1.2.2 Levels of processing

Another pioneering model of memory is the levels of processing framework by Craik and Lockhart (1972). Unlike the previous model, it is not a model about how memory is organised or structured per se, but rather describes memory as a by-product of processing (Craik & Lockhart, 1972; Lockhart & Craik, 1990). The central notion is that the more in-depth information is processed, the longer it will remain in memory. If

information is processed shallowly (such as through repetition), then it will only be remembered for a short time. If the processing is more elaborative and deep, such as the processing of meaning or relating the to-be-remembered information to stored knowledge, then it will be remembered for much longer. Shallow processing occurs acoustically (i.e., processing the sound of a word) or visually (i.e., processing the colour, size, font etc. of a word), and is kept in memory via maintenance rehearsal, whereas deep processing occurs when information is processed semantically (i.e., processing the meaning of a word).

The theory was shown in practice by Craik and Tulving (1975). They presented participants with a set of sixty words; for each word, participants answered a question about the word's visual, acoustic, or semantic properties. The visual questions lead to shallow processing (such as processing the colour of the words), the acoustic questions concerned rhyming (such as whether the presented word rhyme with the word 'new'), and was described as intermediate processing, and the semantic questions resulted in deep processing (processing words in terms of categories and sentences). Participants were then tested on their free recall, cued recall and recognition of the presented words. Results showed semantically processed words were remembered better than visual and acoustically processed words. Additionally, these findings were corroborated by many similar studies (for a review of studies both in support of and against the levels of processing theory, see Cermak and Craik (1979).

The levels of processing model is able to explain why we remember some things better than others, such as why processing the meaning of information in an essay results in better recall than simply repeatedly reading the essay, and furthermore, it shows that encoding is multi-dimensional. This distinction between different types of

encoding was later introduced in Atkinson and Shiffrin (1968)'s model, in which they introduced a second type of rehearsal; elaborative rehearsal. This differs from maintenance rehearsal (repetition), and involves the integration of to-be-remembered information with stored information (Raaijmakers & Shiffrin, 2003).

Although the levels of processing is an intuitive theory, it has been critiqued for being rather vague in defining what 'deep' processing refers to (see Lockhart & Craik, 1990, for a discussion of these critiques). Moreover, it's reasoning is circular, explaining that the deeper something is processed the better it is remembered, whilst how well something is remembered is predicted by how deep it is processed (Eysenck, 1978). Furthermore, there are cases in which deep (semantic) processing cannot explain good memory. Transfer appropriate processing (Morris, Bransford, & Franks, 1977) shows that semantic encoding only leads to enhanced memory when the test requires the recall of semantic memory. In this classic study, subjects were given words to learn either semantically or phonetically. The words were presented in congruent (e.g., sentences that semantically made sense, or that rhymed) or incongruent sentences. During the recognition test, subjects that received a rhyming recognition test and learned the words in semantically congruent sentences, performed poorer than those who received the rhyming test and learned the words in phonetically congruent sentences. The authors concluded that:

[T]here are no inherent differences in the nature of the memory traces resulting from semantic versus non-semantic levels of processing. Instead the emphasis is on the activation of appropriate skills and knowledge structures that "set the stage" for knowing precisely how and in what ways certain inputs differ from other potential inputs. (Morris et al., 1977, p. 529).

Thus, although the levels of processing theory established that semantic information is often well remembered, it failed to account for the relationship between acquisition and retrieval, which far better explains the durability of memory traces.

1.2.3 Working memory model

Baddeley and Hitch (1974)'s working memory model developed from Atkinson and Shiffrin (1968)'s multi-store model, and is an expansion of their short-term component of memory³. The model proposes that short-term memory is not unitary, rather, it is comprised of several components. The visual store (visual-spatial sketchpad) and the phonological store (phonological loop) are referred to as the 'slave systems', and are controlled by the central executive. Information that is detected by the senses is transferred to the appropriate slave system, where it is temporally stored and maintained via rehearsal. For example, auditory information is sent to the phonological loop and is maintained through vocal rehearsal (Baddeley, 2012). Both systems are limited in capacity, but the limits are independent. Furthermore, the systems are directly linked to long-term memory, meaning that information from long-term memory can influence working memory, and vice versa (Baddeley, 2012).

The central executive is responsible for controlling the slave systems, ensuring that the correct type of information is sent to the correct system, and can also combine auditory and visual information into integrated units. It also controls mental processes, deciding what we should and should not attend to (Baddeley & Hitch, 1974). Thus,

³ Despite differences in the models, working memory and short-term memory are often used interchangeably (Aben, Stapert, & Blokland, 2012).

working memory comprises of both manipulation and storage of information, whereas the model of short-term memory encompasses only the storage of information.

A fourth component was later added, named the episodic buffer (Baddeley, 2000). The episodic buffer was introduced to account for the lack of temporary storage for manipulated information. As we often combine visual and auditory information, this integrated information needs to be temporally stored. The central executive cannot store this integrated information, due to it not having a storage element (Baddeley, 2012), thus the episodic buffer fulfils this role. It holds integrated information in the form of episodes or chunks, whilst retaining chronological order, meaning that information can be recalled in sequence, such as details of a story. It also is linked to long-term memory.

Unlike Atkinson and Shiffrin (1968)'s unitary model of short-term memory, this model is able to account for cases in which some elements of short-term memory remain intact, whilst others are lost (e.g., the case study of K.F). Furthermore, it explains why memory retention is minimally disrupted in parallel tasks that recruit the different slave systems (e.g., an auditory task alongside a spatial task), compared to parallel tasks that recruit one slave system (e.g., two auditory tasks; Cocchini, Logie, Della Sala, MacPherson, & Baddeley, 2002). In the first example, information is processed in two separate systems, and thus the capacity is the capacity of the two systems. In the second example, information is processed by one system, and is thus restricted to the capacity of one system, meaning that not all information can be maintained.

Although the working memory model is an improvement on the unitary model introduced by Atkinson and Shiffrin (1968), it has been criticised for its lack of

specificity. For instance, little is known about the central executive, due to difficulties with directly testing it, leading to proposals that it's only function is to explain performance that the slave systems cannot, "[t]he central executive is a concept that emerges from research by default when more rigorous theoretical constructs cannot handle the data." (Parkin, 1998, p. 521). Despite this, the working memory model provides a framework which is generally accepted today, and from which alternative theories have been developed (Baddeley, 2012).

1.2.4 Declarative and non-declarative systems

As with short-term memory, long-term memory is not unitary. Early research distinguished between two long-term memory systems: declarative and procedural (Cohen & Squire, 1980). Declarative memory is memory for facts and events that can be consciously retrieved and explicitly expressed, with conscious retrieval referring to the awareness of bringing information to mind. Declarative memory is usually measured using recall and recognition tasks (Squire, 1992a)⁴. Procedural memory refers to memory for skills and habits, such as remembering how to ride a bike. These procedural memories are unconscious and occur without awareness, as such, these memories are expressed implicitly and shown through performance and behaviour, rather than conscious recollection (Squire & Dede, 2015). For instance, when learning how to ride a bike, you may deliberately remember the last time you tried in order to progress with learning; this is declarative (conscious) memory. However, when you

⁴ Although declarative memories are usually verbally expressed (i.e., through recall and recognition tasks), they can also be expressed non-verbally through behaviour (e.g., remembering that I left my shopping in the boot of the car is expressed through my action of opening the car boot).

have successfully learnt to ride a bike, the ability to cycle will come automatically, without conscious recall of the learning process; this is procedural (un-conscious memory).

The distinction between declarative and procedural memory was partly due to case studies of amnesia, which showed instances of intact procedural memory in the absence of declarative memory. For example, the ability to acquire and maintain skills, such as tracing an outline using only a reflected mirror image, and reading words from a reversed mirror image, without the ability to recollect the learning process (Cohen & Squire, 1980; Gabrieli, Corkin, Mickel, & Growdon, 1993). One of the most cited examples of this dissociation is the case study of H.M (Scoville & Milner, 1957), who suffered from a deficit in declarative memory (as a result of bilateral removal of the hippocampus and surrounding areas), whilst his procedural memory remained intact. H.M was able to learn to trace the outline of a star when the star and his hand were only visible as a reflection in a mirror. He retained this information over days, however, he could not recall ever having done the task before (Milner, 1962, as cited in L. R. Squire, 2009), suggesting that his memory of the event (declarative memory) was lost, but his learnt skill (procedural memory) remained. Similar findings have also been reported more recently in larger population samples, and using different types of procedural tasks (e.g. Cavaco, Anderson, Allen, Castro-Caldas, & Damasio, 2004), indicating that the dissociation between procedural and declarative memory is fairly robust.

Further research with amnesiac populations (e.g. Bayley, Frascino, & Squire, 2005; Hamann & Squire, 1997; Levy, Stark, & Squire, 2004; Reber & Squire, 1994) has shown that procedural memory is not the only type of memory to be dissociated

from declarative memory, rather there are other types of memory that are intact when declarative memory is lost, such as priming and habit (Tulving, Schacter, & Stark, 1982). Priming refers to the facilitative effect that previous exposure to a stimulus has on the subsequent processing of a related (or the same) stimulus (Tulving et al., 1982). For instance, response time to the target “gorilla” will be faster when preceded with the related word “chimpanzee”, as opposed to the un-related word “blue”. A critical study in support of the distinction between declarative memory and priming highlighted the importance of task instructions on performance (Graf, Squire, & Mandler, 1984). In this study, amnesiacs were poor at free recall and recognition of previously presented words (declarative memory), but performed as well as control subjects in a stem-completion task (in which the start of a word is presented, and subjects are asked to complete the word). However, when presented with the stem-completion task and asked to use the stems to help recall the words from the previously presented list, performance was below controls. Thus, amnesiacs performed well only when the task instructions were directed away from the memory elements of the task (i.e., when participants were not instructed to explicitly try and retrieve a memory).

The dissociation between declarative and other non-declarative systems (e.g., priming, habit and procedural memory) is further supported by brain imaging and experimental animal studies, which show that specific brain regions are recruited in declarative but not non-declarative memory (Squire & Zola-Morgan, 1991). For example, Malamut, Saunders, and Mishkin (1984) found that rhesus monkeys with limbic lesions (amygdaloid and hippocampal ablations) were unable to learn to discriminate between a familiar and novel stimulus (recognition memory), but were fully capable of learning an associative task. They presented monkeys with two objects;

one which covered a peanut (sample object), and one which did not. After a thirty second delay, the sample object was presented again, along with a new object that had not been seen before. Monkeys with limbic lesions were unable to learn to select the sample object within one-thousand trials, even with an inter-trial retention period of only thirty seconds, whereas control subjects all learnt within one-thousand trials. However, the monkeys with limbic lesions were just as efficient as controls when the task was to discriminate between two familiar items (one which had been rewarded and one which had not), even with a retention period of twenty-four hours between trials. The performance difference between the two tasks shows that when monkeys needed to use recognition memory (i.e., to discriminate between a familiar and new stimulus) they failed. However, when they needed to discriminate between a familiar positive and a familiar neutral stimulus (akin to habit) they were successful, suggesting that hippocampal and amygdaloidal regions are necessary for declarative, but not habit memory.

In the case of human populations, Reber, Wong, and Buxton (2002) asked two sets of participants to complete one of two tasks whilst in an fMRI scanner. In one task, subjects indicated whether a pattern of dots came from the same category or different category as previously seen patterns (non-declarative task), whilst in another task they indicated whether they had seen the pattern of dots before (recognition memory). A control task (in which they counted dots) allowed for activity associated with counting to be subtracted from the analysis, resulting in only task specific differences to be compared. The two tasks activated brain regions to different extents, with the declarative task showing more activity in seven regions, including the region of the

posterior right hippocampus, suggesting that declarative and non-declarative memory differ at the neural level.

The dissociation between multiple types of memory and declarative memory suggests that a two-memory system model is too simplistic. Indeed, there are now thought to be numerous non-declarative systems, such as a procedural, priming, non-associative and classical conditioning systems (see Squire, 1992a). These systems all fall under the umbrella of non-declarative memory, and differ from declarative memory in terms of lacking conscious recollection (Squire & Zola-Morgan, 1988). Furthermore, although the systems are independent, they work together in parallel to guide behaviour and learning. For instance, Packard and McGaugh (1996) showed that rats could use two types of learning in order to find a food item in a maze. They could learn the place of the food (i.e., on the left arm), or they could learn using a response (i.e., always turn left). They initially used place learning, and then later switched to response learning. However, when the caudate nucleus was temporally inactivated (via injections of lidocaine), they reverted to place learning, meaning that place learning was preserved, even though response learning was the dominant response. Thus, two types of learning were used in parallel by the rats; a spatial learning method and a stimulus response method. Likewise, Brown and Robertson (2007) showed that the systems can interact with each other, with procedural learning interfering with declarative consolidation, and vice versa.

Although many accept the traditional distinction between declarative and non-declarative systems, there are alternative conceptions. One viewpoint suggests that declarative and non-declarative systems do not dissociate, but rather vary along a continuum with regards to consciousness and other variables, such as the level of

intention (Dew & Cabeza, 2011). For instance, both non-declarative and declarative memories can be triggered by external stimuli, suggesting there may be mechanisms which transition the processing from unconscious to conscious (Dew & Cabeza, 2011). Similarly, although many amnesiac patients seem to show intact non-declarative memory and impaired declarative memory (suggestive of a dissociation between the systems), there is evidence to suggest that their memory deficit may not be a loss of declarative memory per se, but rather a deficit in binding (Rosenbaum, Gilboa, Levine, Winocur, & Moscovitch, 2009; Schacter, 1997). For example, amnesiacs perform poorly when they are required to bind or integrate information and create complex associations, regardless of whether the task is declarative or non-declarative (see Schacter, 1997). As such, although the distinction between declarative and non-declarative systems is generally recognised, alternative notions propose that the distinction is not so black and white.

1.2.5 Episodic and semantic memory

Within the declarative memory system, a further distinction is made between two types of memory: semantic and episodic memory (Tulving, 1972). Semantic memory refers to memory for facts, knowledge, and concepts, and includes words, objects, places, people, and the relations among them. Episodic memory is memory for personally experienced episodes or events, and includes spatial and temporal information, such as what happened, where and when. Semantic memory lacks this spatial-temporal information, and although it can refer to the past, it is not autobiographical (personally experienced). For example, my memory of the first time I was introduced to a chimpanzee draws upon episodic memory, however, my knowledge that a chimpanzee

is a primate is semantic, as it does not require a specific experience of having met a chimpanzee. Semantic memories are obtained through repeated exposures and experiences, whereas episodic memories are of single, specific events. The two types of memory are thought to be independent subsystems of the declarative system (Squire & Zola, 1998; Tulving, 1983), but see below for an alternative theory. They differ in numerous ways, such as organisation (temporal vs conceptual), and reference (self vs world). For a summary of the key differences see Tulving (1983, table 3.1, p. 35).

Over the years, Tulving (1972)'s original definition of episodic memory has been expanded. It now incorporates autonoetic conscious, defined as a recollective experience of remembering, and chronesthesia, described as a subjective sense of time, or a knowledge and awareness of one's own personal past and future (Tulving, 1983, 2001). When these elements go wrong, disorders of memory such as *déjà vécu*⁵ can occur (Moulin, Conway, Thompson, James, & Jones, 2005). It is these components that Tulving (2005) has argued are unique to humans, and by extension, that episodic memory is unique to humans. The question as to whether non-human animals (here after, animals) have episodic memory is the key motivation behind this thesis, and is discussed later in this chapter.

Tulving (1989) was one of the first to show evidence of the dissociation between episodic and semantic memory in healthy subjects. Using measures of cerebral blood flow, he showed that episodic and semantic memory retrieval have different levels of activation in different brain regions, with broadly speaking, more activation in the anterior regions for episodic remembering, and more activation of posterior regions

⁵ a feeling of reliving the present moment again.

with semantic retrieval. Dissociations in brain regions for semantic and episodic remembering have also been replicated more recently (Prince, Tsukiura, & Cabeza, 2007; Wiggs et al., 1998). For instance, the extent of damage to the hippocampus is related to the severity of deficit to episodic memory, but not semantic memory (Rosenbaum et al., 2008), and episodic memory retrieval often involves activation in the right prefrontal cortex, whereas semantic retrieval does not (Nyberg, Cabeza, & Tulving, 1996).

Clinical populations, specifically amnesiac patients, also support the dissociation. K.C (1951-2014) suffered from anterograde amnesia and temporally graded retrograde amnesia, after severe bi-hippocampal damage caused by a motorcycle accident (Rosenbaum et al., 2005). He was unable to recollect or form any new memories of personal experiences, nor form new semantic memories. However, his semantic knowledge from prior to the accident was unaffected, showing a dissociation between retrograde episodic and semantic memory (Tulving, 1989). Similar findings were obtained by Vargha-Khadem et al. (1997), who studied three patients with early-onset bilateral hippocampal pathology. These patients could not form episodic memories, but were able to acquire general knowledge and language, as evidenced by their (near) normal intelligence, suggesting that episodic memory, but not semantic, is dependent upon the hippocampus. Many similar observations have been shown in other amnesiac patients (see Nadel & Moscovitch, 1997), with the hippocampal formation found to be crucial for episodic, but not semantic, memory (Press, Amaral, & Squire, 1989).

Research consistent with a dissociation between episodic and semantic memory was first thought to provide evidence of independence of two separate sub-systems;

however, a more recent proposal suggests that episodic memory is an extension of semantic memory, rather than an independent system (Tulving & Markowitsch, 1998). The proposal suggests that declarative memory embodies the commonalities between episodic and semantic memory, and that episodic memory is a sub-system of declarative memory that contains unique features that are absent from semantic memory, such as auto-noetic consciousness (Tulving & Markowitsch, 1998). Furthermore, episodic memory is dependent upon semantic memory, meaning that it cannot function without intact semantic memory. Although this theory is consistent with the many findings from amnesiac patients (in which episodic memory is often absent whilst semantic memory remains intact), the theory fails to take account of cases in which episodic memory is present in the absence of semantic memory; namely in semantic dementia (see Hodges & Graham, 2001).

An alternative view proposes that episodic and semantic memory are not different types of memory per-se, but rather are the result of the networking of memories, whereby the hippocampus stores not only unique episodes, but also integrates information from these unique episodes with stored knowledge (Eichenbaum, 1997). Similarly, evidence suggests that semantic memory may aid with the formation of new episodic memories, by providing a framework with which episodic information can be integrated (Kan, Alexander, & Verfaellie, 2009).

As such, although there is substantial evidence showing that semantic memory can occur independently of episodic memory (and sometimes vice versa), the exact relationship between the two is not yet clear (see Greenberg & Verfaellie, 2010). Despite a lack of clarity on the exact relationship between the two types of memory,

there is general agreement that episodic memory is concerned with recollecting past experiences, and semantic memory with general knowledge and factual information.

1.2.6 Conclusions

Although there is not complete agreement upon the structure and systems of memory, it is widely accepted that memory consists of multiple systems (Eichenbaum & Cohen, 2001; Schacter & Tulving, 1994). These systems are independent, yet interact with one another. Indeed, to date we are still learning about the way memory systems interact; recent findings have shown that memories are not created in the hippocampus and later transferred to long-term storage, rather, they are simultaneously formed in both the hippocampus and prefrontal cortex, and change in their levels of activation over time (Kitamura et al., 2017). In the next section, I describe how the interaction between encoding and retrieval plays a crucial role in determining whether a memory is successfully recalled.

1.3 Encoding and retrieval

Tulving (1974) described remembering as the product of both encoding and retrieval:

“we remember an event if it has left behind a trace *and* if something reminds us of it” (p.74). Below I describe how the recall of a memory is determined by this interplay.

1.3.1 The encoding specificity principle

The encoding specificity principle (Tulving & Thomson, 1973) states that memory recall is enhanced when information that was encoded with the memory trace is present during retrieval. That is, information in the current environment that was encoded with the memory trace can serve as an effective cue to trigger recall of the memory.

Crucially, for the cue to be effective, it must be related to the way the target was encoded. For instance, the retrieval cue ‘hot’ would not be helpful if the target word ‘sun’ was encoded as ‘part of the solar system’, but would be effective if the target word was encoded as ‘made of fire’. Thus, it is not enough for the retrieval cue to be merely related to the target, rather, it must be related to the way in which the target was encoded. The encoding specificity has important implications for the recall of episodic memories, in particular the recall of involuntary memories (see page 59), which are often triggered by features in the present external environment that were encoded at the time of the event (Berntsen, 1996).

1.3.2 Cue-overload

The effectiveness of the retrieval cue also depends on the number of memory traces to which it is associated, referred to as cue-overload (Watkins & Watkins, 1975). That is,

a feature that is present in many memory traces is less likely to be an effective retrieval cue than a feature that only occurs in one memory trace. For instance, a list of different animals can be cued by the category ‘animal’; however, the probability of recalling an item from the list declines as the category size increases. Introducing a new category cue, such as ‘mammal’, will increase recall of individual items, as it reduces the number of items associated to a particular cue. Cue over-load is also an important concept in episodic memory, in particular involuntary episodic memory (Rasmussen & Berntsen, 2009).

1.3.3 Outshining and over-shadowing

Outshining refers to the failure to use contextual retrieval cues even when they have been encoded and stored (Smith, 1994; Smith, 2013; Smith & Vela, 2001). It occurs when other retrieval cues are present that are stronger or more efficient (Watkins & Watkins, 1975), thus outshining is not a failure of encoding, but a failure to detect the information that was encoded. Outshining can occur due to various reasons, such as cue-overload (as described above), redundancy of information (i.e., the cue adds no more information than another cue, see Smith, 1994), or lack of saliency of the information (Smith, 1984).

Overshadowing is similar to outshining, but is the failure to store the information, as opposed to the failure of detecting the stored information. A feature may not be encoded when other more salient information is present because of the limited attentional capacity to encode and store information (Smith, 1994; Smith, 2013; Smith & Vela, 2001). Overshadowing can be seen as one stimulus blocking the encoding of another stimulus, that in isolation, would have been successfully encoded

(Kamin, 1969). Thus, the extent to which information can successfully act as a retrieval cue depends on whether the information is outshined or overshadowed.

1.3.4 Conclusions

The interplay between encoding and retrieval determines the success or failure of retrieving a memory. Although intuitively, one would expect that increasing the number of overlapping cues would increase the chance of successful retrieval, this is not necessary nor sufficient (Nairne, 2002). Rather, successful retrieval is dependent upon the value of a given cue; a cue that is overloaded, overshadowed or outshined will not be effective, no matter if present in great number. In contrast, a cue that is unique to a specific memory trace, and processed in the same way as the memory trace, is much more likely to lead to successful recall, even if presented in isolation.

For the remainder of this thesis, the focus turns to memory in animals. I begin with a brief overview of the potential evolutionary purpose of memory, and the memory systems evidenced in animals, before focusing on episodic memory.

1.4 Memory in animals

Memory is not unique to humans, rather it is present in many other species (see Chapter 7, Shettleworth, 2010). As such, it is not a specific adaptation that evolved in humans, but is a widespread mechanism that has a long evolutionary history. For something to have continued down the evolutionary line, its function and purpose must be valuable to all organisms that have it; namely to promote survival and to reproduce (Nairne, 2010). Memory facilitates survival and reproduction by enabling us to learn and adapt from our past experiences. Drawing upon past information means that we can predict and plan for similar future experiences, and adapt our behaviour accordingly (Roediger, Dudai, & Fitzpatrick, 2007). For instance, remembering that you are allergic to nuts will aid you in avoiding eating nuts in the future. Without the ability to do this, we may repeat bad or unsuccessful experiences, which may come at a cost to our fitness. Thus, without memory, the inability to learn and adapt from past experiences may hinder our survival success.

Early research with primates led to observations that they could remember information over long periods. Köhler (1925) noted that chimpanzees that had learnt various discrimination tasks more than one year earlier, showed performance that resembled learning that occur only a few days ago. Similarly, Tinklepaugh (1932) found that chimpanzees were just as accurate as humans at recalling which one of two paired containers had been baited with food. Since then, many commonalities have been found between human and animal memory. For instance, honeybees trained to forage at different food sites that vary in scent and colour, can remember the location of a specific food site when cued with the associated scent or colour (Reinhard, Srinivasan, Guez, & Zhang, 2004). Hummingbirds can recall multiple pieces of

information, such as which flower was in which location in a particular context (Jelbert, Hurly, Marshall, & Healy, 2014), and primates can use memory to plan ahead in a maze just as well as young children (Beran, Parrish, Futch, Evans, & Perdue, 2015). A vast amount of research has also demonstrated that many animals have multiple memory systems, such as short-term and working memory (Beran, Beran, & Menzel, 2005; Dunnett & Martel, 1990; Fujita & Matsuzawa, 1990; Hoffman & Beran, 2006; Inoue & Matsuzawa, 2007; MacDonald & Agnes, 1999; Maki, 1979; Menzel, 1979; Mishkin & Delacour, 1975; Rodriguez, Zurcher, Bartlett, Nathanielsz, & Nijland, 2011), declarative memory (Ban, Boesch, & Janmaat, 2014; Bednekoff, Balda, Kamil, & Hile, 1997; Beran, 2004; Crystal & Babb, 2008; Hunt & Chittka, 2015; Janmaat, Ban, & Boesch, 2013; Jelbert et al., 2014; Martin-Ordas, Berntsen, & Call, 2013; Mendes & Call, 2014; Menzel, 1999; Vander Wall, 1991; Wilson, Pizzo, & Crystal, 2013), and non-declarative memory, such as priming and habit (Broadbent, Squire, & Clark, 2007; Malamut et al., 1984; Resende, Tavares, & Tomaz, 2003; Tu & Hampton, 2013).

Multiple memory systems may have evolved because they serve unique and important functions. Sherry and Schacter (1987) propose that multiple memory systems arise as a response to specific environmental problems, resulting in specialised systems that are limited in flexibility. They term this inflexibility ‘functional incompatibility’. To illustrate this, they use the example of caching and bird song: some birds are able to learn a specific song in order to attract a mate, a song that is remembered over multiple breeding seasons, and is never changed or altered. Some birds also frequently cache food; food caching requires the ability to remember numerous different food locations, and to recall them several days later. These two types of memory are fundamentally

very different from each other, and without distinct types of memory, both functions would not be possible. For instance, if birds applied their long lasting and fixed memory for bird song to food caching, food cache locations would never be forgotten, even when they have been recovered.

Although there is evidence for multiple memory systems in animals, Schacter and Tulving (1994) make the important point that because each species has its own unique environmental pressures, they evolve differently. This makes comparisons between species difficult, and as such, evidence for multiple memory systems in one species is not evidence for all species. Nonetheless, evidence from one animal species serves to show that multiple memory systems can (and do) exist in species other than humans. The specifics as to which memory systems and which types of memory are present in animals is less clear. In particular, the question as to whether episodic memory is unique to humans has been intensely debated. In the next section, I review the on-going debate as to whether animals remember episodically.

1.4.1 Episodic memory in animals

As described previously, episodic memory is memory of personally experienced past events. It has been widely researched in humans, not only in clinical patients, but also in healthy subjects, such as through the use of diary studies and the remember know-paradigm. The remember-know paradigm is employed in recognition tasks to determine whether participants recognise stimuli through familiarity based retrieval, or through episodic recollection (Gardiner, 1988; Rajaram, 1993). Here participants are asked whether they remember seeing the stimulus (conscious recollection), or simply know that the stimulus was there because it feels familiar (familiarity based recognition).

From studying humans, we know that episodic memory is one of the last types of memory to emerge in development. It typically does not begin to appear until around the age of three (Hayne & Imuta, 2011; Perner & Ruffman, 1995; Scarf, Gross, Colombo, & Hayne, 2013), with improvement through the preschool years (Newcombe, Balcomb, Ferrara, Hansen, & Koski, 2014). Likewise, it is one of the first types of memory to decline with age (Nilsson et al., 1997), and is often first affected in degenerative diseases such as Alzheimer's (Greene, Baddeley, & Hodges, 1996; Weingartner, Grafman, Boutelle, Kaye, & Martin, 1983). Recently, there has been a surge of interest as to whether episodic memories may also exist in animals (see Dere, Kart-Teke, Huston, & De Souza Silva, 2006; Malanowski, 2015; Pause et al., 2013). Tulving (among others) claims that episodic memory is a uniquely human ability, "[e]pisodic memory is a recently evolved, late-developing, and early-deteriorating past-oriented memory system, more vulnerable than other memory systems to neuronal dysfunction, and probably unique to humans" (Tulving, 2002, p5.). However, others propose that episodic memory is unlikely to be confined to humans (Clayton & Russell, 2009; Crystal, 2013; Zentall, 2006). For instance, Conway (2005) proposes that animals may have the basic functions of episodic memory, allowing them to behave effectively and adapt to their environments, but lack the organisational structure present in human episodic memory. Furthermore, directly contrasting Tulving (2005)'s notion of episodic memories as recently evolved and late developing, Conway (2005) proposes the converse; with episodic memories as the first to develop.

From an evolutionary perspective, there is good reason to assume that episodic memory exists in animals. Episodic memory enables us to travel back in time and recall experiences and events that happened to us. Further still, it allows us to travel forward

in time to anticipate future scenarios and plan ahead (Allen & Fortin, 2013). Such a system allows us to learn and adapt from past experiences, enabling us to avoid behaviours and situations that caused fitness costs in the past, and instead repeat behaviours that resulted in fitness gains. For instance, an animal that regularly uses a particular food source discovers that one day the food source has been depleted. As a consequence, the animal stops returning to this location, and instead finds a new location in search of food. Thus, the animal modifies its behaviour based on a past experience. If the animal were unable to encode, store, and retrieve the episode in which it found the food source to be depleted, it would lack the information needed to modify its behaviour. Consequently, the ability to recall the outcome of a scenario provides us with valuable information for future scenarios, and thus from a survival and fitness perspective, episodic memory is crucial to animals.

Furthermore, it has also been proposed that episodic memory is important for the processing and use of social information (Clayton, Griffiths, Emery, & Dickinson, 2001; Schwartz & Evans, 2001), such as remembering who has been cooperative and who has been aggressive; information which changes over time and thus may depend on the ability to recall individual experiences (Allen & Fortin, 2013). Evidence of the ability to keep track of past social interactions has been found in primates (Bohn, Call, & Tomasello, 2016; Cheney & Seyfarth, 1990), birds (Bond, Kamil, & Balda, 2004) and rats (Dolivo & Taborsky, 2015). Failure to remember the previous actions of an individual may mean that establishing bonds and relationships is difficult. This goes directly against the (generally) highly social behaviour observed in primates, rodents and birds, all of which are at the forefront of investigation of episodic memory (Allen & Fortin, 2013).

Anatomically, animals have the capacity for episodic memory. Research has shown that brain regions responsible for episodic memory in humans are also present in animals. The hippocampus and surrounding para-hippocampal region are important for the formation of episodic memories (Press et al., 1989; Vargha-Khadem et al., 1997), and these areas are, for the most part, structurally and functionally conserved across mammals (Manns & Eichenbaum, 2006). For instance, the hippocampus is not only important for spatial memory in animals but is also involved in the integration of information in memory (Squire, 1992b); a key feature of episodic memory.

Taken together, the adaptive function and capacity for episodic memory in animals makes a compelling basis for researching its presence in animals. However, when it comes to showing episodic memory in practice, animal research has been hindered by the stringent and changing criteria that arise from Tulving's (1972, 1983, 1984, 1985, 2002, 2005) many definitions. Specifically, accessing whether animals experience conscious recollection and chronesthesia is impossible to either verify or falsify without the use of language, making it impossible to test for episodic memory in animals using the same criteria used for humans. As such, research has focused on testing for the observable prerequisites of episodic memory, such as the integration of what, when, and where information, the binding of contextual details, the recall of the temporal order of information, and free recall. In the following sections I provide an overview of the main research paradigms designed to test for episodic memory in animals. Each focus on different aspects of episodic memory, but taken together provide substantial evidence of episodic memory in animals. A summary of research

can also be found in Table 1.1⁶, and extensive reviews have been covered by Crystal (2009), Pause et al. (2013), and Dere et al. (2006).

1.4.1.1 *What-where-when (episodic-like memory)*

Episodic memory was first investigated in animals using a pioneering paradigm developed by Clayton and Dickinson (1998), which took advantage of the natural caching behaviour of scrub jays. The paradigm focuses on Tulving's (1972) original definition of episodic memory, which described episodic memory as the recall of what, where, and when information, from a single event (it was not until later that autonoetic consciousness was added to the definition). In the paradigm, they presented scrub jays with two types of food: highly preferred wax worms, and non-preferred peanuts. The birds learnt (through repeated exposures) that the wax worms degraded and were inedible after 124 hours, whereas the peanuts were always edible. During the first caching, the birds were presented with a sand box and one of the food items, and given fifteen minutes to cache the food item on one side of the sand box (the other side was blocked by a Perspex cover). During the second caching, they were presented with the other food item and had access to the other side of the sand box. The two cachings were separated by 120 hours, and the test began four hours after the second caching. This meant that the food that was cached first was cached 124 hours ago (and in the case of the wax worms, was now inedible), and the food that was cached second was cached only four hours ago (in this case, both foods were still edible). The birds completed multiple cachings (trials), which were made unique by using different backgrounds in

⁶ This table is not an exhaustive list of research on episodic memory in animals, but provides a range of studies, using different techniques and in different species.

each sand box. At test, the birds were presented with one of the sand boxes, and allowed to search for the cached food (all cached food was removed to prevent the birds from locating the desired food by smell or sight). The authors predicted that the birds should preferentially inspect the side where the worms were cached, but not if they were cached 124 hours ago (and were now inedible); in these cases, they should preferentially inspect the peanut side. The results confirmed these predictions, suggesting that the birds recalled what food they had hidden where, and crucially, when they had hidden it. Clayton and Dickinson (1998) termed this recall of what-where-when information as episodic-like memory, due to meeting the content criteria of episodic memory, but lacking evidence of conscious recollection.

Although this study shows the impressive memory of scrub jays, subsequent reviews have cast doubt on whether the birds did indeed recall all three what-where-when details, or whether the birds could have used simpler strategies to recall the preferred food item. For instance, they may have learnt to recover the wax worms after the short retention period and avoid them after the long period, without recalling where the peanuts were. That is, they recalled and searched for wax worms after long time periods, but after short periods instead of recalling where the peanuts were, they simply recalled where the wax worms were and avoided those. In this instance, they need only recall where and when the wax worms were hidden, and not what was hidden (Livia de Hoz, personal communication, cited in Clayton, Yu, & Dickinson, 2001).

Additionally, rather than keeping track of what item was cached and when, the birds may have used familiarity to guide their behaviour; that is, when their memory of the location of wax worms was strong they recovered the wax worms, when it was weaker they instead recovered the peanuts. In this case, they need only remember what they hid

where, and not when (Hoffman, Beran, & Washburn, 2009; Suddendorf & Corballis, 2007). Furthermore, performance that is based on familiarity is not likely to be episodic in nature, due to dissociable differences between familiarity and episodic recall (Aggleton & Brown, 1999; Jacoby, Woloshyn, & Kelley, 1989). Rather, familiarity based performance reflects a more automatic and unintentional recognition response, compared to a response based on recollection (Jacoby, 1991).

Clayton and colleagues aimed to address some of these issues with a revised definition of episodic-like memory (Clayton, Buss, & Dickinson, 2003; Clayton, Yu, et al., 2001). The revision included the *integration* of what, where and when features (i.e., the storage of information as a single unit, rather than three individual features), and flexible deployment (i.e., using the information alongside previously stored knowledge in order to guide behaviour). To demonstrate this, they modified their original paradigm by introducing an additional perishable food; crickets. Both the worms and crickets were preferred to the peanuts, however, the worms degraded after 28 hours, and the crickets after 100 hours, whereas peanuts always remained fresh. The birds were given the opportunity to cache peanuts on one side of the sandbox, and either crickets or meal worms on the other side. In order to obtain the preferred food when it was still edible, the birds needed to remember three things: first, they needed to recall which side of the sand box they had cached the preferred food. Second, to recall when they had cached the food, and third, to recall whether they had cached worms or crickets. Only by recalling where they had hidden what, and when, could they determine the location and edibility of the cached food; results confirmed that the birds were successful at this (Clayton, Yu, et al., 2001). In a later experiment, the birds needed to update their memory of caching with new information post caching, in order

to avoid perished food. If the birds relied only on familiarity, they would search for a food item that had perished. This was not the case, showing that the birds don't simply use a rule based strategy to determine 'when' something occurred, and are able to flexibly update their behaviour (Clayton, Yu, & Dickinson, 2003).

However, Roberts et al. (2008) points out that often 'when' is confounded with 'how long ago'. That is, an animal may simply recall whether something occurred a long or short time ago, rather than at a specific time of day; a proposal which he demonstrated with rats. In his experiment, one group of rats completed study phases at a consistent time of day, and then completed tests after varying retention intervals. Another group had the test phases at a constant time of day, and study phases at different times to vary the retention interval. For rats in the 'when' group, food was available on trials that had a consistent study phase, thus the rats needed to recall when the study phase occurred. In the 'how long ago' group, it was available on trials with a consistent retention interval, thus rats did not need to recall when the study phase occurred, but rather how long had elapsed between study and test. The 'when' group were unsuccessful, but the 'how long ago' group were able to successfully learn the discrimination, suggesting that rats don't recall when food was encountered, but rather, how long ago. However, Zhou and Crystal (2009) did find that rats can make use of 'when' cues, as long as the 'how long ago cues' are irrelevant to the replenishment of food.

Other criticisms have been levied at the birds innate ability to cache and recall the location of food items, suggesting that episodic-like memory may appear only in species that have specific selection pressures (Dere et al., 2006). For instance, there are cases in which monkeys (Hampton, Hampstead, & Murray, 2005) and rats (Bird,

Roberts, Abroms, Kit, & Crupi, 2003) have failed to recall the ‘when’ component. As monkeys and rats don’t instinctively rely on food caches for survival, knowing when something was cached is not a naturally occurring ability in these animals. Similarly, Hampton et al. (2005) suggest that, “it may be that the birds expression of natural caching behaviour merely provides a particularly convenient “window” through which to see evidence of WWW memory” (p. 257). As such, it may that episodic-like memory is more likely to be observed in different species if we use paradigms that are more suited to their natural behaviours. Indeed, modified versions of this paradigm have found similar results in other bird species, (Jelbert et al., 2014; Zinkivskay, Nazir, & Smulders, 2009) rodents (Babb & Crystal, 2006b; Dere, Huston, & De Souza Silva, 2005b; Naqshbandi, Feeney, McKenzie, & Roberts, 2007), and primates (Hoffman et al., 2009; Martin-Ordas, Haun, Colmenares, & Call, 2010). For example, Babb and Crystal (2006b) showed that rats could recall that preferred food items (grapes and raspberries), as opposed to non-preferred chow, replenished after long but not short intervals. Moreover, the rats could adjust their behaviour when pre-fed (and subsequently satiated to one of the preferred flavours) by revisiting the non-satiated preferred flavour more than the satiated flavour. Additionally, when presented with a new, preferred food type (chocolate), they found that the rats updated their preference of chocolate over chow when they were injected with lithium chloride after eating chocolate (by reducing visits to the location where the chocolate was).

Evidence from bees also suggests that episodic-like memory may manifest itself in different ways, dependent upon the species (Pahl, Zhu, Pix, Tautz, & Zhang, 2007). Here bees learnt that a side of a maze with a specific colour and pattern (e.g., blue horizontal) was rewarded in the afternoon, whereas the other side (e.g., blue vertical)

was not. Another maze in another location was rewarded in the morning on one side (e.g., yellow vertical pattern), but not the other side (e.g., yellow horizontal pattern). The bees were able to successfully select the correct maze and side when the colour cue was removed, thus were able to use time of day to distinguish which pattern was rewarded where. Furthermore, when a novel maze was presented in a novel location, they used time of day to select the correct pattern and colour. The bees were thus proficient at encoding and recalling the 'when' component of episodic memory. The authors propose bees are efficient at using temporal information because they use circadian time to determine when nectar and pollen are at their highest levels. Such examples suggest that certain elements of the what-where-when paradigm may manifest themselves more naturally in animals that instinctively use this information.

Aside from these potential difficulties, a more fundamental criticism targets the validity of the what-where-when paradigm as a test for episodic-like memory. Specifically, this paradigm involves extensive training of a particular rule, and repeated testing of the same question (what is where, and when). Such a paradigm favours rule based learning and semantic encoding, as associations between items and locations are learned, and an expectation of being tested on the information occurs (Zentall, 2006). For example, if a bird experiences repeated tests about where, and when, worms were cached, the bird may learn to explicitly encode the details about when, and where, the worms were cached, and subsequently recall these details without recalling the specific episode of caching (i.e., recall of knowledge rather than recollection of an episode). Consequently, this paradigm may recruit semantic, rather than episodic, memory.

However, an adapted version of this paradigm has succeeded in avoiding the use of extensive training, by taking advantage of the innate preference for novelty

observed in rats (Kart-Teke, De Souza Silva, Huston, & Dere, 2006). Rats were first presented with four copies of an object, which were placed in four of eight possible locations. During a second presentation, the previous four objects were replaced with four new objects; two of these objects occupied places that the previous objects were in, the other two were placed in positions not previously used. At test, the rats were presented with two objects from the first presentation (old familiar), and two objects from the second presentation (recent familiar). One object from each type was located in the same position as was previously encountered (stationary objects), the other object was located in a different position (displaced objects). The authors predicted the rats would spend more time exploring the old familiar stationary object, compared to the recent familiar stationary object, and the displaced object, more than the stationary object of the same type. The results confirmed these findings (with the exception of the stationary old familiar object, which received more exploration time than the displaced old familiar object). The authors concluded that the rats integrated and recalled which object (what), was placed where, and how long ago (when). Other paradigms using the innate novelty preference of rats have also found evidence of the ability to integrate information (Eacott, Easton, & Zinkivskay, 2005; Eacott & Norman, 2004), suggesting that episodic-like memory can be evidenced in the absence of extensive training.

1.4.1.2 The unexpected question and single trial events

Episodic memories are often encoded without the subject's awareness, and without knowledge that the memory will be requested at a later time (Buckner, Wheeler, & Sheridan, 2001; Holland & Smulders, 2011). As previously explained, paradigms that use repeated test trials or exposures may lead to the expectation of a test, and result in

explicit, intentional encoding. That is, if one expects to be tested upon a previous experience, details of that experience may be encoded in a way that optimizes performance at test, such as categorizing the information in a specific way, or generating a planned action in advance. At recall, this information is then recalled in the absence of any recollective experience of the event, and often results in enhanced performance (Bransford & Johnson, 1972; Martin-Ordas, Atance, & Call, 2014). For example, when staying at a hotel, every morning at breakfast I am asked for my room number. The first time I am asked this question, I mentally travel back in time and recall entering my room and seeing the number written on the door (episodic recollection). However, after the second or third day of breakfast at the hotel, I come to expect to be asked for my room number, and intentionally encode the number so that I can later recall it in absence of any recollective experience. Intentional encoding is not only a problem for the episodic-like memory paradigm just described, but also for some human episodic memory tasks. For example, in the remember-know paradigm, the subject is often instructed to memorize the material and told that a memory test will follow.

The ‘unexpected question’, as termed by Zentall, Clement, Bhatt, and Allen (2001), avoids this potential problem by testing subjects when they have no expectation of being tested. Consequently, any information that is recalled at test is likely to have been encoded incidentally, and subsequently recalled through recollection. Zentall et al. (2001) put this unexpected question into practice using pigeons (see also Singer & Zentall, 2007). Here, pigeons were trained to peck or not to peck a particular pattern, and to then respond as to whether they had previously pecked or not pecked, by choosing a red or green light respectively. Next, the pigeons were taught to peck on

presentation of a yellow light, but not when presented with a blue light. Crucially, the two training regimes were never presented together. At test, the two training regimes were put into a novel manipulation. Here the pigeons were presented with a green and red light, after presentation of either a blue or yellow light; this was the first time these colours had been presented together in this way. If the pigeons could recall what they had just done (pecked or not pecked), they should respond appropriately to the question ‘what did you just do’, by selecting either the green or red light. The authors found this to be the case, and more importantly, that they could do so during the first four trials (in later trials, the test may have become expected). However, although this paradigm likely measured incidental encoding, the length of time between pecking or not pecking and answering the question ‘did you just peck?’ was a matter of seconds, and thus is more consistent with working memory than episodic memory.

With regards to longer retention intervals, numerous studies have shown that apes can recall details from single trials or limited exposures (Kano & Hirata, 2015; Martin-Ordas et al., 2013; Mendes & Call, 2014; Menzel, 1999; Schwartz, Colon, Sanchez, Rodriguez, & Evans, 2002), which are likely to be incidentally encoded due to minimal reinforcement and lack of opportunity for rule learning. Furthermore, other paradigms have modified Zentall et al. (2001)’s version of the unexpected question, to show recall of incidental information over longer time periods (Fugazza, Pogány, & Miklósi, 2016; Zhou, Hohmann, & Crystal, 2012). For instance, Zhou et al. (2012) first presented rats with a T-shaped maze, where they learnt to ‘report’ on whether they had been presented with food. They were rewarded for turning left if they had been given food, and for turning right if they had not. Thus, they learnt the rule, turn left if there was food, turn right if there was no food. To incorporate this rule based learning into an

unexpected question, the rats were presented with a 5-arm maze, in which they either found food or did not find food. They were then unexpectedly presented with the T-maze. They found that the rats were able to successfully report on whether they had found food in the 5-arm maze, even though they were not expecting to be tested on this information. Furthermore, they found that by temporally inactivating the rats' hippocampus, they failed to answer this unexpected question, but were able to answer an expected question using a similar task to the T-maze task learnt previously. The findings suggest that rats can unexpectedly recall events after incidental encoding, and furthermore, that this relies on the hippocampus; the area crucial to episodic memory, therefore providing both behavioural and anatomical evidence for prerequisites of episodic memory.

Interestingly, the unexpected question has also been found to predict episodic memory in humans (Holland & Smulders, 2011). Performance on a what-where-when paradigm was predicted by performance on an episodic memory task when the test was unexpected; yet, when the test was expected, performance only predicted the 'what' component. This suggests the importance of the unexpected question for the episodic-like (what-where-when) paradigm. However, other evidence suggests that unexpectedness may not be a crucial prerequisite for episodic memory. As stated previously, intentional encoding often results in better recall, as one is able to encode the information in a structured and meaningful (semantic) way, to plan subsequent behaviour for a later test. However, there are cases in which intentional encoding has no advantage over incidental encoding in episodic tasks, suggesting that semantic processing is not occurring. For instance, Shimamura and Squire (1987) tested recall of amnesiac and control subjects on a semantic and episodic memory task. Amnesiacs

performed poorly in both tasks, regardless of whether they were told about the impending test (intentional encoding), or not (incidental encoding). Likewise, controls showed no difference in performance as a function of encoding. Thus, intentional encoding did not improve performance on the episodic task, suggesting that episodic tasks don't always result in semantic encoding when intentional encoding takes place.

Additionally, it is unlikely that one trial learning (in which a test is unexpected), is neither sufficient, nor necessary, for episodic memory. There are cases in which one trial is enough to learn an association between a stimulus and response, such as taste aversion (Garcia, Kimeldorf, & Koelling, 1955). The subsequent behaviour of avoiding that stimulus in the future is not necessarily based on recollecting the specific experience with that stimulus, but is likely implicitly based (Morris, 2001). As such, although the unexpected question may avoid the possibility of semantic encoding in episodic tasks, it is not a definitive approach to the question of whether animals have episodic memory.

1.4.1.3 *Free recall*

Another proposed prerequisite of episodic memory is free recall; that is, episodic memories are recalled in the absence of cues (Tulving, 1983). In the human literature, participants are often instructed to freely recall items from a list, or describe a past event in the absence of cues. In animals, such instructions cannot be given, and thus paradigms often use recognition tasks, or provide external cues as prompts. As such, cases of free recall in animals is uncommon. An early anecdotal example of free recall in a chimpanzee was described by Menzel (1973). Here, a chimpanzee watched as food

was hidden in various locations. The chimpanzee was then later tested on the route he took to retrieve the hidden food. Menzel (1973) reported that:

[O]n several trials, a striking example of sudden recall occurred while an animal was apparently asleep. After having eaten many pieces of food and lain supine with his eyes closed for up to 30 minutes, the test animal suddenly jumped to his feet and ran 10 to 30 m straight to a hidden piece of food (Menzel, 1973, p. 944).

In terms of direct evidence, a chimpanzee named Panzee was also able to recall the locations of various hidden food items without any prompts (Menzel, 1999). Panzee is able to use lexigram symbols to communicate about numerous foods, tools, locations and actions, meaning that she is able to communicate about where a particular food item has been hidden. In this experiment, Panzee watched as an experimenter hid food items in various locations in an area outside her enclosure (Panzee did not have access to these locations). After a delay, which varied from minutes to an overnight duration, the test phase began. During this phase, an uninformed person (someone that had not seen the food being hidden) was in the vicinity of Panzee; this person went about his daily routine, and did not initiate any interactions with Panzee. The authors found that Panzee spontaneously recruited and communicated with the uninformed person (using lexigrams, gestures, gazing and vocalisations) about what food was hidden where. For instance, Panzee pointed and gazed towards an object, and her vocalisations became more intense as the person got closer to the object. Thus, Panzee spontaneously, and without cues, recalled the locations of items that had been hidden.

Although the memory Panzee shows is extremely impressive, there are again concerns that the memory is not necessarily episodic. Panzee sees food being hidden that presumably she wishes to obtain, as such she may rehearse the locations and types of food until an opportunity presents itself to retrieve it. Thus, the study is subject to the same issue in which information may be encoded semantically in anticipation of later recall. Moreover, the notion that free recall is necessary in episodic memory is also debatable. It is likely that the recall of all explicit memories involves some type of cue, whether it be an external cue from the current environment, or an internally generated cue, such as an emotion (see Pause et al., 2013). For instance, involuntary episodic memories are often triggered by current external cues that share some similarity to the stored memory (see page 59 for details regarding involuntary episodic memories). If episodic memories are not triggered by a cue, then their retrieval would be uncontrolled and highly disturbing (Berntsen, 2009). As such, tests that are ‘absent’ of cues are not necessary, nor sufficient, to test for prerequisites of episodic memory.

1.4.1.4 *Temporal order*

When we remember an event, we recall the details in a temporally organised structure. For example, when recollecting what I ate for breakfast, I remember opening the fridge to find no milk, and deciding instead to have toast for breakfast, and subsequently putting bread into the toaster. Thus, when I recall this event, I recall what happened in chronological order. Additionally, we often recall multiple events within a temporally organised structure, for example, I remember that I watched the finish of the first stage of the Tour de France in my home town, the day before I moved to Leipzig. This ability to recall the temporal order of an event, and order events in time, is thought to be a

crucial feature of episodic memory (Roberts, 2002), and is one of the key features that distinguishes episodic from semantic memory (Tulving, 1983).

There is evidence to suggest that rats (Allen, Morris, Mattfeld, Stark, & Fortin, 2014; Ergorul & Eichenbaum, 2004; Fortin, Agster, & Eichenbaum, 2002) and primates (Schwartz, Hoffman, & Evans, 2005) can recall the temporal order of an event. Fortin et al. (2002) presented rats with a series of five odour cups. The odour cups were presented sequentially, and contained a reward buried in sand that the rat had to dig through to obtain. After a delay of three minutes, the rats were presented with two odour cups from the series of five, and were rewarded for choosing the odour that had appeared earliest in the series. The rats successfully learnt to select the cup that appeared earliest, but failed to do so after hippocampal lesions. On a recognition task, hippocampal lesions did not impair performance, indicating that rats' ability to recall temporal order is dependent upon the hippocampus.

Similarly, Schwartz et al. (2005) tested a gorilla named King on his ability to recall the order in which he received specific food items. Here King was given three food items, one at a time. After five minutes, he was presented with five cards depicting food; three of the cards depicted the three foods he had just eaten (in a previous task King had been trained to give the card that represented the food; Schwartz et al., 2002). In order to receive a food reward, King had to exchange the food items in the reverse order in which he had been given them (the order was in reverse due to King always responding with the most recent item during pilot testing). The authors found that King was above chance at recalling all three foods in the correct order, suggesting that he recalled which food he had eaten, and in which order.

Although these paradigms suggest that rats and apes can recall the temporal order of a past event, they are subject to similar criticisms as the what-where-when paradigm. For instance, due to repeated testing and reinforcement for a correct response, the subjects may have learnt over time to encode information about order, and subsequently not needed to recollect the actual events to perform correctly. Additionally, King's preference for returning the most recent food item first may be due to a familiarity based response; that is, he had a preference for returning the most recent item first, which was also the most familiar. Moreover, the necessity of temporal order in episodic memory has been questioned, due to research that suggests events are often not time 'stamped' and represented along a linear time scale. Rather, memory for when an event occurred is more inferential, and judged by references and links to other stored memories (see Friedman, 1993; Friedman, 2007). Indeed, Eacott and Norman (2004) propose that the temporal element of episodic memory can be considered as an occasion marker that distinguishes one episode from another, and that an occasion marker can be represented by aspects other than time, such as the context and environment in which an episode takes place. This idea is at the forefront of the final paradigm I will cover; contextual binding.

1.4.1.5 Contextual Binding

Binding is an essential characteristic of episodic memory (Chalfonte & Johnson, 1996; Moscovitch, 1994; Raj & Bell, 2010). Impairments in episodic memory, such as source memory failure, can result from difficulties with binding stimuli or reconstructing the bound information at retrieval (Schacter & Addis, 2007; Schacter, Norman, & Koutstaal, 1998). Information that is bound together can act as a distinct, unique cue at

retrieval, distinguishing memories that share many of the same features from one another. For instance, my office, my colleague and my collection of English tea may be associated with many individual, separate memories, but the combination of all three of these features is associated with only one memory; the memory of my colleague asking me for recommendations for tea whilst we were both working in the office. Thus, presentation of these features is likely to result in recollection of that particular episode, as opposed to a different episode involving my colleague in the office.

As mentioned previously, Clayton, Buss, et al. (2003)'s revised definition of episodic-like memory required that what-where-when information be recalled in an integrated unit, and not as individual, separate pieces of information. However, given that time may not be such a crucial component for episodic retrieval (Friedman, 2007), alternative approaches have looked at the binding of contextual information as a prerequisite for episodic memory (Eacott et al., 2005). Rubin and Umanath (2015) recently proposed an alternative conceptualization of episodic memory based on this, named as event memory. Event memory is defined as “the mental construction of a scene, real or imagined, for the past or the future” (Rubin & Umanath, 2015, p.1). Scene construction refers to the mental generation of a scene or event, which is achieved by binding multiple pieces of information into a coherent and spatially organized representation (Hassabis & Maguire, 2007; Lind, Williams, Bowler, & Peel, 2014; Raffard, D'Argembeau, Bayard, Boulenger, & Van der Linden, 2010; Rubin & Umanath, 2015). Event memory removes some of the restrictive criteria imposed by the consciousness based conception of episodic memory, and instead focuses on binding of contextual features as the core requirement for recall of an event (see also Hupbach,

Hardt, Gomez, & Nadel, 2008, who propose that context provides the scaffold to which episodic memories are bound).

Rodents, birds, and primates can successfully bind contextual features to distinguish between events that share many of the same features (Clayton, Yu, et al., 2001; Crystal & Smith, 2014; Eacott & Norman, 2004; Kart-Teke et al., 2006; Martin-Ordas et al., 2013). For example, Eacott et al. (2005) showed that rats can bind the location of a preferred (novel) object to a specific contextual background. Rats were habituated to two different mazes, one smooth black maze and one wire mesh maze. From the start of each maze, two different objects could be seen; one to the left and one to the right. The position of the objects was switched between contexts (e.g., in the black maze object A was on the left and object B on the right, in the wire maze object B was on the left and A on the right.) The rats received two exposures with each maze, so that they could learn that the location of the objects within a context stayed the same within a day, and received daily trial-unique objects. In the next stage, the rats were habituated to one of the objects, resulting in one object being novel in comparison to the other (as rats have a novelty preference, they preferentially explore novel objects). During test phases, the objects were not visible from the starting position; thus, in order to locate the novel item, the rats needed to recall in which context the novel item was located. The authors found the rats successfully located the novel object.

Similarly, a clever study by Crystal and Smith (2014) looked at binding of multiple features in context, using trial-unique baiting locations. They developed a paradigm in which rats could only distinguish between two similar episodes by binding the information from each unique episode into a unique unit. The events contained multiple pieces of information, such as what food (chocolate or chow) was where in the

maze, what the source of the food was (human or self-generated) and what the room looked like (context). After a delay, the chocolate was replenished at the location in which it was self-generated, but not where it was human generated. None of the chow locations replenished. Crucially, the baiting locations differed between the two episodes, with one episode occurring in room A and the other in room B. Thus, the two episodes shared many overlapping features, but were distinguishable by their context. In order for the rats to successfully retrieve the chocolate, they needed to recall the features within the context (i.e., to bind multiple features together). The authors found that the rats were able to do this, as evidenced by visiting the replenished locations more than the non-replenish, and the chow.

Additionally, they provided further support for the bound hypothesis by manipulating the similarity and difference between the baiting configurations in the two episodes. If the rats used un-bound features, performance should be better when the two baiting configurations are the same, compared to when they are different, as the food location is the same for both episodes. Whereas, when the baiting configuration is different, recalling features in the absence of context may result in the wrong configuration being recalled. In contrast, if the features are bound to context, the configuration of the baiting should have no difference on performance. The results confirmed the later predictions; that is, the rats' performance did not differ as a function of the baiting configuration.

Binding has also been evidenced in orangutans and chimpanzees (Martin-Ordas et al., 2013). Here, apes witnessed two similar events, in which a tool was hidden that was required to obtain food from a piece of apparatus. Many of the features from the two events overlapped, such as the experimenter that was present, the room, and the use

of a tool task. At test, in order to remember which tool was hidden where, the apes needed to bind the relevant contextual features together in order to create a cue that was unique, and diagnostic of one of the hiding events. If the cues were not integrated into this unique cue, it would not be possible to distinguish one event from the other (or indeed, other similar events with the same experimenter, room, and tool task), due to the high degree of overlapping contextual features.

Although such studies show evidence of binding in animals, they too are associated with many of the issues discussed above, such as the use of extensive training and repeated testing, and thus may also be indicative of semantic memory, as opposed to episodic memory.

1.4.1.6 Other paradigms

The paradigms presented above are not an exhaustive list of the ways in which elements of episodic memory have been tested; rather, they represent an overview of the vast and varied research conducted in this field. For instance, there is a large branch of research that focuses on the ability to use past events to guide and plan future behaviour, referred to as episodic foresight or future mental time travel (see Suddendorf & Corballis, 2010; Zentall, 2006). Similarly, there is much research regarding metamemory. Metamemory refers to the cognitive monitoring of one's own memory, and is useful in distinguishing between explicit and implicit memory (as implicit memories cannot be monitored due to the lack of awareness of such memories). As such, evidence that animals can monitor their own memory, such as by avoiding a test when they do not know the correct response (e.g. Hampton, 2001), implies that they have explicit memories; an important prerequisite for episodic memory. Taken

together, the vast amount of research investigating various aspects of episodic memory provides compelling evidence for at least some form of episodic remembering in animals.

Table 1.1 An overview of research investigating elements of episodic memory in animals. Studies are grouped by the type of paradigm used, the species tested, and the findings. Superscript letters represent limitations of the study (see below).

Paradigm	Species	Confirmatory findings	Non-supportive findings
<i>What-where-when</i>	Primates	^{a,d} Hoffman et al. (2009) ^{a,b} Martin-Ordas et al. (2010)	^a Dekleva, Dufour, de Vries, Spruijt, and Sterck (2011) - failed to recall what, where and when, and instead used an association based strategy. ^a Hampton et al. (2005) – failed to recall when.
	Rodents	^a Babb and Crystal (2006a) ^a Babb and Crystal (2005) ^b Dere, Huston, and De Souza Silva (2005a) ^{a *} Ergorul and Eichenbaum (2004) ^a Ferkin, Combs, Pierce, and Franklin (2008) ^b Kart-Teke et al. (2006) ^{a,b} Naqshbandi et al. (2007) ^a Veyrac et al. (2015) Fellini and Morellini (2013)	^a Bird et al. (2003) – failed to recall when.

<i>Unexpected question and single trial events</i>	Birds	a,b Clayton and Dickinson (1998) a,b Clayton, Yu, et al. (2001) a Clayton, Yu, et al. (2003) a,b Zinkivskay et al. (2009) a,b Feeney, Roberts, and Sherry (2009)	a, d Skov-Rakette, Miller, and Shettleworth (2006) - individual, but not integrated, recall of what, where, when.
	Other	Bees: ^{a,c} Pahl et al. (2007) Cuttlefish: ^{a,b} Jozet-Alves, Bertin, and Clayton (2013)	
	Primates	a,b Schwartz et al. (2002) a,b Schwartz, Meissner, Hoffman, Evans, and Frazier (2004) ^e MacDonald (1994)	
	Rodents	Zhou et al. (2012)	
	Birds	d,e Singer and Zentall (2007) d,e Zentall et al. (2001)	
<i>Free recall Temporal order</i>	Other	Dogs: ^e Fugazza et al. (2016)	
	Primates	Menzel (1999)	
	Primates	^b Schwartz et al. (2005)	
	Rodents	a,d Allen et al. (2014) ^a Fortin et al. (2002)	a,c Roberts and Roberts (2002) – Failed to use sequence or time to retrieve a large food reward.
<i>Contextual Binding</i>	Primates	Martin-Ordas et al. (2013) ^e Mendes and Call (2014)	
	Rodents	^a Eacott et al. (2005) a,b Eacott and Norman (2004) ^a Crystal and Smith (2014)	

Birds	a,c Jelbert et al. (2014)	
Other	Pigs: ^b Kouwenberg, Walsh, Morgan, and Martin (2009) Zebrafish: ^b Hamilton et al. (2016)	

^a Extensive training with test material and or/ multiple test trials may lead to rule learning or semantic encoding in anticipation of a test.

^b Familiarity/memory trace strength may guide performance.

^c Not tested on a trial unique event/ single study episode, thus likely to be general memory not a unique episodic memory.

^d Delays of only seconds, thus likely to be working memory not episodic memory.

^e Does not explicitly test for integration/binding of features.

* Although it's possible the rats used familiarity of the odour to guide performance, removal of the hippocampus lead to poor performance in trials in which spatial and odour cues were provided, but good performance when only odour cues were present. This suggests that spatial and odour trials relied on integration of what-where-when, and odour trials on familiarity.

1.5 Aims and objectives

In order to better understand our own memory systems, it is important to establish the differences and similarities between human and animal memory. Although much can be learnt by studying developmental changes within humans (i.e., comparing children and adults), a comparative approach allows us to discover what may be unique to us as humans, and what is shared among species.

In this thesis, I aim to investigate the similarities and differences between human and great ape episodic memory. Great apes are our closet living relatives, whom we share many complex cognitive abilities with, and thus likely have the potential for episodic remembering (that is not to say that other distantly related species do not). Although there are numerous insightful studies that have shown elements of episodic memory in a variety of species, including apes, there is still controversy as to whether animals have episodic memory, in part due to the limitations of the paradigms. For example, Suddendorf and Busby (2003) have argued that even if animals can show integrated recall of what, where, and when information from a single event, it does not necessitate that they recollect the event in order to recall this information. They point out that although you may know where, when, and what happened at your birth, you do not remember the event. Similarly, you can recollect an event without being able to recall accurately when it was. Likewise, Klein (2013) argues that the content criteria of episodic memory is not indicative of episodic memory, but rather it is shared with semantic memory. Additionally, he advocates additional criteria necessary for episodic memory, termed ‘enabling systems’. Such critiques ultimately lead back to the problem of being unable to assess whether an animal consciously recollects an event, resulting in the possibility that recalled information is simply known, and not recollected.

In addition to the inability to demonstrate the phenomenological components of episodic memory in animals, the many behavioural criteria imposed upon animal research has led to an unworkable definition of episodic memory. This is in contrast to the testing of episodic memory in humans, in which, “[i]f one applies all the behavioural and phenomenological criteria that have been put forward for animal studies to current human studies, these unfortunately fall short of measuring episodic memory” (Dere et al., 2006, p1221).

Consequently, episodic memory research in animals has reached somewhat of an impasse, whereby the definition of the phenomenon has limited progression and understanding of the similarities and differences between the way humans and animals recall past events (Basile, 2015; Templer & Hampton, 2013). For instance, Shettleworth (2007) observes that searching for a definitive answer as to whether an animal shares a particular cognitive ability with humans, removes the focus from investigating what elements of a cognitive ability we may, or may not, share with other species. I therefore aim to make progress in understanding what elements of episodic memory we may share with great apes. To achieve this, I focus less on demonstrating the mass of criteria proposed as evidence for episodic memory in animals (e.g., showing flexible integration of what happened, when, and where, after a single exposure, with no training, when the test was unexpected etc.), and instead investigate new avenues and under-explored areas relating to the recall of past events, that focus on just a single element of episodic memory. Investigating additional and under-explored aspects of episodic memory is a near impossible task if one is expected to meet all the criteria proposed so far. As a result, the research in this thesis is not unique in that it is free of the criticisms levelled at episodic research in animals (as described previously).

On the contrary, the research conforms less to the definitions provided by Tulving (1972, 1984) and others, and is thus open to many potential critiques. Yet, it advances our understanding of the similarities and differences between human and animal memory for past events by focusing on elements we know little about, as opposed to fulfilling an almost exhaustive list of criteria.

Currently, evidence suggests that numerous species are capable of recalling what happened where, with some species also recalling when something happened, or in which context. We have also seen that some species can recall this information unexpectedly, or after a single exposure, and can recall the temporal order, or sequence of an event (see Table 1.1). Despite the diversity in approaches to studying episodic memory in animals, many of the paradigms do not go beyond providing evidence for the content criteria of episodic memory, as defined by Tulving (1972). Conversely, when looking to the human literature, much more is investigated beyond the content of episodic memory. For instance, we know that episodic memories are influenced by emotion and significance (Brown & Kulik, 1977; Hirst, 2016; Kensinger, 2009), are highly fallible to error (Hyman, Husband, & Billings, 1995; Loftus & Palmer, 1996), and are more vulnerable to disease and normal ageing than other types of memory (Greene et al., 1996; Nilsson et al., 1997; Weingartner et al., 1983). As such, I aim to investigate whether great ape's memories of past events are subject to similar phenomena. I describe the phenomena to be investigated, and the specific aims of the three experimental chapters (Chapters 3-5) below. Chapter 2 describes the general methods of the experimental chapters.

1.5.1 The distinctiveness effect.

The distinctiveness effect refers to the general memory enhancement of unusual information compared to common information. von Restorff (1933) most famously demonstrated the effect using an isolation paradigm. She showed, across a series of experiments, that an item that is different in respect to a series of similar items is remembered better than the other items. For instance, in a list of colours, any non-colour will be recalled better than any colour (e.g., house will be recalled better than yellow). The distinctiveness effect is dependent upon context; that is, the extent to which something is distinctive is directly related to its context, and is not a property of a stimulus itself. For example, in a list of colours, the word house is distinctive, but in list of buildings it is not. Distinctiveness effects can occur when stimuli are distinctive in comparison to the immediate context (primary distinctiveness), or distinctive in comparison to information stored in memory (secondary distinctiveness; Eysenck, 1979; Schmidt, 1991).

In terms of the mechanisms of the distinctiveness effect, there are multiple proposals. Most focus on encoding, such as distinctive stimuli receiving more rehearsal (Rundus, 1971) and greater attention (Jenkins & Postman, 1948) than non-distinct items (for an in-depth review of the distinctiveness effect and proposed mechanisms see Hunt & Worthen, 2006). Encoding proposals lead to the assumption that distinct items should receive more processing time, and consequently that divided attention should show a reduction in distinctiveness effects; however evidence of this is mixed (McDaniel & Geraci, 2006).

An alternative approach to the distinctiveness effect proposes that distinctiveness is the result of processing both similarity and difference, rather than an independent variable describing a stimulus in a certain context (Hunt, 2006; Hunt & McDaniel, 1993). At encoding, two types of processing occur: relational processing and item-specific processing⁷. Relational processing is the processing of commonalities between all stimuli, leading to stimuli being organised in a related structure, and results in the retrieval of one item aiding the retrieval of other items. Item-specific processing is the processing of features that are unique to individual stimuli, and not shared with any of the other stimuli. This means that items are not processed in an organised structure, but are processed in terms of individual discriminability. Distinctiveness occurs when both processing occurs together; the processing of common features between items provides a context in which the unique features of an item ‘stands out’. Hunt and McDaniel state that, “[t]he significance of the two processes is manifested at retrieval. The combination of relational and distinctive processing provides high diagnostic value for unique convergence on a particular item” (Hunt & McDaniel, 1993, p. 429). As such, distinctiveness is proposed to be a result of encoding both the commonalities between items, and the uniqueness of an item, resulting in highly diagnostic information pertaining to a specific item (see also McDaniel & Geraci, 2006).

The distinctiveness effect is not confined to isolation paradigms that involve the recall of lists and similar ecologically limited material, but occurs in a variety of contexts, such as face recognition (Valentine & Bruce, 1986) and the recall of past

⁷ Relational processing and item-specific processing were first proposed as a model for recognition memory by Humphreys (1976).

events, often referred to as ‘flashbulb memories’ (Brown & Kulik, 1977; however see Schmidt, 2007 for a caution on interpreting distinctiveness and emotion/significance). The distinctiveness effect also has important implications for involuntary memory (discussed in the next section), as cue discriminability is key to the retrieval of such memories (Staugaard & Berntsen, 2014).

In terms of animal research, the distinctiveness effect has received little attention, but has been evidenced in primates and rats, predominantly in isolation paradigms. For instance, rats show enhanced recall of a food location in a maze when one of the locations is accompanied by a distinctive feature (e.g., a tone; Reed & Richards, 1996), or by a unique visual context (McLaughlin, Cicala, & Pierson, 1968). In a matching to sample task, monkeys show less recognition errors when the target is an isolate from a previously seen list, as opposed to when the target is a homogenous item from the previously seen list (Parker, Wilding, & Akerman, 1998). A similar effect is also seen in chimpanzees, using category (rather than colour) as the context in which items are homogenous or isolated (Beran, 2011). Regarding past events, there is some evidence that primates remember distinctive events well, however, such studies lack a control comparison (Kano & Hirata, 2015; Martin-Ordas et al., 2013). Chapter 3, therefore, investigates whether great apes are more successful at recalling where an item of food was hidden during an event, when elements of the event are distinctive, as opposed to non-distinct. As such, the chapter focuses on the binding criterion of episodic memory, investigating the recall of ‘where’ information within a distinctive or non-distinctive context, in the absence of training.

1.5.2 Involuntary memory

Previously, I described the difference between declarative and non-declarative memory as one of consciousness; that is, non-declarative memories are unconscious, recalled without awareness, and expressed through behavior and performance. In contrast, declarative memories are conscious and explicitly expressed. Although this is true, it is also true that conscious memories can be further divided into two types of memory: voluntary and involuntary (Berntsen, 1996; Ebbinghaus, 1885, 1964). Voluntary memories are memories that are deliberately and intentionally brought to mind, usually for some purpose or goal. Conway (2005) refers to this goal-directed search process as generative retrieval. For instance, when trying to remember where I left my keys, I recall the sequence of events leading up to when I last had them. Conversely, involuntary memories occur spontaneously, (i.e., without any previous attempts at retrieval), and are non-goal directed, a process referred to as direct retrieval (Conway, 2005). One of the most famous examples of an involuntary memory comes from Proust (1981), who described the taste of madeleine dipped in lime tea eliciting his childhood memory of visiting his aunt on Sunday mornings:

And once I had recognized the taste of the crumb of madeleine soaked in her decoration of lime-flowers which my aunt used to give me . . . immediately the old grey house upon the street, where her room was, rose up like the scenery of a theatre (Proust, 2006, p. 63).

Involuntary memories have largely been overlooked when it comes to memory research (Berntsen, 1996; Rubin, Boals, & Berntsen, 2008), and have typically received

attention in clinical settings, such as their occurrence as flashbacks of events after severe trauma (Berntsen, 2001; Rubin et al., 2008). However, more recently, autobiographical⁸ research has shown that involuntary memories are not limited to negative experiences, but that they are also often positive (Berntsen, 2001; Berntsen & Rubin, 2002). Furthermore, they occur regularly in our day to day lives, occurring at least as frequently, if not more, than voluntary memories (Rubin & Berntsen, 2009).

Involuntary memories are often triggered by external cues that share unique features with the present situation and the remembered event (see Berntsen, 2009; Rasmussen & Berntsen, 2009). In terms of successful retrieval, it is not the extent to which the cues overlap, but rather the uniqueness of the overlap that is important (Nairne, 2002). If many of the features occur in many other memories, it is unlikely they will lead to the spontaneous recall of a specific memory; however, if the constellation of cues is unique to a specific memory, recall is likely (i.e., recall is related to the extent to which the cue is diagnostic of a specific memory). Thus, involuntary memory has direct links to the encoding specificity, cue-overload and distinctiveness - external features that are present at the time of encoding and retrieval (encoding specificity), that are unique to one event (un-overloaded), act as highly diagnostic cues that will likely lead to spontaneous recall of a specific event. The more distinctive the event, the more unique the cues will be.

As involuntary memories are retrieved associatively, they are often retrieved much faster than voluntary memories (Berntsen, Staugaard, & Sorensen, 2013;

⁸ Autobiographical memory is a system containing episodes and knowledge pertaining to oneself. Information is structured according to three main levels of specificity: life time periods, general events and specific (episodic) events (Williams, Conway, & Cohen, 2008).

Schlagman & Kvavilashvili, 2008), and do not rely heavily on executive control processes or recruit pre-frontal brain regions as much as voluntary memories (Hall, Gjedde, & Kusters, 2008; Hall et al., 2014). Consequently, they are considered to be a basic mode of remembering that precedes the evolutionary development of voluntary memory (Berntsen, 2010; Rasmussen & Berntsen, 2009). Recently, it has been proposed that animals may also recall past events through this involuntary mode (Berntsen, 2010; Berntsen & Jacobsen, 2008; Clayton, Bussey, Emery, & Dickinson, 2003; Rasmussen & Berntsen, 2009); yet, there is only limited evidence of this to date (e.g., Martin-Ordas et al., 2013). Chapter 4, therefore, aims to investigate whether apes can spontaneously recall a distinctive past event, when presented with features that are diagnostic of the event. Chapter 4 also draws upon the distinctiveness effect from Chapter 3, by comparing the recall of an event that is highly distinctive, to one that is less distinctive. In terms of episodic memory criteria, this chapter presents the apes with a unique, one-time event, and therefore fulfils the unexpected question prerequisite of episodic memory.

1.5.3 Binding of social information

Research into binding in animal episodic memory has generally comprised of the integrated recall of what, where, when, or which (context) features. The ‘what’ element has generally focused upon food, such as what food was cached or found in a particular location. Food is particularly salient to animals (and humans), due to the reliance on it as an energy source. Likewise, spatial (where) and contextual (which) information may be particularly salient due to the need to remember in which environments, and which locations in those environments, food and resources are located. Indeed, evidence

suggests that primates are adept at mapping information in their environment to recall the location of food (Janmaat et al., 2013; Normand, Ban, & Boesch, 2009; Noser & Byrne, 2007). For instance, a study by Menzel (1999) showed that a chimpanzee (Panzee) could recall the hiding location of numerous food items. Panzee successfully recalled each of the hiding locations with great accuracy, and additionally which item was hidden in each location, showing evidence of binding the ‘what’ and ‘where’ features into memory. Consequently, it may be that such information is encoded effortlessly, or is easily bound to information in memory.

The extent to which primates can bind and recall information other than what, where, when, and which, is largely unknown. In human memory, when recalling a past event we often remember who was present, or a particular social interaction. Moreover, people are often identified as triggers of involuntary memories of past events (Berntsen, 1996; Berntsen & Hall, 2004), suggesting that social information is a prominent feature in episodic memory. Regarding animals, it has been suggested that episodic memory is particularly important for the processing and use of social information, enabling individuals to remember past cooperative or hostile interactions (Cheney, Seyfarth, & Smuts, 1986). Despite this, very few studies have tested the ability of animals to encode and recall social information embedded in past events. As such, Chapter 5 aims to address the lack of research into binding and social information, by assessing whether apes can learn to bind an item (what), with a person (who), and later recall this.

Chapter 2 | General methods

Here I describe the general methods used throughout the experimental chapters (Chapters 3-4). First, I introduce the Wolfgang Köhler Primate Research Centre (WKPRC), in Leipzig, Germany, and the apes that are housed there. I then provide an overview of the testing facilities, general testing procedure, sampling method, data collection and analyses. Specific methodological details for each experiment can be found in their respective chapters.

2.1 Research centre and apes

The WKRPC is a project of the Max Planck Institute for Evolutionary Anthropology (MPI-EVA), in collaboration with the Leipzig zoo. The focus of research is on the behaviour and cognition of the four great ape species: chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*), orangutans (*Pongo pygmaeus*), and bonobos (*Pan paniscus*). All research is strictly non-invasive, and visitors to the zoo can also observe testing take place in specially designed observation rooms.

During my period of testing (October 2014 - September 2017), the WKRPC housed fifty-four apes (see Table 2.1): thirty chimpanzees (9 male), eleven bonobos (6 male), five gorillas (1 male), and eight orangutans (3 male). The majority of these chimpanzees are the Western chimpanzee subspecies (*Pan troglodytes versus*), with the others being Western and Eastern chimpanzee hybrids (*Pan troglodytes versus/schweinfurthii*). The gorillas are all Western lowland gorillas (*gorilla gorilla gorilla*), and the orangutans are Sumatran (*Pongo pygmaeus abelii*). The apes are socially housed within their own species, with the chimpanzees housed in two separate groups; the A-chimpanzees consist of twenty-one individuals (8 male), and the B-

chimpanzees consist of nine individuals (1 male). Each species has access to its own indoor and outdoor enclosure, as well as separate sleeping rooms. The age of the apes ranges from under one year, to fifty-one years of age, and the majority were reared by their parents, with some hand-reared. Although the population was fairly stable during my three-year testing period, some changes occurred due to births and transfers to/from other zoos.

Table 2.1 Demographics of the Leipzig zoo ape population. Ages are shown in years and are calculated from birth to present day (present day at the time of calculation was the 01.01.2017). Participation indicates which experimental chapters the apes participated in.

Name	Sex	Species	Age	Birth place	Rearing history	Duration in Leipzig	Participation (chapter no.)
Tayo	M	Bonobo (<i>Pan paniscus</i>)	0	Leipzig	Parent	Birth - present day	None
Yaro	M	Bonobo (<i>Pan paniscus</i>)	3	Leipzig	Parent	Birth - present day	None
Kasai	M	Bonobo (<i>Pan paniscus</i>)	4	Leipzig	Parent	Birth - present day	None
Fimi	F	Bonobo (<i>Pan paniscus</i>)	8	Leipzig	Parent	Birth - present day	3-5
Gemena	F	Bonobo (<i>Pan paniscus</i>)	11	Twycross Zoo, GB	Parent	15/05/2013 - present day	3-5
Luiza	F	Bonobo (<i>Pan paniscus</i>)	11	Leipzig	Parent	Birth - present day	3-5
Lexi	F	Bonobo (<i>Pan paniscus</i>)	17	Jacksonville	Hand-reared	22/05/2012 - present day	3-5
Yasa	F	Bonobo (<i>Pan paniscus</i>)	19	Twycross Zoo, GB	Parent	26/05/2004 - present day	3-5
Kuno	M	Bonobo (<i>Pan paniscus</i>)	20	Wilhelma Zoo (Stuttgart)	Hand-reared	08/03/2001 - present day	3-5
Jasongo	M	Bonobo (<i>Pan paniscus</i>)	26	Wuppertal	Parent	24/05/2011 - present day	3-5
Joey	M	Bonobo (<i>Pan paniscus</i>)	34	Royal Zool. Society of Antwerp	Hand-reared	05/03/2001 - present day	3
Ohini	M	Chimpanzee (<i>Pan troglodytes verus</i>)	0	Leipzig	Parent	Birth - present day	None

Azibo	M	Chimpanzee (<i>Pan troglodytes verus</i>)	1	Leipzig	Parent	Birth to present day	None
Bangolo	M	Chimpanzee (<i>Pan troglodytes verus</i>)	7	Leipzig	Parent	Birth to present day	3-5
Kara	F	Chimpanzee (<i>Pan troglodytes verus</i>)	11	Leipzig	Parent	Birth - 24/02/2016	3,4
Kofi	M	Chimpanzee (<i>Pan troglodytes verus</i>)	11	Leipzig	Parent	Birth - present day	3-5
Kisha	F	Chimpanzee (<i>Pan troglodytes verus</i>)	12	Osnabrück	Parent	19/09/2013–present day	3
Lobo	M	Chimpanzee (<i>Pan troglodytes verus</i>)	12	Leipzig	Parent	Birth - present day	3-5
Tai	F	Chimpanzee (<i>Pan troglodytes verus-schweinfurthii hybrid</i>)	14	Leipzig	Parent	Birth - present day	3-5
Lome	M	Chimpanzee (<i>Pan troglodytes verus</i>)	15	Leipzig	Parent	Birth - present day	3-5
Bambari	F	Chimpanzee (<i>Pan troglodytes verus</i>)	16	Ostrava	Parent	03/02/2016 - present day	3
Swela	F	Chimpanzee (<i>Pan troglodytes verus</i>)	21	Basel	Parent	15/03/2005–present day	3,4
Sandra	F	Chimpanzee (<i>Pan troglodytes verus-schweinfurthii hybrid</i>)	23	Rijswijk	Parent	28/02/2001–present day	3,4
Frodo	M	Chimpanzee (<i>Pan troglodytes verus</i>)	23	Rijswijk	Parent	28/02/2001–present day	3-5
Maja	F	Chimpanzee (<i>Pan troglodytes verus-schweinfurthii hybrid</i>)	30	Hannover	Parent	03/02/2016–present day	None
Natascha	F	Chimpanzee (<i>Pan troglodytes verus</i>)	36	Rijswijk	Hand-reared	28/02/2001–present day	3,4
Dorien	F	Chimpanzee (<i>Pan troglodytes verus</i>)	36	Rijswijk	Hand-reared	28/02/2001–present day	3-5
Ulla	F	Chimpanzee (<i>Pan troglodytes verus</i>)	39	Rijswijk	Hand-reared	28/02/2001 – 24/02/2016	3,4
Riet	F	Chimpanzee (<i>Pan troglodytes verus-schweinfurthii hybrid</i>)	39	Rijswijk	Hand-reared	28/02/2001–present day	3,4
Corrie	F	Chimpanzee (<i>Pan troglodytes verus</i>)	40	Rijswijk	Hand-reared	28/02/2001 – present day	3,4

<i>Fraukje</i>	F	Chimpanzee (<i>Pan troglodytes verus</i>)	40	Rijswijk	Hand-reared	28/02/2001– present day	3-5
<i>Robert</i>	M	Chimpanzee (<i>Pan troglodytes verus</i>)	41	Rijswijk	Hand-reared	28/02/2001– present day	3,4
<i>Alex*</i>	M	Chimpanzee (<i>Pan troglodytes verus</i>)	15	Safaripark Plaisance du Touch	Hand-reared	08/05/2002 – present day	3-5
<i>Alexandra*</i>	F	Chimpanzee (<i>Pan troglodytes verus</i>)	17	Rijswijk	Hand-reared	15/06/2001 – 24/02/2016	3,4
<i>Annett*</i>	F	Chimpanzee (<i>Pan troglodytes verus</i>)	17	Rijswijk	Hand-reared	15/06/2001 – 24/02/2016	3,4
<i>Zira*</i>	F	Chimpanzee (<i>Pan troglodytes verus</i> - <i>schweinfurthii</i> <i>hybrid</i>)	19	Ostrava	Parent	03/02/2016– present day	5
<i>Jahaga*</i>	F	Chimpanzee (<i>Pan troglodytes verus</i>)	24	Rijswijk	Parent	28/02/2001- 24/02/2016	3-5
<i>Hope*</i>	F	Chimpanzee (<i>Pan troglodytes verus</i>)	26	Jerusalem	Parent	03/02/2016- present day	3,5
<i>Daza*</i>	F	Chimpanzee (<i>Pan troglodytes verus</i>)	31	unknown	Unknown	27/05/2013- present day	3,4
<i>Frederike*</i>	F	Chimpanzee (<i>Pan troglodytes verus</i>)	43	unknown	Unknown	27/05/2013- present day	3-5
<i>Jeudi*</i>	F	Chimpanzee (<i>Pan troglodytes verus</i>)	51	unknown	Unknown	27/05/2013- present day	3,4
<i>Kianga</i>	F	Gorilla (<i>Gorilla gorilla gorilla</i>)	0	Zoo Leipzig	Parent	Birth - present day	None
<i>Diara</i>	F	Gorilla (<i>Gorilla gorilla gorilla</i>)	2	Zoo Leipzig	Parent	Birth - present day	None
<i>Kumili</i>	F	Gorilla (<i>Gorilla gorilla gorilla</i>)	13	Chessington	Parent	29/11/2012 – present day	None
<i>Kibara</i>	F	Gorilla (<i>Gorilla gorilla gorilla</i>)	13	Leipzig	Parent	Birth - present day	None
<i>Abeeku</i>	M	Gorilla (<i>Gorilla gorilla gorilla</i>)	17	Rotterdam	Parent	20/08/2012 – present day	None
<i>Tanah</i>	F	Orangutan (<i>Pongo abelii</i>)	7	Leipzig	Parent	Birth - present day	4
<i>Suaq</i>	M	Orangutan (<i>Pongo abelii</i>)	7	Leipzig	Parent	Birth - present day	3-5
<i>Batak</i>	M	Orangutan (<i>Pongo abelii</i>)	7	Leipzig	Parent	Birth - present day	None
<i>Raja</i>	F	Orangutan (<i>Pongo abelii</i>)	13	Leipzig	Parent	Birth - present day	3-5
<i>Padana</i>	F	Orangutan (<i>Pongo abelii</i>)	19	Leipzig	Parent	Birth - present day	3-5

<i>Dokana</i>	F	Orangutan (<i>Pongo abelii</i>)	27	Dresden	Parent	06/05/2002 - present day	3-5
<i>Pini</i>	F	Orangutan (<i>Pongo abelii</i>)	28	Leipzig	Parent	Birth - present day	3-5
<i>Bimbo</i>	M	Orangutan (<i>Pongo abelii</i>)	36	Duisburg	Hand- reared	22/12/2000 - present day	3-5

*B- Chimpanzee group

2.2 Testing facilities

Testing of the apes was possible between the hours of 8.30am and 12.30pm every day. For the chimpanzees, gorillas, and orangutans, it was possible to test them in either their sleeping rooms or in their observation rooms (here-after described as testing rooms). For the bonobos, testing took place in their sleeping room. The testing rooms consisted of multiple enclosures (from three to five), connected by hydraulic doors. Testing was possible in any of the enclosures, with the connecting doors open or closed as required. Additionally, each testing room contained an experimenter area in which the experimenter stood during testing. This area was never accessible to the apes, meaning that the experimenter and ape were always separated (see Figure 2.1 for examples of two testing rooms. All other testing rooms used in the experimental chapters can be seen in the Appendix A). The experimenter could interact with the apes through testing panels and meshing. The testing panels came in various designs (e.g., with varying numbers of holes of varying sizes) and were interchangeable; however, the meshing was fixed and could not be changed or removed. Apparatus could be attached to the meshing and panels, such as folding tables, sliding tables, and feeders (see Figure 2.2). Each species had its own separate apparatus to avoid any cross-species pathogen transmission. In cases where this was not practical (e.g., when custom made

apparatus was required), the apparatus was thoroughly disinfected after use with each species. All apparatus was approved by the ethics committee (see below).

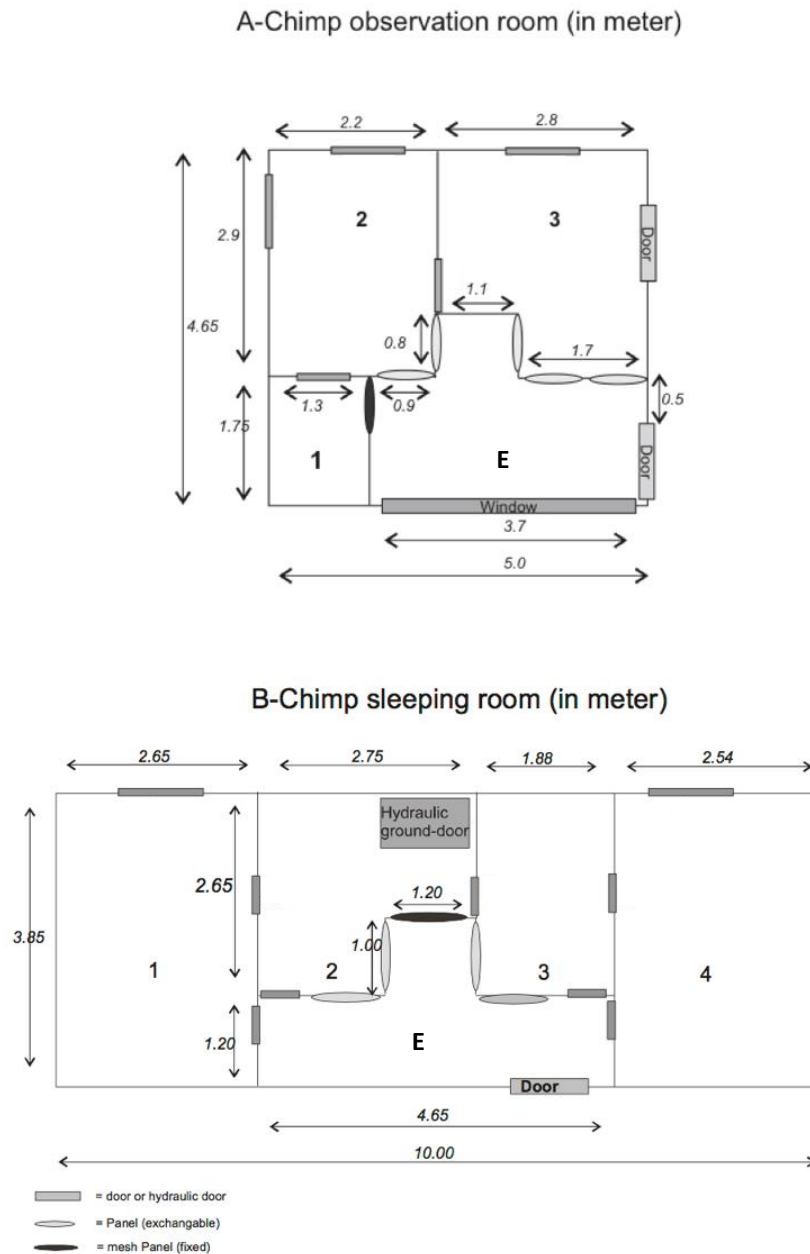


Figure 2.1. A-chimp observation room and B-chimp sleeping room specifications. Enclosures are numbered from 1-4 (1-3 for the A-chimp observation room). E indicates the experimenter area. Figure reproduced with permission from MPI-EVA.

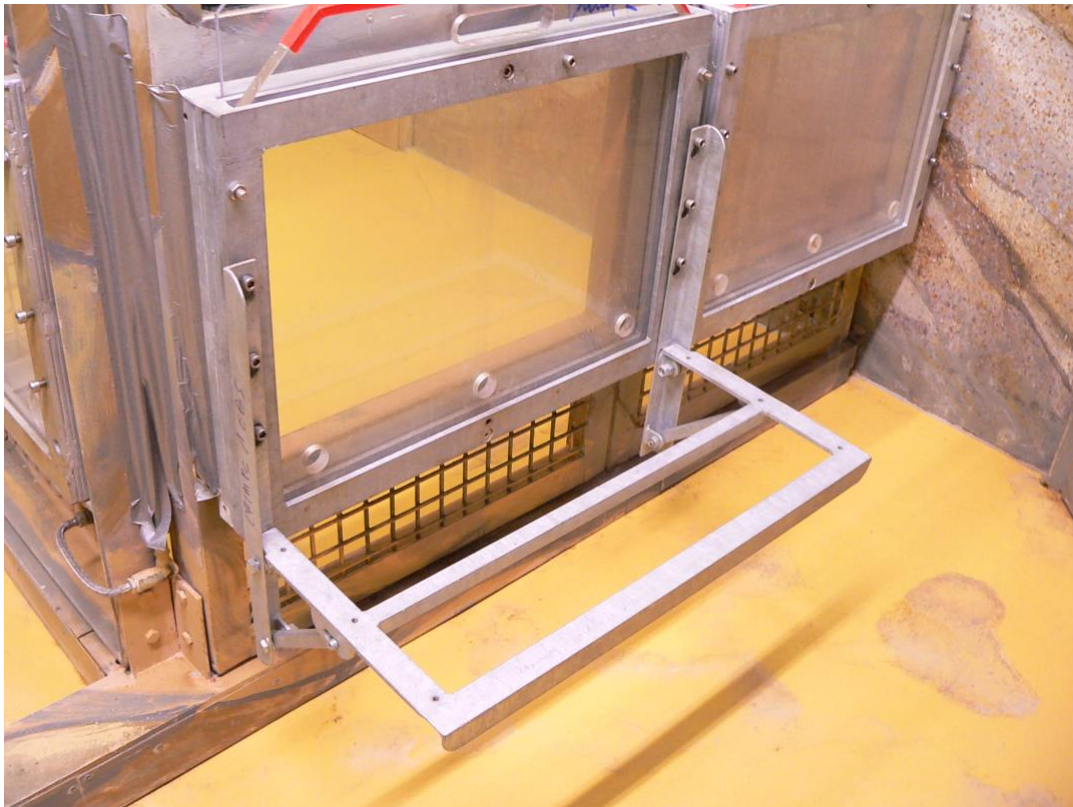


Figure 2.2 A folding table attached to a testing panel. Photo printed with permission from MPI-EVA

2.3 General testing procedure

All testing was approved by the MPI-EVA, the Leipzig zoo ethics committee, and the ethics committee of the School of Psychology and Neuroscience at the University of St Andrews. Apes were not food or water deprived during testing, or any time prior to or post testing, and all received a healthy and balanced diet. It was possible to test all apes (apart from infants), and none of the apes were ever forced to participate. Apes never participated in more than three tests per day, and the amount of food they received during tests was controlled to prevent over-feeding. The keeper was responsible for

deciding which apes could be testing on any particular day, for instance, if an ape was sick or had recently given birth, testing was not possible.

Apes were tested individually, this meant that subjects were temporally separated from the group during testing, except for mothers and infants who were never separated. In most cases the subject was alone in the testing room whilst the rest of the group remained in the indoor enclosure (the indoor enclosure was connected to the testing rooms, but was not visible from them). Sometimes other members of the group would be inside the testing room in an enclosure not needed for testing (e.g., the subject to be tested was in enclosure 1, and another group member in enclosure 2). This was often the case for juveniles, with the mother present in the adjoining enclosure. In situations where observing another member participating in a test would impact subsequent test performance, occluders were used to block the observers view. In cases where this was not possible, the observer was not included in the test.

At the start of a testing session, all apparatus and equipment was set-up prior to the ape entering the enclosure. Often none of the apes would be inside the testing room at this point, but occasionally one or more apes would be in the room in an enclosure not being used for testing. Once the test was ready to begin, the keeper checked all doors and panels were secured. The keeper was responsible for moving the ape into and out of the testing room, or between enclosures within the testing room, which was done by the opening and closing of hydraulic doors. If the subject was already inside the testing room inside an enclosure not being used for testing, the keeper opened the door to the testing enclosure so that the ape could enter. Sometimes food was used to encourage the ape to enter if they were reluctant, but usually the apes enter of their own accord. If the ape to be tested was outside the testing room (i.e., in the indoor

enclosure), the keeper would open the door to the indoor enclosure and call the ape by name. Again, food would sometimes be used to encourage the ape. No ape was forced to enter the enclosure and participate. Once the ape was inside the enclosure, the keeper left the testing room.

During testing the apes would participate in various tasks (see specific methods in Chapters 3-5), and were rewarded with food during, or after, a testing session. The food reward ensured that the apes were never in a situation in which they saw food but did not receive any (e.g., in the case of incorrect choices or non-reinforced testing procedures). Food was given to the ape through the testing panels or the meshing, a feeder could also be used if preferred. Contact with the apes (other than through feeding) was strictly prohibited, and where possible the experimenter kept a distance of at least 20cm between themselves and the ape. If an ape showed any signs of distress or became unmotivated and stopped participating, the test ended and the ape re-joined the other group members. If at any point during the test there was a problem, such as with the ape or apparatus, the keeper could be reached via radio. At the end of a testing session the ape re-joined the other group members.

2.4 Sampling

Where possible all apes were tested, except for gorillas (see Table 2.1). As there were only three gorillas available for testing, statistically controlling for any potential species differences with gorillas in the sample would not have been possible. All of the experiments involved between-subject designs, as such, apes were allocated to conditions using stratified sampling based on three variables: species, age, and sex. This reduced the possibility that any differences in performance between conditions

would be explained by these variables, as opposed to the manipulation of conditions. Additionally, species was controlled for in the statistical analyses where possible. Likewise, for within-subject variables, all ordering was counterbalanced between subjects. For example, in Chapter 3 subjects trained with two experimenters; half trained with experimenter A then B, and half with experimenter B then A.

2.5 Data collection and analysis

All testing sessions were video-taped using a standard portable video camera, and the video files were stored on a file server of the MPI-EVA. Where possible, data was coded live on coding sheets, which was later checked by playing back the video recording after the session ended. In cases where data could not be coded live (e.g., when the experimenter was not in the testing room, or when the apes' responses were too fast to record), the video file was used to code the data. In these cases, an additional person (blinded to condition) coded the data from the video file, and inter-observer reliability was measured. All data was analysed using SPSS version 20.0.0 or R Studio version 0.98.1091, with the alpha level set to 0.05 (unless otherwise stated). The specific statistical analyses for each study are described in their relevant chapters.

Chapter 3 | Distinctiveness

3.1 Introduction

Research suggests that primates are able to bind and recall multiple features from past events, such as what was where (Mendes & Call, 2014; Menzel, 1999), and when (Martin-Ordas et al., 2010), or in which context (Martin-Ordas et al., 2013); however, not all research has found confirmatory results (Dekleva et al., 2011; Hampton et al., 2005). Consequently, this chapter⁹ aims to further investigate the binding and recall of details from a past event in great apes. Crucially, the research described here differs from previous research by assessing binding from the perspective of the distinctiveness effect, a phenomenon that has received little attention in animal research.

As previously mentioned, the distinctiveness effect refers to the enhancement of memory as a result of the processing of both difference and similarity (Hunt, 2006). At the core of the distinctiveness effect is context; information is processed in relation to the differences and similarities with the current (primary distinctiveness), or stored (secondary distinctiveness) context. For example, in a list of words, in which all are types of food except for the word ‘tree’, ‘tree’ is more likely to be recalled than the other words. This is because encoding the similarity between the words establishes a context in which ‘food’ is the common theme, whilst processing the differences results in the observation that ‘tree’ does not correspond to the common theme. Subsequently, ‘tree’ is distinctive in this context. The distinctiveness effect therefore involves the

⁹ This chapter formed the publication by Lewis, Call, and Berntsen (2017a; see appendix B). Many of the themes and ideas that are expressed in the publication are expressed here, with some text and figures reproduced verbatim. Instances of reproduction are for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.

encoding of multiple features, as information is not encoded in isolation, rather it is encoded in relation to its context. Indeed, the distinctiveness effect would not occur without relational processing, “it is critical to cue the relational information at retrieval to obtain the distinctiveness effect” (Geraci & Rajaram, 2006, p. 218). As such, evidence of a distinctiveness effect is also evidence for the encoding of multiple pieces of information in an integrated unit (i.e., binding).

The distinctiveness effect is a well-established phenomenon in the human literature, and has been investigated in numerous paradigms, such as the isolation effect (von Restorff, 1933), flashbulb memories (Brown & Kulik, 1977; Edery-Halpern & Nachson, 2004), and the expectation violation paradigm (Hirshman, Whelley, & Palij, 1989). Below I review the literature on the distinctiveness effect in animals, followed by the aims and predictions of this study.

3.2 Previous research

As mentioned in Chapter 1, the majority of research investigating distinctiveness in animals has focused on the isolation effect, whereby items on a list or in a particular location are recalled better when they are distinctive as opposed to when they, or other items, are not (Beran, 2011; McLaughlin et al., 1968; Parker et al., 1998; Reed, Chih-Ta, Aggleton, & Rawlins, 1991; Reed & Richards, 1996). For instance, Reed et al. (1991) showed that rats remember an item in the middle of a series better when the item is made distinctive, as opposed to when it's not. Rats were rewarded for entering a novel box, but not for entering a box that had previously been entered. After learning to enter only novel boxes, the rats were placed into a Y-maze with unique boxes at the end of each arm. The boxes were made unique by having different textures and designs, and

containing different items. Each of the arms opened one at a time and in a particular order, so that the rat could only enter the boxes at the ends of the arm in a specified order. On some trials, when entering the third box, the lights were either turned on or off at entry; this did not occur for any of the other boxes, and was thus intended to make this box distinctive. After entering all the boxes, the rat was placed in to a blank box (free of any pattern or item) and remained there for twenty seconds. Following this retention period, the rat was presented with a choice between one of the boxes that it had previously entered in the Y-maze, or a novel box. Rats showed a recency and primacy effect; that is, they selected the novel box more often when given a choice between a novel box and the first or last (fifth) box they had entered in the Y-arm maze. They performed worst when the choice was between a novel box and the third box from the maze; however, performance greatly improved on trials in which the third box was distinctive, showing a clear distinctiveness effect.

These results were replicated in a similar study, in which rats recalled which arms in a maze they had previously entered by avoiding those arms at test (Reed & Richards, 1996). When one of the arms was made distinctive (by the accompaniment of a tone or human handling), rats made fewer re-entries to that arm in comparison to when the distinctive element was absent.

Although these studies show that distinctiveness enhances memory for isolate items, they are limited with regards to what they tell us about memory of past events. Typically, they involve rule learning and repeated testing, and use retention periods more consistent with working memory than episodic memory (i.e., seconds; although Reed and Richards (1996) incorporated a delay of 16minutes). As such, it is likely that recollecting a past event is not necessary for successful performance. Research with

primates, however, suggests that past events that are distinctive can also be well remembered. Mendes and Call (2014) showed that chimpanzees could recall the location of hidden food after minimal exposure to a novel event. During the event, chimpanzees discovered hidden food in a specific location in their enclosure (in total, the chimpanzees participated in four foraging events, in each event a different location was baited). The event was particularly distinctive, as the chimpanzees were released into the enclosure in pairs, and an experimenter stood on an observation platform in full view of the subjects. These aspects were unique to this experiment, and thus distinctive in comparison to other foraging events the apes had experienced. Twenty-four hours later, the apes were released in the same pairs and the same experimenter stood on the observation platform, thus, the distinctive features of the event were present during encoding and retrieval. The authors found that the chimpanzees successfully recalled the food locations, as evidenced by searching the correct location more often than not, and revisiting the locations faster than during the initial discovery. Furthermore, three months later when presented with the same cues (experimenter on the platform and being released in the same pair), the chimpanzees again searched the previously baited locations more often than a baseline condition in which no cues were presented.

Similarly, an innovative method by Kano and Hirata (2015) involved the use of eye tracking technology, and showed that apes could remember what happened in a movie (see Chapter 4 for additional study details). The apes watched a clip of an actor dressed in a King Kong suit performing an aggressive act. Twenty-four hours later, when watching the same clip again, the apes were able to predict what would happen next through the use of anticipatory looks (i.e., they looked at the location in which

King Kong would appear *before* he appeared). Thus, the apes recalled the previously encoded information in anticipation of what was coming next.

These studies suggest distinctive events are well remembered, however, they provide limited evidence regarding the distinctiveness effect for two reasons. First, as neither study explicitly aimed to establish if distinctive events are well remembered, they did not provide a baseline memory performance (i.e., there is no non-distinctive event to compare recall performance to). Second, although both events were novel, they were not designed with the purpose of being distinctive, as such, it is unclear how distinctive the events were to the apes. In the Mendes and Call (2014) study, the apes may have experienced occasions in which they have foraged and found food in pairs outside of an experimental manipulation, which would undermine the novelty of this event. Furthermore, as they participated in multiple events (4 foraging events), each event was likely less distinctive than the former (due to being identical except for the food location), yet performance did not differ between events. In the Kano and Hirata (2015) study, the authors state that the movie clip was designed to be emotionally stimulating due to apes encoding emotional material better than neutral material. Thus, the event may have been well remembered due to its emotional content rather than distinctiveness. As such, it is not clear whether the events were well remembered because they were distinctive, or simply if they were well remembered for other reasons, such as the positive reinforcement from receiving food, or due to the emotional content of the event.

3.3 Aims

This chapter presents a series of three experiments aimed at establishing whether ape's memory performance on a simple memory task is enhanced when the event in which the task occurs is distinctive, as opposed to non-distinctive. The events were designed to be distinctive with regards to previously experienced events in the same room and with the same type of task, thus they incorporate secondary distinctiveness as opposed to primary distinctiveness (Eysenck, 1979; Hunt & Worthen, 2006; Schmidt, 1991). The experiments also aimed to separate performance based on distinctive processing from performance based on associative learning. Often in animal studies, associative learning is argued to be a simpler explanation of performance on a task, as opposed to an explanation that favours a higher cognitive capacity (Beckers, De Houwer, & Dwyer, 2016). Associative learning refers to the influence of paired events on behaviour (De Houwer, Hughes, & Barnes-Holmes, 2016), and encompasses both classical and operant conditioning (see Grant, 1964). These experiments focused on operant conditioning, specifically positive reinforcement, which is the pairing of a desired behaviour with a reward, resulting in an increase in the desired behaviour. For each experiment, two predictions for performance are provided: one based on distinctive processing, and one based on associative learning (measured via positive reinforcement).

3.4 General methods

Due to the similarity between the three experiments, I first describe the general methods. Additional methodological details for each of the experiments can be found under their respective specific methods. In all three experiments, apes were presented

with a memory task in which banana slices were hidden under one of three containers. Two weeks later, the apes were tested on their memory of which container had previously been baited with banana. As previous research using a similar experimental task has shown that apes can recall the location of a baited container after twenty-four hours (Martin-Ordas & Call, 2011), and that a distinctive hiding event that was seen once was successfully recalled two weeks later (Martin-Ordas et al., 2013), a two-week retention period was used to see whether a common baiting task could be successfully recalled when presented within a distinctive context. Across the three experiments, the distinctiveness of the context in which the baiting took place, the number of overlapping cues at encoding and retrieval, and the extent to which the apes were reinforced for selecting the baited container was manipulated (see Table 3.1).

Table 3.1 Experimental variables shown by Experiment and condition. Modified from Lewis et al. (2017a), in accordance with Wiley Terms and Conditions for Self-Archiving.

	Condition	<i>Distinctive context</i>	<i>Large reinforcement</i>	<i>Small reinforcement</i>	<i>No reinforcement</i>	<i>Overlapping Experimenter</i>
Experiment 1	Mask	✓	✓	-	-	✓
	No Mask	*	✓	-	-	✓
Experiment 2	Reinforced Matching	-	-	✓	-	✓
	Non-reinforced Matching	-	-	-	✓	✓
	Reinforced Non-Matching	-	-	✓	-	-
	Non-reinforced Non-matching	-	-	-	✓	-
	Reinforced	-	✓	-	-	✓
Experiment 3	Non-reinforced	*	-	-	✓	✓

✓ Variable included

- Variable absent

* Variable unintentionally included

3.4.1 Subjects

The majority of apes housed at the WKPRC participated in this study (see Table 3.2).

Where possible, the same apes participated in all three experiments (see specific

methods of each experiment for full details). Additional demographic information about each ape can be found in Table 2.1 (Chapter 2). Apes were tested during the period July 2015 to February 2016, and an additional six chimpanzees were tested in Experiment 2 during January 2017.

Table 3.2 Subject demographics. Age shows the age that the subjects were at the start of the first experiment they participated in. Modified from Lewis et al. (2017a), in accordance with Wiley Terms and Conditions for Self-Archiving.

Subject	Species	Age (years)	Sex	Experiment participation
<i>Fimi</i>	Bonobo	7	Female	1,2,3
<i>Gemena</i>	Bonobo	9	Female	1,2,3
<i>Luiza</i>	Bonobo	10	Female	1,2,3
<i>Lexi</i>	Bonobo	15	Female	1,2,3
<i>Yasa</i>	Bonobo	17	Female	1,2,3
<i>Kuno</i>	Bonobo	19	Male	2,3
<i>Jasango</i>	Bonobo	24	Male	1,2,3
<i>Joey</i>	Bonobo	32	Male	1,3
<i>Bangolo</i>	Chimpanzee	7	Male	2
<i>Kara</i>	Chimpanzee	10	Female	1,2
<i>Kofi</i>	Chimpanzee	11	Male	2
<i>Lobo</i>	Chimpanzee	11	Male	1,2,3
<i>Tai</i>	Chimpanzee	12	Female	1,2,3
<i>Kisha</i>	Chimpanzee	12	Female	2
<i>Lome</i>	Chimpanzee	13	Male	1,2,3
<i>Alex*</i>	Chimpanzee	14	Male	1,2,3
<i>Alexandra*</i>	Chimpanzee	15	Female	1,2,3
<i>Annett*</i>	Chimpanzee	15	Female	1,2
<i>Bambari</i>	Chimpanzee	16	Female	2
<i>Swela</i>	Chimpanzee	20	Female	2
<i>Frodo</i>	Chimpanzee	21	Male	1,2,3
<i>Sandra</i>	Chimpanzee	22	Female	1,2,3

<i>Jahaga*</i>	Chimpanzee	22	Female	1,2,3
<i>Hope*</i>	Chimpanzee	26	Female	2
<i>Daza*</i>	Chimpanzee	29	Female	1,2,3
<i>Dorien</i>	Chimpanzee	34	Female	1,2,3
<i>Natascha</i>	Chimpanzee	35	Female	2,3
<i>Riet</i>	Chimpanzee	37	Female	1,2
<i>Corrie</i>	Chimpanzee	38	Female	1,2,3
<i>Ulla</i>	Chimpanzee	38	Female	1,2
<i>Fraukje</i>	Chimpanzee	39	Female	1,2,3
<i>Robert</i>	Chimpanzee	39	Male	1,2,3
<i>Frederike*</i>	Chimpanzee	41	Female	1,2,3
<i>Jeudi*</i>	Chimpanzee	49	Female	1,2,3
<i>Suaq</i>	Orangutan	6	Male	2,3
<i>Raja</i>	Orangutan	11	Female	1,2,3
<i>Pini</i>	Orangutan	17	Female	1,2,3
<i>Padana</i>	Orangutan	19	Female	1,2,3
<i>Dokana</i>	Orangutan	26	Female	1,2
<i>Bimbo</i>	Orangutan	34	Male	2,3

* B-group chimpanzee; see Chapter 2.

3.4.2 Apparatus

Chimpanzees from the A-group were tested in their observation room. Testing of the chimpanzee B-group, bonobos and orangutans took place in their respective sleeping rooms (see Testing Facilities in Chapter 2 and Appendix A). A sliding table was attached to the meshing of the enclosure. The table was designed so that the bottom half was fixed in position, but the top half could slide. This enabled the table (and its contents) to be pushed towards the apes to indicate that they should make a choice, and to be pulled back from the apes after a choice was made. Three containers were positioned on the sliding table, approximately 16cm apart. The containers differed

slightly in each of the three experiments (see specific methods for each experiment), this was to reduce proactive interference¹⁰ from one experiment to the next, whilst keeping the task demands the same by not making some containers more or less distinctive than others. Above the sliding table was a testing panel with three circular holes, each hole was in alignment with one of three containers. Figure 3.1 shows the set-up for Experiment 1; the set-up for Experiments 2 and 3 was the same, except for the containers and the plastic tray on which they sit, which were unique to Experiment 1.



Figure 3.1. Set-up of the apparatus for Experiment 1. The banana is hidden under the container positioned on the left. Photo printed with permission from MPI-EVA.

¹⁰ Proactive interference refers to the reduction in memory performance for recently stored information, as a result of previously stored information that is similar (Anderson & Neely, 1996).

3.4.3 Design

All experiments used a between-subjects design, with the dependent variable as ‘choice at test’, defined as the container the subject selected at test. Each experiment consisted of an exposure, followed by a test two weeks later. There were two trials at exposure, one immediately preceding the next. The trials were identical in all aspects, meaning that exactly the same container was baited in each trial (e.g., the left). If an incorrect choice was made during a trial an additional trial was administered, and if subjects made two incorrect choices they were dropped from the experiment. Subjects needed to complete two trials correctly for two reasons: first, to make sure they were paying attention to which container the food was hidden under. Second, to make sure that they could recall the food location after a brief period (i.e., the time taken from observing which container the food was hidden under, to the time of choice). At test, all subjects only received one trial, and the container that was baited was the same container that had been baited during exposure. It was not possible to give subjects more than one trial, as apes received feedback as to which container was baited after they made a choice. As such, performance on subsequent trials may have been based on the feedback they received during test, as opposed to their memory of the baiting event.

The location of the baited container was counterbalanced between subjects, and within subjects between experiments (e.g., for Lome, the left container was baited in Experiment 1, the right in Experiment 2 and the center in Experiment 3. For Alex, his order was right, center, left). This minimized the effect of any potential side biases on performance (i.e., an ape may prefer the right side as opposed to the centre or left), and the possibility that the apes could select the correct location by learning that the baited container always appeared in one location throughout all three experiments.

3.4.4 Procedure

During the exposure, three containers were positioned on to the sliding table, one to the right, center and left. The experimenter (E) hid banana under one of the containers; this was either done outside of the testing room (Experiment 1), or behind an occluder inside the testing room (Experiments 2 and 3). E made sure that no traces of the banana were visible from the ape's point of view, so to avoid unintentionally showing the ape the location of the banana. The remaining two containers remained empty.

E then called the subject by name, only once the subject had looked directly at E did the trial begin, ensuring the ape had seen the identity of E. E first lifted the container under which the banana was hidden (the baited container). Once the subject had seen the banana, the container was replaced so that the banana was hidden once again. The remaining two containers were then simultaneously lifted to reveal that no banana was there. Once the subject had seen this, they too were replaced. The sliding table was then pushed towards the subject, indicating that they should make a choice. When pushing the sliding table, E made sure to push it from the centre and not to look at any of the containers, so to minimize any unintentional cues E may give as to where the banana was hidden. A choice was defined as the subject pointing or reaching through one of the holes, with the container nearest the hole taken as their choice (e.g., if they pointed through the centre hole, the centre container was the subject's choice). If a subject pointed to more than one hole, E said to the ape "one" and waited for the subject to choose again. If the subject chose the baited container (a correct choice), E lifted the container to reveal the banana and gave it to the ape through the hole in the testing panel aligned with the baited container (e.g., if the baited container was on the left, the food was given through the left hole). The remaining two containers were lifted

to reveal that they were empty. If the subject made an incorrect choice by choosing one of the un-baited containers, the chosen container was lifted to reveal it was empty, and the remaining two containers were lifted (one of which had banana). In this instance, the banana was not given to the subject. This marked the end of a trial, with a trial lasting approximately 90-seconds. After two successful trials the session finished.

Two weeks later, subjects completed a test consisting of only one trial. The test took place in the same room as the exposure and followed the same procedure, with the same container being baited. However, there was one crucial change: the location of the banana was not revealed to the subject before they made a choice. As such, the apes had to rely on their memory of the exposure to determine which container the food was hidden under.

3.4.5 Data analysis

For all three experiments, the main question was whether the apes could remember which container was baited two weeks previously. Successful performance was defined as selecting the baited container above chance (as there were three possible choices, the probability of selecting the baited container by chance was 0.33). To test this, the number of times the baited container was selected in each condition was compared to the expected number if performing at chance, using two-tailed binomial tests (two-tailed tests were used to reduce the chance of a type-1 error). Where additional analyses were run, the details can be found in the specific methods section of each experiment. Only non-parametric tests were used due to the dependent variable being dichotomous, and a small sample size.

3.5 Experiment 1 | Distinctiveness

3.5.1 Aims and predictions

The first experiment aimed to compare whether performance in an event with a highly distinctive feature was better than performance in an event without this feature. Apes received the same amount of reinforcement (reward) for selecting the baited container in both events. As such, it was predicted that performance would be better in the distinctive event due to distinctive processing (binding of contextual features); however, if performance reflected associative learning (rather than distinctive processing), performance will not differ between events, due to the same reinforcement value in both.

In the distinctive event, a facial mask was worn by E that depicted the face of the apes' keeper. In the non-distinctive event this mask was absent. Four different masks were used, one for each species. The masks were made using high quality headshots of four of the keepers: a bonobo keeper, an orangutan keeper and two chimpanzee keepers (one for the A group and one for the B group). Previous research has shown that primates are capable of recognizing human faces in the form of 2D facial images (Martin-Malivel & Okada, 2007; Sliwa, Duhamel, Pascalis, & Wirth, 2011; Tomonaga, 1999), thus, a photographic mask depicting the keepers face should be recognizable to the apes. The apes only saw the mask of their own keeper, for example, bonobos only saw the mask of the bonobo keeper.

Masks of the keepers were used for two reasons: first, to ensure the event was distinctive; the apes are very familiar with their keeper, and have been tested multiple times with E and on similar platform tasks, but they have never experienced E wear a mask, nor the face of their keeper appear on the body of another person. Thus, the

situation was very distinctive with regards to the apes' previous experiences, and conflicted with what they know about their keeper and E. Second, the event needed to be distinctive, but by no means frightening to the apes. By using faces of familiar keepers, the apes should be surprised, but not frightened.

3.5.2 Specific methods

3.5.2.1 *Subjects*

A subset of thirty apes participated in this experiment (see Table 3.2): nineteen chimpanzees ($M = 26$ years), four orangutans ($M = 18$ years) and seven bonobos ($M = 16$ years).

3.5.2.2 *Apparatus*

Three blue opaque containers (length= 7cm, width = 10cm, height =10cm) were positioned onto a tray. The tray was used to transport the containers into and out of the testing room (see Figure 3.1). For half of the subjects, a laminated cardboard mask depicting the face of a keeper was worn by E. The mask covered the entire face E, except for the eyes. Each species only saw a mask depicting the face of their own keeper (i.e., bonobos only saw a mask of the bonobo keeper). There were four masks in total, one for each species and each chimpanzee group (see Figure 3.2).

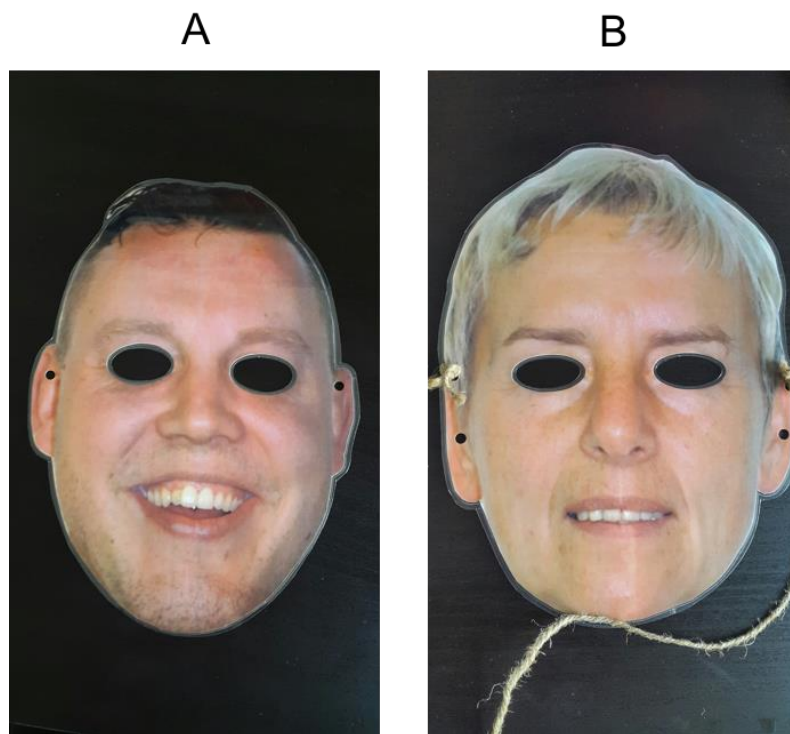


Figure 3.2. Two of the masks worn by the experimenter. A depicts the mask for the chimpanzee A-group, B depicts the mask for the chimpanzee B-group. The string (see B) was used to attach the mask to E's face.

3.5.2.3 Design

Apes were allocated to one of two conditions: mask (two orangutans, four bonobos and nine chimpanzees, age range 10-41 years, $M = 22$ years) or no-mask (two orangutans, three bonobos, ten chimpanzees, age range 7-49 years, $M = 23$ years).

3.5.2.4 Procedure

The procedure followed the procedure detailed in the general methods, with the following changes: E hid half a sliced banana (cut into 5 pieces) under one of the containers whilst outside the testing room. The containers were all posited onto a tray,

which was used to transport the containers into the testing room. In the no-mask condition, E carried the tray into the testing room and positioned it onto the sliding table, with care taken not to displace or move any of the containers. The procedure then followed that of the general procedure. At the end of a trial, E lifted the tray with the containers still on it, and left the testing room. In the mask condition, whilst outside the testing room, E secured a mask of a keeper to her face, making sure her entire face (except for her eyes) was concealed. E then repeated the procedure described above whilst wearing the mask.

At test (13-17 days later), the procedure above was repeated, except subjects received only one trial and the location of the banana was not revealed. Additionally, in the mask condition, E wore the same mask that was worn during exposure. Thus, the difference between the two conditions was only the wearing (or not wearing) of a mask at exposure and test.

3.5.2.5 Data analysis

The main analysis is described in the general methods section.

3.5.3 Results

All subjects required only two trials during exposure, meaning that no subject made an incorrect choice. This shows that all subjects attended to and recalled the baited container after a minimal delay (seconds). At test, recall in both conditions was significantly better than chance. In the mask condition (N=15), the baited container was selected 60% of the time, which was significantly greater than chance ($p = 0.05$, 95% confidence interval (CI) lower, upper [0.32, 0.84]). In the no-mask condition (N=15)

the baited container was selected 80% of the time, significantly greater than chance ($p < 0.001$, 95% CI [0.52, 0.96]). Thus, subjects in both conditions were able to successfully recall the location of the baited container after a two-week retention period.

As both conditions showed above chance performance, an additional analysis assessed whether performance was better in one condition compared to the other. A two tailed Fisher exact test found no significant difference between conditions ($df= 1, p = 0.43$), indicating that although the baited container was selected more in the no-mask condition, it was not significantly greater than in the mask condition (see Figure 3.3). Thus, subjects in both conditions were equally good at recalling the location of the baited container after two weeks¹¹.

¹¹ Although no significant difference was found, it's possible this was due to a lack of power.

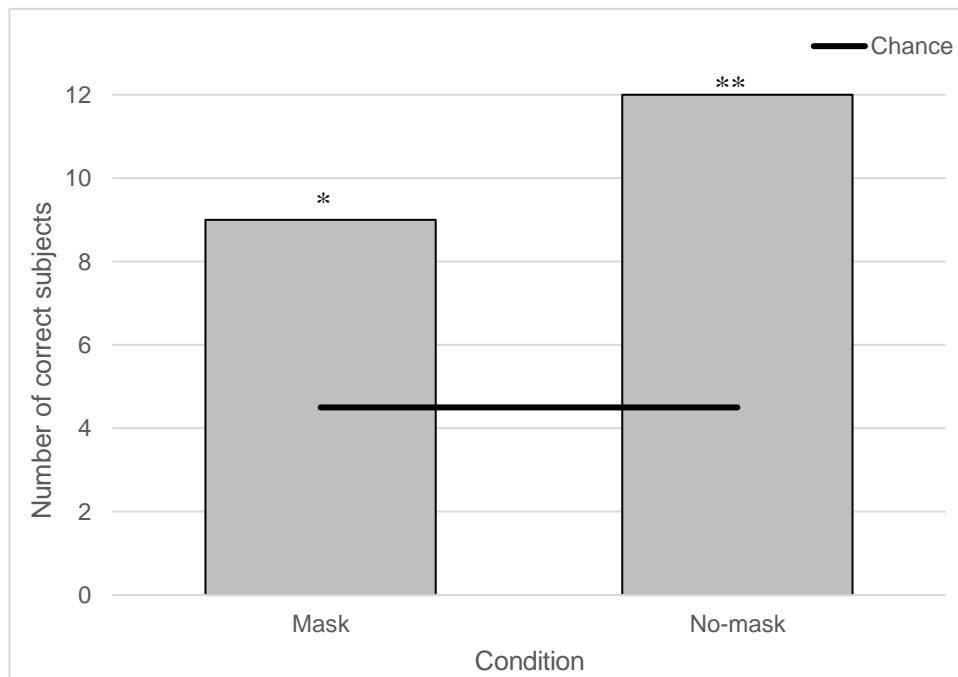


Figure 3.3. Number of correct choices in the mask and no-mask condition.

Chance shows the number of choices that would be correct if the apes were performing at chance. *= 0.05 **=<0.001. Figure reproduced from Lewis et al. (2017a), in accordance with Wiley Terms and Conditions for Self-Archiving.

3.5.4 Discussion

The results indicate that the apes were able to remember the location of the baited container after a delay of two weeks. Additionally, performance was very high in the no-mask condition. This was somewhat surprising given the difficulty of the task; the apes had to distinguish this task from many similar tasks (e.g. Call, 2004), to distinguish the containers used from other similar containers in other tasks (e.g. Call, 2006), and to recall the exact location of the baited container in an array in which the containers were extremely close together (see Figure 3.1).

Performance between the two conditions did not differ, which is in line with predictions from an associative learning based account, rather than a distinctiveness effect. The good performance in both conditions may be explained by associative learning, due to the large reinforcement for choosing the baited container (i.e., the likelihood of choosing the same container again is increased with a positive reward). Despite these findings, there are other potential explanations for these results. First, the lack of difference in performance may have been a result of the high performance in both conditions, leaving little room for improvement in the distinctive condition; however, as performance was not at ceiling (and was better in the no-mask condition), this is unlikely. Second, the results may reflect the influence of emotion on memory. The mask was intended to be distinctive by eliciting surprise, and indeed, a number of individuals produced a physical reaction to the mask (prolonged looking, wariness, aggression). In both the human and animal literature, emotion enhances memory, however, the effect is focal (Burke, Heuer, & Reisberg, 1992; Easterbrook, 1959; Kensinger, 2009; Schmidt & Saari, 2007). That is, individuals often remember central aspects of the event that are directly linked to the emotional source, but do so at a cost to the peripheral aspects, which are often forgotten. This is likely due to focal features capturing attention, resulting in fewer cognitive resources to encode the peripheral details (Easterbrook, 1959; Kensinger, Piguet, Krendl, & Corkin, 2005). In this case, the mask (a central feature directly linked to the emotional arousal) may have captured attention, but at a cost to the peripheral details, such as the position of the baited container. This may explain why performance was not better in the mask condition relative to the non-mask condition. Third, the high performance in the no mask condition may be a result of a distinctiveness effect occurring. Although it was only

intended for the mask condition to be distinctive, it's possible that the unusual baiting procedure (baiting outside the testing room) and unusually large amount of food reward (the apes usually receive a small slice of food) was distinctive without the addition of a mask. Consequently, the results may reflect distinctive processing in both conditions.

3.6 Experiment 2 | Baseline

Experiment 2 was designed to further investigate the findings from Experiment 1.

This experiment aimed to establish a baseline level of memory performance by using a standard baiting procedure that was absent from any unusual features. In Experiment 1, it was possible that the unusual procedure and large reinforcement led to distinctive processing in both events. As such, this experiment was designed to provide a true control performance. It was predicted that performance in this task would be poorer than performance in Experiment 1.

Additionally, this experiment aimed to further assess whether the performance in Experiment 1 may have been explained by reinforcement alone. As such, the reinforcement value was manipulated, with the prediction that an event with no reinforcement would result in poorer performance than an event with reinforcement. No difference in performance between events would suggest that reinforcement is not a predictor of performance. Finally, it was investigated whether performance may differ as a result of the retrieval cues present at test. To achieve this, for half the subjects the retrieval cues consisted of features that were present at the time of encoding, for the other half, one of these features (the identity of the experimenter) differed. In line with the encoding specificity principle, it was predicted that performance would be best when encoded features are present at retrieval.

The procedure thus differed from Experiment 1 in four ways: first, no masks were worn by E in any of the conditions. Second, the amount of banana was reduced to one piece, a standard amount for these types of task. Third, E began inside the testing room, rather than outside of the testing room, and the containers were baited behind an occluder. This is common procedure for testing with the apes in this laboratory, that is,

experimenter(s) are normally present and waiting in the testing room when the ape enters the enclosure, and containers are baited behind an occluder. Fourth, the experimenter at retrieval was one of two experimenters; either the experimenter who conducted the exposure, or an experimenter who did not.

3.6.1 Specific methods

3.6.1.1 *Subjects*

All apes from Experiment 1 took part, except for one bonobo (Joey) who was unwilling to participate. In addition, one bonobo (Kuno), two orangutans (Suaq, Bimbo) and seven chimpanzees (Hope, Bambari, Swela, Bangolo, Kofi, Kisha, Natascha) that were unwilling, unavailable, or not at the zoo during testing of Experiment 1 took part here. All of these additional chimpanzees (except for Natascha) took part during the later testing period (January 2017) and only completed this experiment. They were only tested in Experiment 2, as the design of this experiment meant that more subjects were required here than the other two experiments. A total of thirty-nine apes participated in this experiment (see Table 3.2): 26 chimpanzees ($M = 24$ years), 7 bonobos ($M = 14$ years), and 6 orangutans ($M = 19$ years).

3.6.1.2 *Apparatus*

Three containers of the same style and measurements as the containers in Experiment 1 were used, but were red instead of blue. Additionally, an occluder was used during the baiting process. This was a plastic rectangular shaped cover, which when placed on the sliding table obscured the apes' view of the containers and E's hands during the baiting process. This enabled the experimenter to bait the container inside the testing room

whilst the ape was present, but without the ape seeing which container was being baited; this is a common baiting procedure in this laboratory.

3.6.1.3 *Design*

A 2x2 between-subjects' design was used. Apes were assigned to one of two exposure conditions: reinforced (R) or non-reinforced (NR), and one of two test conditions: matching experimenter (M) or non-matching experimenter (NM). The R exposure followed by the M test represented a standard baiting task procedure.

3.6.1.4 *Procedure*

The procedure followed the procedure detailed in the general methods, with two changes. First, baiting during the exposure took place inside the testing room. E sat down in front of the sliding table and covered the containers with the occluder. Before baiting the container, E first showed the subject a piece of banana and then placed the banana under one of the containers (only one slice of banana was used). The subject could see that E was placing banana somewhere, but their view was obscured by the occluder. The occluder was then removed and the trial followed the procedure described in the general methods. At the end of a trial, E positioned the occluder back on the sliding table.

Second, the procedure differed depending on which exposure condition the subject was in. In the R condition, the procedure was as described, with subjects receiving the banana upon a correct choice. In the NR condition, subjects who chose the correct container did not receive the banana, instead E threw the banana into an opaque bucket positioned next to E. Thus, the conditions differed in terms of

reinforcement, with subjects in the R condition being reinforced for choosing the correct container, whereas subjects in the NR were not reinforced.

The test followed two weeks later (13-15 days). E began in the testing room and baited the container the same way as described above. The test then followed the procedure described in the general methods, except for one change: the experimenter that was present varied depending on which condition the subject was in. In the M condition, E was the same experimenter that had conducted the exposure. In the NM condition, E was an experimenter who had not conducted the exposure. Thus, the two conditions differed in terms of whether the identity of E was consistent across exposure and test, or changed between exposure and test. All subjects were rewarded for a correct choice regardless of which exposure condition they had previously received.

3.6.1.5 Data analysis

The data analysis is described in the general methods section. An additional analysis was conducted on the subjects that participated in both this experiment and Experiment 1 (N=27). The performance of these subjects was compared between experiments (conditions pooled) using an exact McNemar test, to see whether overall performance was poorer here compared to Experiment 1.

3.6.2 Results

The majority of subjects required only two trials during exposure. Two subjects (Daza and Ulla) failed after three and were subsequently dropped from the experiment. Ulla was in the NR exposure, and during the first trial she immediately selected the correct container. However, during the second and third she took her time before selecting an

incorrect container. Thus, it's possible she quickly learnt to avoid the correct container after not being rewarded for choosing it. Daza was incorrect in trials 1 and 3, and thus it seems she did not understand the task, or could not recall where the food was after the short delay. However, as she was able to pass the exposure in Experiment 1, her performance may be a result of lack of motivation for a small food reward.

Results showed that subjects performed at chance in all conditions (all $p > 0.31$). Furthermore, performance between the non-reinforced matching (NR-M), reinforced non-matching (R-NM) and non-reinforced non-matching (NR-NM) was identical, with only 2 of 9 (22.22%) subjects selecting the baited container. Performance in the reinforced matching (R-M) was slightly better, with 5 of 10 subjects selecting the baited container (see Figure 3.4). In order to investigate this further, an additional analysis compared the performance of the R-M condition to the three other conditions pooled together. A fisher exact test revealed no significant difference ($df = 1$, $p = 0.13$), indicating that performance was not significantly better in this baseline condition. Thus, subjects were equally poor in all conditions, regardless of whether they were reinforced or whether the experimenter identity was consistent across encoding and retrieval. Furthermore, an exact McNemar test revealed that subjects that participated in both the present experiment and Experiment 1 performed better in Experiment 1 (Mean proportion of correct subjects = 0.78, $SD = 0.42$) compared to Experiment 2 ($M = 0.33$, $SD = 0.48$), $p = 0.004$, suggesting that some element(s) of Experiment 1 (the large food amount or baiting procedure) resulted in enhanced memory performance compared to when this/these element(s) were absent.

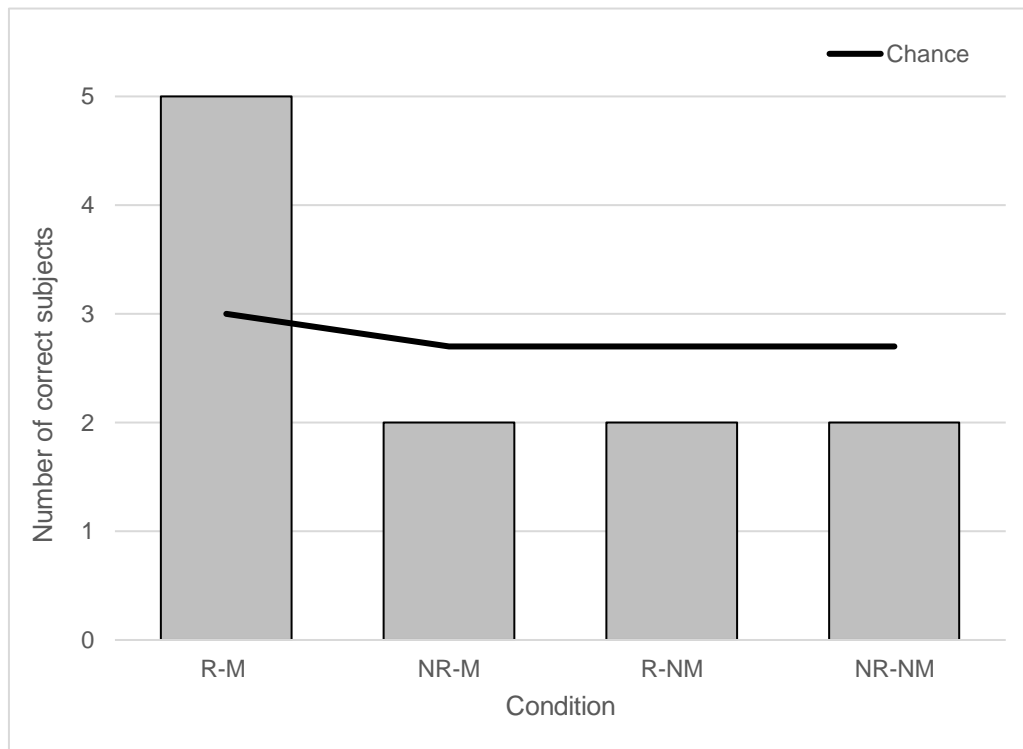


Figure 3.4 Number of correct choices in each of the four conditions. R-M = reinforced matching, NR-M = non-reinforced matching, R-NM = reinforced non-matching, NR-NM = non-reinforced non-matching. Chance shows the number of choices that would be correct if the apes were performing at chance. Figure reproduced from Lewis et al. (2017a), in accordance with Wiley Terms and Conditions for Self-Archiving.

3.6.3 Discussion

Subjects failed to recall the location of the baited container after two weeks.

Performance was below chance in all conditions, suggesting that reinforcement did not influence performance. Moreover, the finding that performance in the true baseline condition (R-M; at chance performance) was poorer than performance in the intended baseline condition of Experiment 1 (no-mask; above chance performance), suggests this no mask condition was not a suitable baseline with which to compare the mask

condition to, and may explain why no difference was found between the conditions in Experiment 1. This is also supported by the finding that subjects as a whole (conditions pooled) performed significantly better in Experiment 1 than in Experiment 2.

Additionally, there appeared to be no effect on performance when the identity of the experimenter at encoding and retrieval did not match, suggesting that the experimenter was not bound to the memory trace. Although this suggests binding did not occur, it is important to note that even if multiple features were bound to memory, the combination of these features at retrieval does not necessarily mean that recall will be successful. This is because the efficiency of cues is not only determined by the overlap of features at encoding and retrieval (encoding specificity principle), but also the extent to which they are overloaded, overshadowed or outshined (see Chapter 1). The cue that was manipulated was the experimenter identity. As the apes are tested by numerous experimenters, and often multiple times per day, it may be that this particular cue was overloaded or overshadowed. That is, the experimenter may not have been an effective cue because it was associated with numerous similar episodes (overloaded), or because the very fact that the apes see experimenters during testing every day meant the experimenter was not salient, and subsequently not encoded (overshadowed). Furthermore, the other relevant cues may also have been overloaded or overshadowed; the location has been used for many other tasks (e.g. Call, 2006), platform tasks have been done many other times (e.g. Call, 2004), and similar containers have been used in other tasks (e.g. Call, 2006). Thus, even if binding took place, there was nothing distinctive about the bound representation to lead to the recall of this specific baiting event. This is consistent with Eysenck's theory of distinctiveness (Eysenck, 1979), in which "performance is assumed to depend far more on distinctive than non-distinctive

overlap” (p.94). As such, the failure to recall the baited location may not necessarily a result of a failure of binding, but rather a lack of distinct information in the bound representation to retrieve a specific memory, and further highlights the influence of distinctiveness on the recall of a past event.

With regards to reinforcement, it may also be premature to conclude that reinforcement had no effect on recall performance. As the reinforcement value in this experiment was small, it may not have been great enough to influence performance in the same way as it may have done in Experiment 1 (in which a large amount of banana was received). Furthermore, due to the small sample sizes in each condition of this experiment, the analyses may have suffered from a lack of statistical power. With more subjects, a significant difference may have emerged between conditions, thus the findings should be taken with caution.

3.7 Experiment 3 | Reinforcement

The final Experiment aimed to clarify the findings from the previous two experiments. In Experiment 1, performance was above chance in both conditions; however, it was unclear as to whether this was due to a large reinforcement in both conditions, or because both conditions were distinctive. In Experiment 2, it was established that the true baseline condition did not result in above chance performance, suggesting that good performance in the intended control condition of Experiment 1 was due to distinctiveness. This was further supported by the finding that reinforced conditions did not result in better performance than non-reinforced conditions, suggesting that reinforcement may not have been the primary influence in Experiment 1. However, as the reinforcement value was low, it is still not certain as to whether performance in Experiment 1 could be explained by a large reinforcement in both conditions. As such, Experiment 3 aimed to directly address the role of reinforcement in memory performance in a non-distinctive event. The difference in reinforcement value between two events was greatly increased, with one event resulting in high reinforcement, and a second event resulting in no reinforcement. If reinforcement explains good memory performance, then performance should be above chance in the highly reinforced event and at chance in the non-reinforced event. Conversely, if distinctiveness predicts performance, then performance in both conditions should be at chance, as neither condition is distinctive. Furthermore, performance should be comparable to Experiment 2, in which none of the events were distinctive, and poorer than Experiment 1, in which both events were distinctive.

3.7.1 Specific methods

3.7.1.1 *Subjects*

Twenty-nine apes took part in this experiment (see Table 3.2): 16 chimpanzees ($M=27$ years), eight bonobos ($M = 17$ years) and five orangutans ($M = 17$ years). The six chimpanzees that only took part in Experiment 2 during January 2017 did not take part here. Additionally, three chimpanzees (Kara, Ulla and Annett) were transferred to other zoos before they could take part, and one orangutan (Dokana) did not take part due to her infant disrupting testing.

3.7.1.2 *Apparatus*

The apparatus was identical to Experiment 2, except that the containers were green with slightly different measurements (Length = 13 cm, Width = 7 cm, Height = 6 cm). Again, this was to reduce proactive interference from the previous Experiments, without substantially changing the task demands.

3.7.1.3 *Design*

Apes were allocated to one of two conditions: reinforced (R) or non-reinforced (NR). In most cases, subjects were assigned to the opposite reinforcement condition they received in Experiment 2 (e.g., If they were assigned to the R condition in Experiment 2, they were now assigned to the NR condition). This was to reduce possible interference from the previous study.

3.7.1.4 Procedure

The procedure at exposure was the same as Experiment 2, except the baiting amount was increased to half a banana (5 sliced pieces). The test procedure was also the same, but with the exclusion of the NM conditions, meaning that the experimenter present was always the one that had conducted the exposure.

3.7.1.5 Data analysis

The data analysis is described in the general methods section. An additional analysis considered whether apes' performance in this experiment differed from performance in Experiment 1 and Experiment 2 (all conditions in each experiment pooled). This was conducted only on subjects that completed all three Experiments ($N=23$), using an exact Cochran's Q.

3.7.2 Results

All subjects required two trials during the exposure, except for Frederike who required three. In the R condition ($N=14$), the baited container was selected 35.71% of the time, which was not different to chance. In contrast, the baited container was selected 60% of the time in the NR condition ($N=15$), which was significantly greater than chance ($p = 0.05$, 95% CI [0.32, 0.84]). Thus, subjects recalled the location of the baited container in the NR but not the R condition (see Figure 3.5).

Performance between the three Experiments differed, $Q(2) = 8.67$, $p = 0.02$.

However, exact McNemar tests (alpha set to 0.025) revealed that performance in this Experiment (Mean proportion correct = 0.52, $SD = 0.51$) did not differ from performance

in Experiment 1 ($M=0.78$, $SD=0.42$), $p=0.09$, or Experiment 2 ($M=0.30$, $SD=0.47$), $p=0.13$.

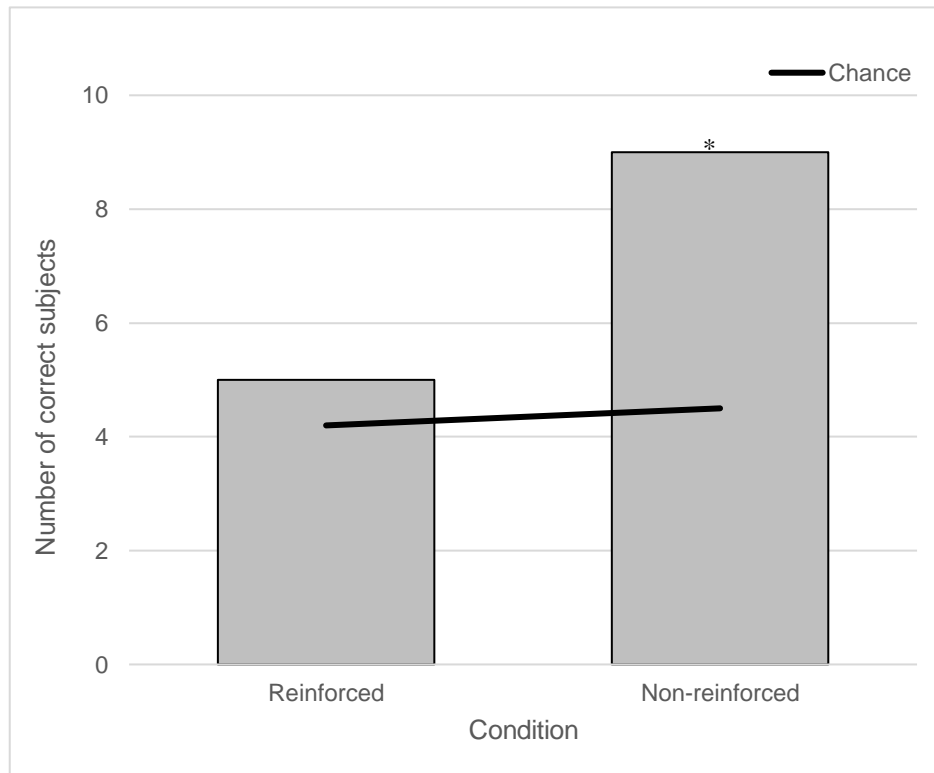


Figure 3.5 Number of correct choices in the reinforced and non-reinforced condition. Chance shows number of choices that would be correct if performing at chance. * = 0.05. Figure reproduced from Lewis et al. (2017a), in accordance with Wiley Terms and Conditions for Self-Archiving.

3.7.3 Discussion

Apes failed to recall the location of the baited container when they were reinforced for a correct choice at exposure, but were successful when the reinforcement was removed. This is surprising, as it is at odds with any law of reinforcement. Furthermore, as the apes were expecting to be rewarded with food upon a correct choice, the ‘throwing

away' of food can be seen as a negative punishment (i.e., removal of a reward). Negative punishment results in the decrease of a behaviour occurring again (the opposite of positive reinforcement), thus if the apes' performance was based on associative learning, they should not only perform well in the positive reinforcement condition (R condition), but poorly in the negative punishment condition (NR condition); the results indicate the opposite finding. As such, apes' memory performance cannot be attributed to associative learning.

However, the findings also do not appear to support the predictions regarding distinctiveness. As both events were not intended to be distinctive, performance between conditions should not have differed. Likewise, performance should have been worse than Experiment 1, in which both conditions were distinctive. However, it may be that the original prediction was misguided; as with baiting the container outside the testing room in Experiment 1, 'throwing' away a large amount of food is not a common occurrence, and is therefore distinctive (different in comparison to the standard procedure). The crucial difference between the throwing away of food in Experiment 2 and this experiment is the amount of food that was thrown away. As the apes rarely receive such large food amounts, it is highly unlikely they have experienced such a large amount being thrown away. In contrast, they have had experience of small amounts being discarded, such as in reverse contingency tasks (Uher & Call, 2008; Vlamings, Uher, & Call, 2006). Furthermore, the apes in the NR condition here were not in either of the NR conditions in Experiment 2 (except for Lome), thus they did not have a recent experience of food being thrown away. Consequently, even though it was not intended to include a distinctive feature to the event, the act of throwing away a large amount of food may have been distinctive, resulting in enhanced performance.

This is further supported by the finding that performance in this condition was comparable to performance in Experiment 1 (i.e., above chance), in which the only common variable between the experiments was distinctiveness.

Such a finding is consistent with distinctiveness effects in human memory, in which distinctiveness enhances memory regardless of reinforcement (Guitart-Masip, Bunzeck, Stephan, Dolan, & Duzel, 2010; Hunt & Worthen, 2006). Furthermore, research with primates suggests that a novel stimulus attracts attention even when it is associated with a negative outcome (Foley, Jangraw, Peck, & Gottlieb, 2014). In the human literature, this effect is referred to as an “attention magnet” (Laney, Campbell, Heuer, & Reisberg, 2004), in which negatively arousing stimuli capture attention and subsequently are remembered very well. This may also explain the results observed here.

Alternatively, the good performance in the NR condition here could be due to the role of experience¹². At the time of this experiment, the apes had already been tested on two very similar tasks (i.e., Experiments 1 and 2). As such, the apes may have anticipated that they would be tested on the location of the baited container. However, if this were the case, performance in the R condition would also be expected to be good, yet here they perform at chance. Furthermore, it would be expected that performance would improve from Experiment 1 to Experiment 3, again this is not the case, with the best overall performance in Experiment 1.

As such, the findings appear to be more consistent with a distinctiveness effect; that is, performance in the R condition was at chance, and the R condition had no

¹² This suggestion was provided by an anonymous reviewer.

distinctive features (although the large food amount was distinctive in Experiment 2, here it was no longer distinctive due to the very fact it had recently occurred in Experiment 1). Thus, just like Experiment 2, a lack of distinct information may have hindered successful recall. Moreover, performance in the NR condition was above chance, even though reinforcement was completely removed, suggesting that distinctiveness, as opposed to reinforcement, is important for successful recall.

3.8 General discussion

The purpose of this study was to investigate the influence of distinctiveness on the recall of a past event. To address the common concern that an animal's performance may be based on simpler associative mechanisms, as opposed to more complex cognitive processes, predictions were generated from the perspective of both distinctive processing and associative learning.

In the first experiment, it was found that apes could successfully recall the location of the baited container after two weeks, and that performance was equally high in both the distinctive and non-distinctive event. As it was unclear as to whether performance was due to the high reinforcement received in both events, or whether the undistinctive event was un-intentionally distinctive, a second experiment was conducted to establish a true baseline condition. Additionally, it was assessed whether performance could be hindered or enhanced from this baseline by manipulating reinforcement, and by matching the experimenter at encoding and retrieval.

The results indicated that the apes failed to remember the location of the baited container in any of the conditions, showing a clear drop in performance from Experiment 1. Furthermore, there was no difference in performance between conditions, indicating that when apes were reinforced for a correct response their performance was not any better than when they were not reinforced. These results suggest that the performance in Experiment 1 was likely due to the distinctiveness of both events, and not due to reinforcement. However, the lack of difference between reinforced and non-reinforced conditions may have been due to the small reinforcement amount in the reinforced conditions. Consequently, Experiment 3 was conducted to clarify if reinforcement may have accounted for the findings in Experiment 1. The

results showed that when apes were reinforced with a large amount of food during an undistinctive event, performance was at chance. When the apes were not reinforced for a correct choice and a large amount of food was thrown away (an act that was likely very distinctive), performance was above chance and comparable to performance in Experiment 1. These results clearly show that reinforcement is not a predictor of performance, and suggest that distinctiveness is.

The results from Experiment 3 clarified that memory performance does not improve as reinforcement value increases, but rather contrary to any law of reinforcement, performance was enhanced when reinforcement was removed. Furthermore, as the apes expected to receive food upon a correct choice, throwing away of food can be seen as a punishment (i.e., choosing the baited container results in a positive stimulus being removed; negative punishment). If the apes' performance was based on associative learning via negative punishment, then they should avoid the baited container and choose one of the other containers. Again, this was not the case. As reinforcement (and negative punishment) cannot explain the successful memory performance in Experiment 3, and did not have an influence on the results in Experiment 2, it is unlikely that it was the sole explanation for the good memory recall in Experiment 1. Conversely, the distinctiveness effect may be a likely explanation for the findings across all three experiments. In Experiment 1, both events were distinctive, due to the use of a novel procedure and a large food reward, resulting in good memory performance. In Experiment 2, all events were undistinctive, and many of cues were overloaded, resulting in poor recall as a result of a lack of any unique or diagnostic information to aid retrieval. In Experiment 3, the standard baiting procedure and large amount of banana were not distinctive (although the large banana was distinctive in

Experiment 1 due to novelty, its very occurrence in Experiment 1 meant it was no longer novel in Experiment 3), and recall was poor. In the non-reinforced condition, in which a large amount of food was thrown away (an event likely never experienced by the apes), recall was good. Thus, the findings across the three experiments suggest that memory was enhanced for distinctive events, irrespective of reinforcement, which is consistent with distinctiveness effects in human memory (Hunt & Worthen, 2006).

Interestingly, the results are also consistent with the enhancement of memory for emotionally arousing events. As previously mentioned, emotion enhances memory for focal information (Burke et al., 1992; Easterbrook, 1959; Kensinger, 2009; Schmidt & Saari, 2007). In the case of Experiment 1, the mask was the focal emotional source of the event, with the location of the containers peripheral to this source. In contrast, in Experiment 3 the focal source of emotional was the throwing away of food from the baited container. Thus, the location of the container was directly tied to the emotional source. The findings that the mask did not enhance performance relative to no-mask, but throwing away food did relative to receiving food, is consistent with this focal memory enhancement. Furthermore, this enhancement effect for focal information has been proposed to be particularly strong for negatively arousing events (Kensinger, 2009), which is consistent with the enhanced memory performance found when a negative punishment was received (i.e., throwing away food). However, as the emotionality of the events was not tested, the influence of emotion in these experiments can only be speculated upon.

Although the findings are more consistent with distinctive processing, as opposed to associative learning by reinforcement, alternative explanations cannot be completely ruled out, especially when the distinctiveness account did not always

directly follow from the data. For instance, a distinctiveness account would predict enhanced performance for the mask condition in Experiment 2, and better performance in the matching condition compared to the non-matching condition of Experiment 1. However, when accounting for other well-known memory concepts, such as cue-overload in Experiment 2 and attention magnets in Experiment 1, the data remain consistent with a distinctiveness account.

Regarding the limitations of this study, it may be argued that the apes did not assume that the same container would be baited after a two-week delay¹³. As the apes are tested on many similar tasks, which are often unrelated to one another, the apes' experimental history may predispose them to assume that tasks separated in time are not related to one another. However, I believe this is not the case for two reasons: first, the apes successfully assumed that food was in the same location in Experiments 1 and 3, as shown by selecting the correct container above chance. Second, previous research from this lab using a similar design has shown that apes can successfully remember the location of a baited container after twenty-four hours (Martin-Ordas & Call, 2011). Thus, the apes are familiar with this type of memory retention task, and have proven to be successful at it.

Another potential limitation is the sample size. Unfortunately, it was only possible for subjects to complete one test per experiment, as during each test, feedback was given about the location of the hidden banana. If subjects were subsequently tested again on the same event, their response may be based on the feedback received at test, rather than their memory of the baiting event. Not baiting any of the containers at test

¹³ This suggestion was provided by an anonymous reviewer

would also not have resolved this problem, as if the subject made a correct choice and found nothing, they may have avoided this container in the subsequent test. Likewise, subjects could not take part in multiple conditions within an experiment, as participation in one condition would likely have influenced performance in another. For example, a subject that sees banana being hidden in the left container in the mask event, followed by the right container in the non-mask event, may perform worse on the non-mask event because of interference from the mask event. This issue could have been resolved by always baiting the same container; however, then the apes could simply learn over time which container is always baited, and would not need to recall the baiting event. Moreover, repeated testing in this way may have lead the apes to anticipate a test, and again to learn to recall a particular location, rather than remember the baiting event. Although this may have occurred in the current testing design (due to completing three similar tests), performance would be expected to improve over time as the subject learned the rule; this was not the case. As such, design constraints and the limited sample size meant that the data set size was modest, and subsequently potential differences between conditions may not have been observed due to a lack of power. This is particularly true in Experiment 2 (as previously mentioned).

As well as a potential lack of power, the limited sample size meant that the same subjects were tested in all three experiments. Consequently, performance may have been driven by certain subjects always performing well, and other subjects always performing poorly. However, inspection of the data revealed that individual performance was inconsistent across experiments; only two of the twenty-three subjects that participated in all three experiments passed all (Tai), or failed all (Luiza) experiments. Additionally, only three of these twenty-three subjects chose the same

location in all three experiments, suggesting the apes did not choose locations based on a location bias.

Finally, as with many other studies investigating the recall of past events in animals, being unable to ask the animals how they selected the correct location leaves open the possibility that performance was not based on recalling a past event. Although it is clear that performance was not a result of associative learning through reinforcement, it is possible that the apes' response may have been based on other non-recollective processes, such as an automatic familiarity response (Jacoby, 1991). In this instance, although the apes may have initially processed the event as distinctive, and encoded multiple elements about the context and other details, they may not have recalled these details at test. Instead, because the very act of distinctive processing leads to greater attention to the item in question, this increased attention may have meant the baited container was chosen at test based on familiarity strength, rather than recollection. That is, apes in the distinctive conditions paid additional attention to the baited container, in comparison to apes in the non-distinctive conditions, and subsequently performed better in distinctive conditions. Although this possibility cannot be ruled out, I believe that memory performance based on familiarity strength would be poor after a two-week retention period, as familiarity strength would diminish over time, a point also made by Schwartz et al. (2005). Furthermore, it would not be unreasonable to assume that subjects also paid more attention to the baited container in comparison to the un-baited containers in both distinctive and non-distinctive events (i.e., their attention was focused on where the food was). Thus, even in non-distinctive conditions, if performance was guided by familiarity they should still show a preference for the baited container (which they do not).

To summarize, the results of these experiments suggest that distinctiveness enhances apes' recall of a past event, irrespective of reinforcement. Although the results do not always follow directly from the predictions derived from a distinctiveness explanation, they are nonetheless consistent with a distinctiveness based account, and in clear contrast to performance based on associative learning. As distinctiveness is dependent upon context, such effects would not have occurred without the apes encoding features within their context, thus the results also suggest the apes were able to bind contextual features. Additionally, the results are consistent with other distinctiveness effects found in insolation paradigms in apes (Beran, 2011; Parker et al., 1998), but moreover, expand these results to memory of past events.

The next chapter aims to assess the influence of distinctiveness on the spontaneous (involuntary) recall of a past event, and to further investigate whether the identity of an experimenter can act as an effective cue if present at encoding and retrieval.

Chapter 4 | Involuntary memory

One way to solve this dispute is to suggest that the involuntary form for mental time travel may be shared among other species.

(Rasmussen & Berntsen, 2009, p. 1146).

4.1 Introduction

As discussed in Chapter 1, the existence of episodic memory in animals is highly debated. Although numerous paradigms, across various species, provide evidence of elements of episodic memory, they fall short of showing Tulving's (1972, 1983, 2001) phenomenological criteria. However, as the dispute so far has centred upon voluntary memory, the above quotation proposes an elegant resolution, whereby animals may have the less cognitively demanding involuntary form of episodic memory. This chapter, therefore, aims to investigate whether great apes may have the involuntary form of episodic memory.

Involuntary memory refers to the spontaneous recollection of personal past events (Berntsen, 1996). Although such memories have been largely overlooked in the human literature, recent research has shed much light on the nature of involuntary memories. We now know that despite the difference in retrieval mechanisms, voluntary and involuntary memories share many commonalities. For instance, they both show recency effects (Berntsen, 1998; Schlagman, Kliegel, Schulz, & Kvavilashvili, 2009), are related to current concerns (Johannessen & Berntsen, 2010), can be negative and positive in nature (Berntsen & Rubin, 2002), and concern both past and future events (Berntsen & Jacobsen, 2008). Involuntary memories occur as frequently as voluntary

memories (Rasmussen & Berntsen, 2011; Rasmussen, Ramsgaard, & Berntsen, 2015), and are evident in many diary studies (e.g. Mace, 2005; Rubin & Berntsen, 2009), indicating that they are a common occurrence.

Such findings suggest that involuntary memories do not occur merely as a dysfunction of normal memory, manifesting only in clinical disorders such as post-traumatic stress (where the focus of investigation has been). Rather, they are a fundamental ‘basic mode’ of remembering, just as voluntary memories are also a fundamental mode of remembering (Berntsen, 2010). Berntsen (2010) proposes four central claims regarding the nature of involuntary memories: first, they are universal; that is, everyone with intact memory has involuntary memories (although she notes that this may be refuted at some stage). Second, they occur frequently, moreover they occur just as often as voluntary memories. Third, involuntary and voluntary memories are not separate systems, rather they are both part of the episodic memory system. They share many commonalities during encoding and storage, but differ in their retrieval mechanisms. Fourth, they are not a dysfunction of memory, but serve the function of enabling us to live beyond the present; if memories were only recalled deliberately (voluntary) as a response to achieving a purpose or goal, the scope and timescale of memories would be very limited. They also enable us to effortlessly retrieve relevant information (via associative retrieval mechanisms), which may then provide us with helpful information on how to act or behave in a current situation (Berntsen, 2009; Rasmussen & Berntsen, 2009).

Recently, it has been proposed that animals may also have this basic involuntary mode of remembering (Berntsen, 2009; Berntsen, 2010; Berntsen & Jacobsen, 2008;

Clayton, Bussey, et al., 2003; Donald, 1991; Rasmussen & Berntsen, 2009). As mentioned previously, involuntary memories arise without strategic effort and are often triggered by external cues in the present environment that overlap with the memory trace. The associative retrieval mechanism of involuntary memory means they rely much less on cognitively demanding executive control processes, and instead by-pass the top-down strategic retrieval mode, resulting in rapid memory formation (Conway & Pleydell-Pearce, 2000). Furthermore, as episodes are often encoded incidentally (i.e., not deliberately), they are more easily retrieved in the same incidental way (i.e., involuntarily; Berntsen & Hall, 2004). Indeed, as episodes tend to be activated by distinct and unique cues, they are difficult to retrieve through top-down, voluntary, search processes (Berntsen, 2009; Rasmussen & Berntsen, 2009). As such, the relative automatic nature of involuntary episodic memories means that they may be more likely to occur in animals than the more cognitively demanding voluntary version (Berntsen, 2009; Rasmussen & Berntsen, 2009).

Direct evidence for a reduction in control processes in involuntary memory retrieval has been shown by reduced activation in brain areas responsible for control processing (Hall et al., 2008; Hall et al., 2014). For instance, Hall et al. (2014) tested participants involuntary and voluntary recall of previously learnt associations. Here, participants first learnt to associate different sounds with different pictures. During the recall phase, they heard the same sounds whilst in an fMRI scanner, and were asked to locate which side (right or left) the sound was loudest. For the voluntary memory group, they were also asked to try and recall which picture was associated with the sound. After the scan, all participants were presented with the same sounds again and asked whether they had recalled the image associated with each sound during the scan,

and if so, how much effort was required to recall the image. Results showed that subjects in the voluntary condition recalled more images, but that subjects in the involuntary condition recalled images with much less effort. Furthermore, the scan results indicated that voluntary and involuntary recall activated many of the same areas associated with successful episodic retrieval (the medial temporal lobe, posterior midline, ventral parietal cortex and sensory reactivation regions), but that voluntary memory additionally activated the left dorsolateral prefrontal cortex, a region that is associated with controlled episodic retrieval.

Consistent with this, research has also shown that involuntary retrieval is quicker than voluntary retrieval, which is indicative of less control processing (Berntsen et al., 2013; Schlagman & Kvavilashvili, 2008). Furthermore, specific memories in older adults tend to be recalled easier if they are retrieved involuntarily, as opposed to voluntary (Schlagman et al., 2009). The relative ease with recalling specific episodes involuntarily, as opposed to voluntarily, likely reflects the reduced control processes required during involuntary recall - older adults tend to show a reduction in cognition (Li, Lindenberger, & Sikström, 2001), therefore a reduction in cognitive processing would aid recall.

The associative retrieval mechanism of involuntary memory means that memories are often retrieved in the absence of goals or specific task demands (Berntsen & Jacobsen, 2008; Johannessen & Berntsen, 2010; Schlagman, Kvavilashvili, & Schulz, 2007), allowing for the “automatic spreading activation that leads to the retrieval of an involuntary memory” (Berntsen, 2010, p. 139). Successful activation is usually triggered by an overlap of unique cues in the current environment that match a memory trace. Thus, the activation of an involuntary memory is closely tied to the

encoding specificity principle, and crucially, the extent to which the cue(s) provides diagnostic information in relation to stored information (Berntsen, 2009), referred to as cue-item discriminability (Rubin, 1995). This means that it is not enough for merely an overlap between the memory and features at retrieval to cue an involuntary memory, rather, the features that overlap must provide enough information to distinguish a specific memory from other memories that share some of the same features present at retrieval. The importance of this point is made particularly evident when one considers how many features in the external environment, at any given time, may match the features of stored memories (e.g., hearing bird song does not trigger all memories that include birds singing). If this were the case, the vast amount of sensory and external information that we perceive in our everyday activities would lead to a bombardment of involuntary memories, which clearly is not the case (Berntsen, 2009).

There are multiple ways in which a cue can successfully isolate a specific memory. For instance, a cue that matches numerous events is more likely to trigger an event that is particularly emotional, that has been rehearsed, or occurred recently, than an event that lacks these qualities (Berntsen, 2009). Of particular relevance to the research in this thesis, cue-overload (a lack of), distinctiveness and binding also result in cue-item discriminability (Berntsen, 2009). A cue that matches multiple events (cue-overload) is *unlikely* to lead to the spontaneous retrieval of a specific memory; however, if one of the events it matches is distinctive from the other events, then recall of that distinctive event is likely (e.g., I have multiple memories of thunderstorms, but upon hearing a thunderstorm I often spontaneously remember the one time when I got caught out in a storm in Leipzig on my bike). Likewise, a cue that features in only one specific event (un-overloaded) is likely to lead to retrieval of that event (e.g., a child

that has only seen a thunderstorm once in his life may remember the thunderstorm the second time he sees one). Additionally, if multiple cues are present at retrieval that individually feature in multiple events, they are unlikely to lead to the recall of a specific event; however, when taken in combination they will likely match one event more than another, and lead to recall of that event (e.g., I have many memories of riding my bike, and many more of spending time with my friends, but only one memory of my friends and I riding a four-person bike around an island in Budapest). Consequently, involuntary memories are most likely to be retrieved when they are of events that are specific and distinctive, and when there are multiple external cues that match the memory. This has been evidenced in diary studies, in which participants report that their involuntary memories often share overlapping features with the external environment (Berntsen, 1996), are of unusual, rather than common events (Berntsen, 1996; Berntsen & Hall, 2004), and are usually specific, unique events, as opposed to general events (Ball & Little, 2006; Berntsen & Hall, 2004), including specific future events (Berntsen & Jacobsen, 2008).

In order to examine whether the involuntary form of episodic memories may exist in animals, this chapter¹⁴ aims to investigate whether great apes can recall a distinctive, specific event, when cued with overlapping external features that are diagnostic of the specific event. As previous research has shown that animals can recall (elements of) past events voluntarily, it follows that they should be able to recall events via the less cognitively demanding involuntary counterpart. Moreover, evidence of

¹⁴ This chapter formed the publication by Lewis, Call, and Berntsen (2017b; see appendix B). Many of the themes and ideas that are expressed in the publication are expressed here, with some text and figures reproduced verbatim. I thank David Rubin for his comments regarding the forgetting curve, and Roger Mundry for his help with the statistical analysis.

involuntary recall of past events may provide somewhat of a resolution to the ongoing episodic memory debate in animals, whereby the evolutionary earlier and less cognitively demanding involuntary retrieval may be shared between species, but the voluntary expression reserved for humans (Berntsen, 2010; Berntsen & Jacobsen, 2008; Clayton, Bussey, et al., 2003; Rasmussen & Berntsen, 2009). In the next section, I discuss the current research relating to involuntary memory in animals.

4.2 Previous research

Research regarding the recall of past events in animals has generally focused on voluntary memory, with the little research there is mostly assessing involuntary memory indirectly. For instance, paradigms that have provided overlapping external cues at encoding and retrieval have shown that animals can recall (elements of) past events (Clayton, Yu, et al., 2001; Crystal, Alford, Zhou, & Hohmann, 2013; Crystal & Smith, 2014; Kano & Hirata, 2015; Mendes & Call, 2014; Panoz-Brown et al., 2016). For instance, scrub jays could recall what was hidden, when, and where, when presented with an external cue (a sandbox) that was unique to a specific caching event (Clayton & Dickinson, 1998). However, as these studies were not aiming to distinguish between involuntary and voluntary recall, they provide only limited support for involuntary memory. This is because they included task demands or goals at test, and used repeated events; characteristics that are more consistent with voluntary, than involuntary retrieval (Berntsen & Jacobsen, 2008).

One particular study that was motivated by research on human involuntary remembering is by Martin-Ordas et al. (2013). They tested chimpanzees and orangutans

on their ability to remember two similar tool hiding events. In the first event, the apes were presented with a task that required a tool to obtain food, but were not provided with the tool. After a delay of fifteen minutes, an experimenter hid two tools in two different locations in the apes' enclosure, one of which was useful to solve the task. The apes were then able to retrieve the tool and obtain the food. They experienced this event four times. Three years later they returned to the same room and were presented with the same task, however, this time the tools were already hidden in the same locations as before. The apes spontaneously and immediately searched the tool locations, and upon finding the appropriate tool successfully completed the tool task. A second experiment followed the same procedure, except the apes were presented with a slightly different task and tool, and were only presented with it once. This time the retention period was two weeks. Again, the apes spontaneously and immediately searched the location in which the tool was hidden two weeks previously, and moreover, did not incorrectly search the location from the previous event. The authors concluded that the apes were able to distinguish between the two events (and other similar events) by binding the relevant external cues at retrieval, resulting in a unique and diagnostic representation. As many of the cues in isolation were common to both events, failure to bind the cues would have resulted in many memory traces matching the cues (see Chapter 1 for details). As involuntary memories are often triggered by discriminable external cues, and are retrieved faster than voluntary memories, the authors suggest the apes' performance is consistent with involuntary memory.

Although this study was the first to specifically address involuntary memory, and provides compelling evidence that apes are able to recall events after extremely long delays, the paradigm is subject to the same limitations as the studies that did not

aim to assess involuntary memory. At test, the apes were presented with a task that required a tool in order to obtain some food, thus they were presented with a goal-directed task. Consequently, they may have deliberately (voluntarily) recalled the memory of the tool hiding event in order to achieve their goal of obtaining the food. Likewise, although it is highly impressive that the apes recalled where a tool was hidden three years ago, the event that occurred three years ago was a repeated event and not a specific event. This is problematic, as the apes may have come to expect to be presented with a task, followed by the hiding of a tool, and strategically encoded where the correct tool was hidden. This information could then be recalled in the absence of contextual details (i.e., recall of semantic and not episodic memory; see Chapter 1). Furthermore, the majority of involuntary memories are of specific and not repeated events. As such, although it's possible that the apes involuntarily recalled the tool hiding event from three years ago, semantic and voluntary episodic memory are also viable explanations for successful performance.

Whilst it is often difficult to present animals with a test that is absent of any goal, a novel and ingenious eye tracking paradigm by Kano and Hirata (2015) was able to do just this. In this paradigm, apes viewed a short movie in which an aggressive 'King Kong' character entered through one of two doors and attacked a human experimenter. Whilst watching the movie, an eye-tracker monitored the ape's gaze. Twenty-four hours later the apes completed a test, in which they simply watched the same movie again whilst the eye tracker monitored their gaze. The results showed that the apes made anticipatory looks towards the door in which the 'King Kong' character would enter; that is, they looked at the door before the character entered, suggesting that they recalled what happened in the movie. In a second movie, one of two weapons (a

hammer and a sword) was selected by a human experimenter, and was then used to attack the King Kong character. The apes made anticipatory looks towards the weapon that would be selected, even when the weapons locations were switched from the original viewing. Thus, the apes demonstrated independent recall of where (which door), and what (which weapon), after a single exposure to each movie. Unlike other paradigms, the apes did not recall these details in order to obtain food or a desired goal, as here the apes were given food to eat during the viewing of the movie, regardless of their gaze behavior. Consequently, these results are consistent with the way in which involuntary memories are retrieved (i.e., triggered by overlapping external features at encoding and retrieval, and in the absence of task demands and goal directed motivations).

Despite the positive findings from this study, and the tentative evidence from other cued recall studies, there is still much research needed to further investigate involuntary memories in animals. For instance, in humans involuntary memories are recalled from various time points in one's past (Berntsen & Rubin, 2002; Rubin & Berntsen, 2009), thus are well remembered over time, and not restricted to memories from days or weeks ago (although most occur within the last three years; Berntsen, 1996). Current evidence with apes suggests involuntary memories can be recalled after twenty-four hours (Kano & Hirata, 2015), but the evidence for longer delays is limited by task designs (e.g., Martin-Ordas et al., 2013). Additionally, we know that involuntary memories are often of distinctive and unique events, and although previous studies have used distinctive events (e.g. Kano & Hirata, 2015; Martin-Ordas et al., 2013; Mendes & Call, 2014), it has yet to be addressed whether a distinctive event is more likely to be triggered by diagnostic overlapping cues than a less distinctive event

(i.e., is involuntary retrieval more likely to occur when the event is distinctive).

Likewise, a distinctiveness effect (see Chapter 3) has been found in various memory tasks in rats (Izquierdo, Barros, Medina, & Izquierdo, 2003; Reed et al., 1991; Reed & Richards, 1996), and primates (Beran, 2011; Lewis et al., 2017a; Parker et al., 1998; see also Chapter 3), but it's yet to be investigated in the recall of an involuntary past event.

We also know very little about the encoding-retrieval match in animals. Although evidence suggests that overlapping information at encoding and retrieval can lead to successful memory recall, as long as it is diagnostic of the event (Crystal & Smith, 2014; Martin-Ordas et al., 2013), it has yet to be determined if certain overlapping features are more effective as retrieval cues than others. In the human autobiographical literature, overlapping features such as activities and objects (what), and people (who), are commonly acknowledged as salient memory cues (Berntsen, 1996; Berntsen & Hall, 2004); however, it has yet to be assessed whether the same cues are just as salient and effective as retrieval cues in animals. For instance, Mendes and Call (2014) incorporated the use of social cues and contextual cues (location, objects) in a foraging event (see Chapter 3 for study details). They found apes could successfully recall the foraging locations, but acknowledged they could not disentangle whether the memory for the locations was cued by the overlapping social, non-social, or combination of cues. Additionally, although the results from Experiment 2 of the previous chapter suggested that social information was not an effective retrieval cue, this may have been because the event was indistinct, and the social cue was not unique to the specific event. As the social cue was overloaded, and the event was undistinctive, the social cue would have likely been ineffective at triggering the target

memory. As such, it is unclear whether social (who) information can be effective as a retrieval cue.

4.3 Experiment 1 | Involuntary recall of a past event

4.3.1 Aims

The primary aim of this study was to investigate whether apes can recall a past event involuntarily. To ask this question, apes were unexpectedly tested on their memory of a distinctive, non-goal-directed, food hiding event that occurred once, after one of three delay periods: two weeks, ten weeks or fifty weeks. The two-week delay aimed to replicate the previous finding by Martin-Ordas et al. (2013), but using a non-goal directed task. The additional longer delays enabled investigation as to whether the apes could recall a non-goal directed event after longer time periods, as is the case in human involuntary recall, and to assess whether forgetting would occur over time. A logarithmic-scale was used that roughly covered a one-year time period, as this scale best reflects the rate of forgetting in human long-term memory (Ebbinghaus, 1964; Rubin & Wenzel, 1996). A similar forgetting curve has also been observed in animal working memory (see White, 2013), yet less is known regarding long-term memory retention over time; evidence suggests memory performance is relatively stable over time, (Bogale, Sugawara, Sakano, Tsuda, & Sugita, 2012), though prone to increased error (Balda & Kamil, 1992), and differs between species (Bednekoff et al., 1997).

To investigate whether a highly distinctive event would be recalled better than an event that was less distinctive (albeit, still distinctive), the type of food hidden during the hiding event was manipulated. Half of the subjects found a large cache of

familiar (but uncommon) bread during the hiding event, whereas the other half found a large cache of cardamom flavored pellets, which were completely novel and surprising in taste. The taste was made distinctive (as opposed to the visual appearance), as currently there is only evidence for a distinctiveness effect on recall with visual information (Beran, 2011; Parker et al., 1998). Furthermore, as odors are often effective as cues for retrieving memories in humans (Aggleton & Waskett, 1999; Pointer & Bond, 1998; Saive, Ravel, Thévenet, Royet, & Plailly, 2013), it is likely they will also be effective in animals.

To investigate whether social information can be an effective retrieval cue, the overlap of social information at encoding and retrieval was manipulated. This was achieved in the same way as Chapter 3, in which the identity of the experimenter at encoding and retrieval either differed, or remained the same. Although this manipulation produced no effect on performance in Chapter 3, the to-be-remembered event was indistinct. In this current experiment, the event is distinctive, and the experimenter is likely more salient due to receiving a more prominent role in the event (see methods for details). Thus, even though the experimenter identity is just as overloaded as in Chapter 3, here it is associated with a unique and distinct event, thus it may prove as a successful retrieval cue.

4.3.2 Methods

4.3.2.1 Subjects

Thirty-three apes participated in this study: nineteen chimpanzees (age range 9–49 years), seven orangutans (age range 5–33 years) and seven bonobos (age range 6–32 years). See Table 4.1 for details. All apes were tested between November 2014 and September 2016.

Table 4.1 Demographics of the apes, and allocation to each of the between-subjects' variables. Age shows the age at the time of the first retrieval session.

Subject	Species	Sex	Age (years)	First condition	Exposure food	Delay (weeks)
<i>Fimi</i>	Bonobo	Female	6	Experimental	Bread	50
<i>Luiza</i>	Bonobo	Female	9	Experimental	Pellet	2
<i>Gemena</i>	Bonobo	Female	9	Control	Pellet	50
<i>Lexi</i>	Bonobo	Female	15	Control	Bread	10
<i>Yasa</i>	Bonobo	Female	17	Experimental	Bread	2
<i>Jasango</i>	Bonobo	Male	24	Control	Pellet	10
<i>Joey^a</i>	Bonobo	Male	32	Control	N/A	N/A
<i>Kara</i>	Chimpanzee	Female	9	Experimental	Pellet	10
<i>Lobo</i>	Chimpanzee	Male	10	Experimental	Bread	50
<i>Tai</i>	Chimpanzee	Female	12	Control	Bread	10
<i>Alex[*]</i>	Chimpanzee	Male	13	Experimental	Pellet	2
<i>Lome</i>	Chimpanzee	Male	13	Experimental	Pellet	10
<i>Alexandra[*]</i>	Chimpanzee	Female	15	Experimental	Bread	2
<i>Swela</i>	Chimpanzee	Female	19	Control	Bread	50
<i>Frodo</i>	Chimpanzee	Male	21	Control	Pellet	50
<i>Sandra</i>	Chimpanzee	Female	21	Control	Bread	50
<i>Jahaga^{b *}</i>	Chimpanzee	Female	22	Experimental	Pellet	50
<i>Daza[*]</i>	Chimpanzee	Female	28	Experimental	Bread	10
<i>Dorien</i>	Chimpanzee	Female	34	Control	Pellet	2
<i>Natascha</i>	Chimpanzee	Female	34	Experimental	Pellet	10
<i>Riet</i>	Chimpanzee	Female	37	Control	Pellet	10
<i>Corrie</i>	Chimpanzee	Female	37	Experimental	Pellet	50

<i>Ulla</i>	Chimpanzee	Female	37	Control	Bread	2
<i>Fraukje</i>	Chimpanzee	Female	38	Experimental	Bread	50
<i>Frederike*</i>	Chimpanzee	Female	41	Experimental	Pellet	2
<i>Jeudi*</i>	Chimpanzee	Female	49	Experimental	Bread	10
<i>Tannah</i>	Orangutan	Female	5	Experimental	Pellet	2
<i>Suaq</i>	Orangutan	Male	5	Experimental	Bread	10
<i>Raja</i>	Orangutan	Female	11	Experimental	Bread	2
<i>Padana</i>	Orangutan	Female	17	Experimental	Pellet	10
<i>Dokana^c</i>	Orangutan	Female	25	Experimental	Pellet	50
<i>Pini</i>	Orangutan	Female	26	Control	Bread	2
<i>Bimbo</i>	Orangutan	Male	33	Control	Bread	50

^a Did not complete an experimental condition

^b Experimental data removed due to error during testing

^c Did not complete a control condition

* B-group chimpanzee; see Chapter 2.

4.3.2.2 Apparatus

All testing was conducted in the testing rooms (see Chapter 2 for details of the testing rooms). Two adjacent enclosures were used (e.g., enclosure 1 and 2). The ape always entered the testing room via one enclosure (e.g., 1), and the food was hidden in the adjacent enclosure (e.g., 2). The enclosures were visible from one another.

The hiding location varied between subjects, due to constraints of the testing rooms, but was always above the eye-line of the ape from ground level and in an area not normally used for testing. For the majority of subjects (A-chimpanzees and orangutans), it was located on a ledge above a hydraulic door, accessible to the experimenter only by ladder (see Figure 4.1). The other locations did not require a ladder, but were elevated from ground level.

Two types of food were hidden (exposure food): bread and cardamom flavoured pellets. The flavoured pellets were very distinctive, as the apes had never tasted cardamom before. Additionally, they looked like regular pellets (eaten on a daily basis), thus when eaten were unexpected and (most likely) surprising. The bread was less distinctive, due to being used as an occasional treat, and was not surprising in taste, but was not common to the apes either. A completely familiar food was not used to ensure that the hiding events were comparable in nature; that is, in both cases the apes found unexpected food, but with the added element of novelty and surprise when they found the flavoured pellets.

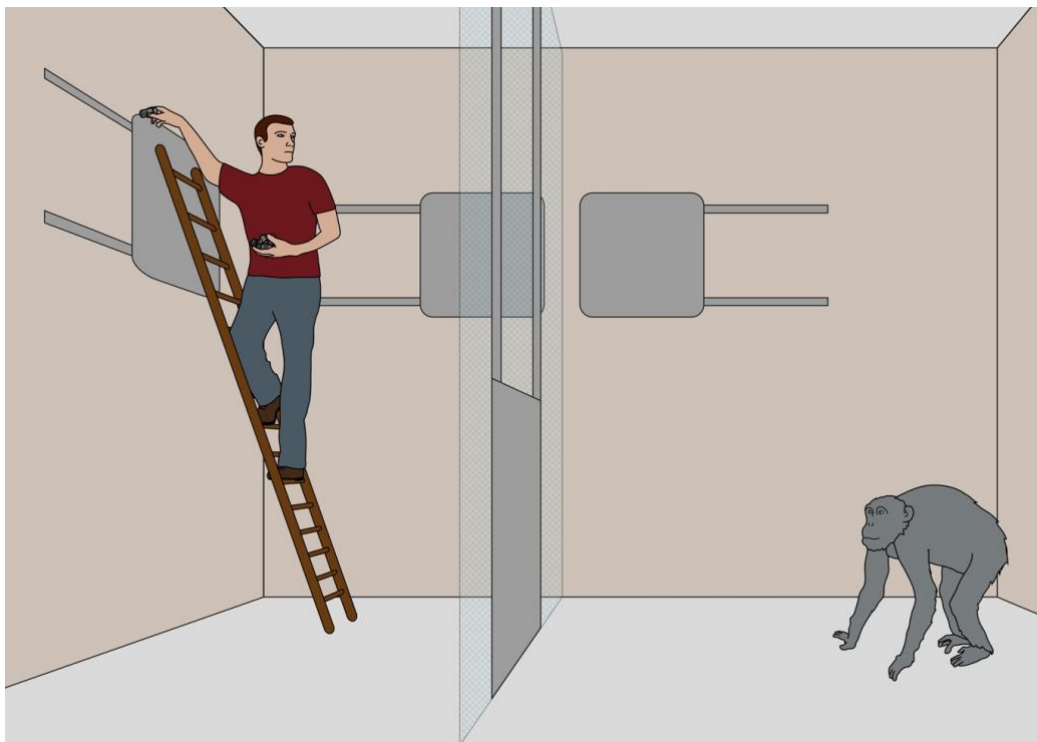


Figure 4.1. Illustration of the hiding event for the A-chimpanzees and orangutans (the set up was slightly different for the bonobos and B-chimpanzees). The ape watched from the enclosure on the right, whilst the experimenter hid food in the enclosure on the left. Once the experimenter had left the enclosure, the connecting hydraulic door (pictured in the centre) was opened and the ape was able to retrieve the food. Figure reproduced from Lewis et al. (2017b).

4.3.2.3 Design

A mixed design was used, with exposure food (bread: N=16, flavoured pellet: N=16) and delay (2 weeks: N=10, 10 weeks: N=11, 50 weeks: N=11) between subjects (see Table 4.1), and condition (experimental, control) and retrieval session (1,2) within subjects. Exposure food referred to the type of food that was hidden during the hiding event. The alternate food type was experienced during the control condition, but was never experienced during the hiding event (see procedure for details).

Apes completed both an experimental and a control condition, which was counterbalanced between subjects (see Table 4.1). There was a minimum of six-months between conditions (range: 182-635 days). In the experimental condition, apes witnessed a hiding event in which the exposure food was hidden. After their allocated delay, they received two retrieval sessions with the exposure food, one-week apart (range: 5-9 days). The control condition differed in that no hiding event occurred before the retrieval sessions and the alternate food was present during the retrieval sessions. This control condition was used as a baseline for comparison with the experimental retrieval performance. As illustrated in Figure 4.2, two different orders were used. In one (a), apes took part in the experimental condition before the control condition, in the other (b), the order was reversed, with the control condition preceding the experimental condition.

The first retrieval session was with an experimenter that was *not* present during the hiding event, and the second retrieval was with the experimenter that hid the food during the hiding event (see Figure 4.2). This enabled comparison between performance when social information (i.e., the experimenter identity) overlapped at encoding and retrieval, forming a social cue. For the first retrieval, the experimenter

was blinded to the condition and delay the subject was participating in (i.e., control or experimental; 2, 10 or 50 weeks), so to avoid any unintentional cueing. It was not possible for the experimenter in the second retrieval to be blinded in this way, as this experimenter was aware who had previously seen (or not seen) a hiding event, and when, due to being present during the hiding event.

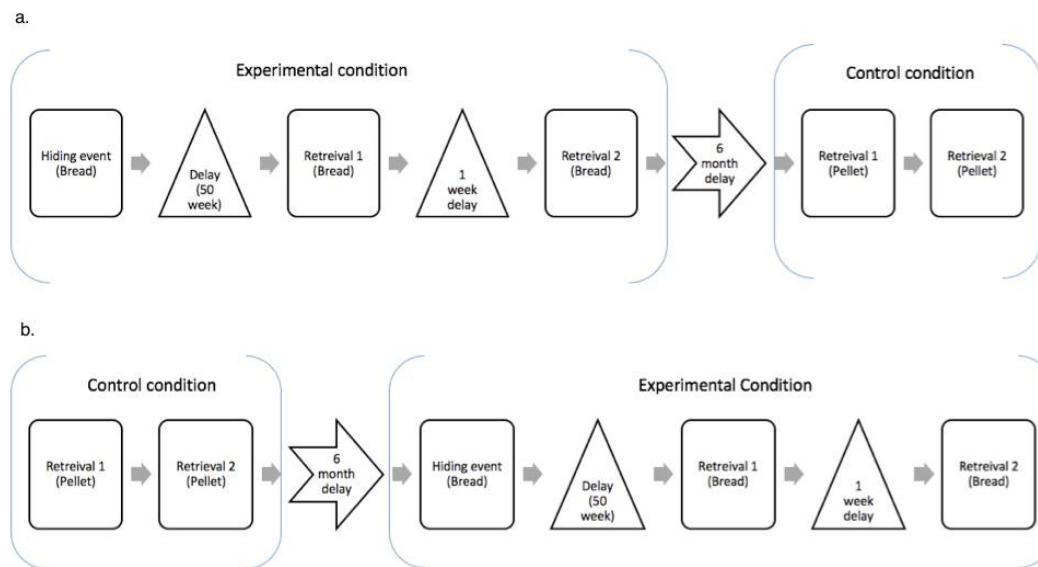


Figure 4.2 Example of the procedure sequence. a) depicts the experimental condition first, followed by the control condition. The subject is in the bread exposure food and 50-week delay group. b) depicts the alternative order, with the control condition first, followed by the experimental. The subject is in the bread exposure food and 50-week delay group. Figure reproduced from Lewis et al. (2017b).

4.3.2.4 Procedure

During the hiding event, the ape began in one enclosure and watched the experimenter (E1) enter the other enclosure with a ladder¹⁵ and six food pellets or pieces of bread in

¹⁵ The ladder was not used with the bonobos and B-chimpanzees (see apparatus)

her hand (exposure food). E1 showed the food to the subject, climbed the ladder and hid the food in the hiding location (see Figure 4.1). The subject could see that the food had been placed there, but could not see the food itself. E1 then left the enclosure and entered the experimenter area. The connecting door between the two enclosures was then opened so that the subject could access both enclosures. Subjects were given a maximum of five minutes to find and eat the food, if the subject failed to do so in this time, the session ended and the subject did not participate any further in the study. Only the experimental condition included this hiding event.

After the allocated delay (2, 10 or 50 weeks), the subject received two retrieval sessions, one-week apart. Retrieval sessions for the experimental and control conditions followed the same procedure. In Retrieval 1, an experimenter that did *not* hide the food during the hiding event (E2) entered the same enclosure in which the food was previously hidden and placed a single piece of the exposure food on the ground, directly below the hiding location. The subject was not present to witness this. E2 then left the enclosure and stood in the experimenter area, before the subject entered the other enclosure. After a ten-second delay, in which E2 was facing the subject and the subject could see the identity of E2, the door connecting the two enclosures was opened and E2 left the testing room. After two minutes had elapsed, E2 re-entered the testing room and stood in the experimenter area so that the subject could again see the identity of E2. E2 did not look at the hiding location during this time. After ten-seconds, E2 left the testing room, and after five minutes the session finished. Retrieval 2 followed the same procedure, except E2 was replaced with the experimenter who hid the food during the hiding event (E1). No food was present in the hiding location during the retrieval to avoid searching as a result of extraneous cues, such as odour.

The control condition differed from the experimental condition in two ways: firstly, subjects did not witness the hiding event, and secondly the food that was on the enclosure floor was not the exposure food in the experimental condition, but the alternate food. For example, if subjects experienced flavoured pellets as the exposure food, they found bread on the floor. Note that two different orders were used; one in which the control condition preceded the experimental condition and one with the reverse order (Figure 4.2).

4.3.2.5 Coding and analyses

All sessions were videotaped and later coded as to whether the subject searched or not. A search was defined as the subject climbing to the hiding location and looking/and or searching the location with hands/feet/mouth. For instances of searching, the time taken from picking up the food from the ground to reaching the hiding location was counted (here-after latency). Twenty percent of the videos were coded by a second coder (see Appendix B, Table B2). Inter-rater reliability for searching was calculated using Cohen's kappa, and Pearson's correlation assessed the inter-rater agreement for latencies. Inter-rater reliability for searching was excellent ($K=1$, $p<0.001$), and for latencies was high ($r=.88$, $N=9$, $p<0.01$).

The main question was whether the apes could successfully recall the hiding event, as measured by searching. To test for this, searching was compared between the experimental and control condition. Additionally, it was tested whether searching was influenced by delay, exposure food, retrieval session and the order of condition. Since it was expected that the effect of these predictors would depend on condition (experimental or control), the respective four, two-way interactions were included (i.e., the interaction between condition and each predictor).

A Generalized Linear Mixed Model with a Poisson error distribution and log link function was fitted¹⁶ (Baayen, 2008; McCullagh & Nelder, 1989). Condition, delay, exposure food, retrieval session and order of condition were fixed effects, species was a controlled fixed effect, and subject a random effect. A Poisson model, rather than a binomial, was used, since the latter was unrealistic with regard to the estimation of the contribution of the random effect of subject, as shown by uncertain stability (see Appendix B.1, model details, for details of this analysis). To keep type I error rate at the nominal level of 0.05, a maximal random slopes structure was included, with condition and retrieval session within subject.

The model was fitted in R (version 3.3.1; Team, 2016) using the function `glmer` of the package `lme4` (Bates, Mächler, Bolker, & Walker 2015). Model stability was checked by comparing the estimates from the full model to those obtained from models with the levels of the random effect (each individual subject) excluded one at a time, which revealed no severe issues with model stability. Variance Inflation Factors (Field, 2005) were obtained from a standard linear model lacking the random effects and the interaction (function `vif` of the R package `car`), to check for absence of collinearity among the predictors, which revealed no issues (maximum Generalized VIF=1.08; Fox & Monette, 1992). Overdispersion was no issue (dispersion parameter: 0.609). As a test of the combined effects of condition, delay, exposure food, retrieval session, order of condition, and the interactions with condition, the full model was compared to a null model comprising only species and the random effects, using a likelihood ratio test (Dobson, 2002; Forstmeier & Schielzeth, 2011).

¹⁶ This model was designed and implemented with the help of Roger Mundry.

Prior to fitting the model, delay was z-transformed to a mean of zero and a standard deviation of one to allow easier interpretation of the coefficients (Schielzeth, 2010). The model suffered from complete separation (Field, 2005), since none of the individuals ever searched in the control condition when this was presented first. To overcome this issue, Goodale, Ratnayake, and Kotagama's (2014) approach was used, in which each of these no-searches was replaced with a search, one at a time, and the model was fitted with the resulting response variable. The results presented are averages across these 30 models. Note that such an approach is conservative, as it makes the difference between the conditions slightly less extreme.

For every instance of searching, the latency (in seconds) from the ape picking up the food on the floor to searching the hiding location was calculated. A paired samples t-test was conducted to see whether search time changed between Retrieval 1 and Retrieval 2 in the experimental condition; subjects that had already searched in Retrieval 1 may be slower in Retrieval 2 because of finding no food in the first session. Additionally, a two-way ANOVA investigated whether search times differed between the two exposure foods, and the three delay groups in the experimental condition. For subjects that searched in both Retrieval 1 and Retrieval 2, a mean search time was calculated.

4.3.3 Results

One subject (Joey) did not complete any experimental sessions as he was unwilling to participate, likewise Jasango was unwilling to participate in his second experimental session. Dokana only completed one experimental session (and no control sessions) as she was unwilling to separate from her offspring. Additionally, Pini's data for the

second experimental session was removed due to her infant searching the hiding location, and Jahaga's experimental retrieval session data was removed from the analysis due to an experimental error during testing. This resulted in a total number of 123 observations from 33 subjects. The full model compared to the null model was significant (likelihood ratio test: $\chi^2=20.404$, $df=9$, $p=0.017$). More specifically, the interaction between condition and order of condition was significant ($\chi^2=6.239$, $df=1$, $p=0.013$; Figure 4.3a). None of the other three interactions were significant (see Figure 4.3c-d; Table 4.2). The interaction showed that subjects searched significantly more in the experimental condition compared to the control condition, when the control condition was completed first (Figure 4.3a). Thus, subjects who had seen the hiding event were searching significantly more than subjects that had yet to see the hiding event (who never searched). Subjects that searched in the control condition when presented second, did so despite experiencing an additional retention period of six months from the initial hiding event and delay period, and crucially, after finding no food in previous experimental retrieval sessions. This included four apes that searched in all four retrieval sessions (Lobo, Lome, Kara, Frederike); one of which received the 50-week delay period, and thus by the fourth retrieval session was still searching, despite the fact that one year and five months had passed since this subject had witnessed the hiding event, and despite finding no food the previous three times.

The lack of any other interaction showed that searching in both conditions did not differ as a result of delay, retrieval session, or exposure food (see Figure 4.3b-d). This finding indicated that subjects recall did not significantly decline over the three test intervals (i.e., from 2 to 10 to 50 weeks after exposure), although the performance did decline from initial exposure to retrieval (see below), and that neither the social cue

nor the distinctive pellet improved recall performance. Additionally, recall performance between Retrieval 1 and 2 in the experimental condition was nearly identical, with all but three subjects consistently searching in both sessions, or consistently failing to search in both sessions, further showing that the social cue did not influence performance.

The fact that no significant decline was observed between the three delay intervals (2, 10, and 50 weeks) does not mean that performance showed no decline from the hiding event to retrieval. Compared with the original 100% search rate during the exposure, a marked decline was seen in the experimental condition at the two-week delay (where 58% searched, see Figure 4.3b) after which the decline levelled. When plotting the rate of searching as a function of days since the observation of the hiding event (estimating the first delay to five minutes = .003 days¹⁷), a standard forgetting curve was observed (see Figure 4.4). Retention by time was best described by a logarithmic function [$y = -4.853\ln(x) + 72.666$. $R^2 = 0.92463$].

¹⁷ Approx. a five-minute delay occurred between the apes witnessing E1 hide the food in the enclosure, to E1 leaving the enclosure, securing the doors, and the ape being given access to the enclosure and retrieving the food.

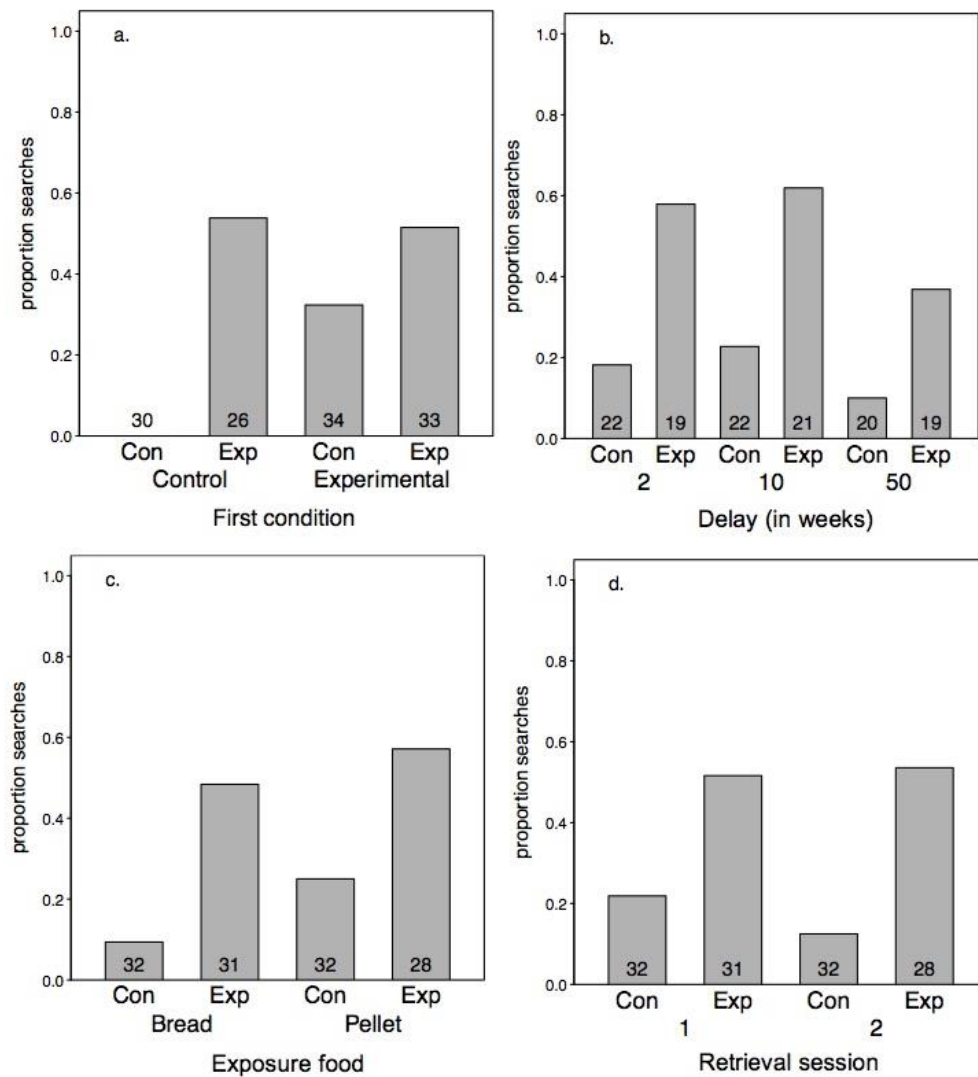


Figure 4.3. Proportion of searches by condition as a function of: a. first condition, b. delay, c. exposure food, and d. retrieval session. Numbers inside the bars represent number of data points (a-c = $N \times 2$ trials; d = N). Con and Exp refer to the Control and Experimental conditions respectively. Figure reproduced from Lewis et al. (2017b).

Table 4.2. Results of the full model. Estimate shows estimated coefficient.

Term	Estimate	SE	95% CI	χ^2	df	<i>p</i>
Intercept	-4.687	1.250	Lower:-7.914 Upper: -2.661			(1)
Delay ⁽²⁾	-0.133	0.357	Lower:-1.119 Upper: 0.428			(1)
Retrieval (session 2) ⁽³⁾	-0.515	0.599	Lower:-1.554 Upper: 0.805			(1)
Species (orangutan) ⁽⁴⁾	1.513	0.770	Lower: 0.212 Upper: 3.587	5.140	2	0.090 ⁽⁵⁾
Species (chimpanzee) ⁽⁴⁾	1.249	0.714	Lower: 0.134 Upper: 3.285			(1)
Exposure food (pellet) ⁽⁶⁾	0.822	0.673	Lower: -0.785 Upper: 1.916			(1)
Sequence (experimental first) ⁽⁷⁾	1.955	1.063	Lower: 0.205 Upper: 4.847			(1)
Condition (experimental) ⁽⁸⁾	2.908	1.168	Lower: 0.912 Upper: 5.819			(1)*
Condition (experimental): Delay	-0.087	0.412	Lower: -0.763 Upper: 0.963	0.143	1	0.805
Condition (experimental): Retrieval (session 2)	0.561	0.699	Lower: -0.965 Upper: 1.775	0.716	1	0.433
Condition (experimental): Exposure food (pellet)	-0.709	0.757	Lower:-1.962 Upper: 1.023	1.000	1	0.365
Condition (experimental): Sequence (experimental first)	-2.264	1.113	Lower: -5.211 Upper: -0.405	6.239	1	0.013

* A main effect of condition was found in the reduced model (with interactions removed):

$\chi^2=9.522$, $df=1$, $p=0.002$,

⁽¹⁾ not shown because of having limited interpretation

⁽²⁾ z-transformed to mean of 0 and standard deviation of 1; mean and sd of the original variable were 20.016 and 20.781

⁽³⁾ dummy coded with session 1 being the reference category

⁽⁴⁾ dummy coded with bonobo being the reference category

⁽⁵⁾ the indicated test refers to the overall effect of species

⁽⁶⁾ dummy coded with bread being the reference category

⁽⁷⁾ dummy coded with control first being the reference category

⁽⁸⁾ dummy coded with control being the reference category

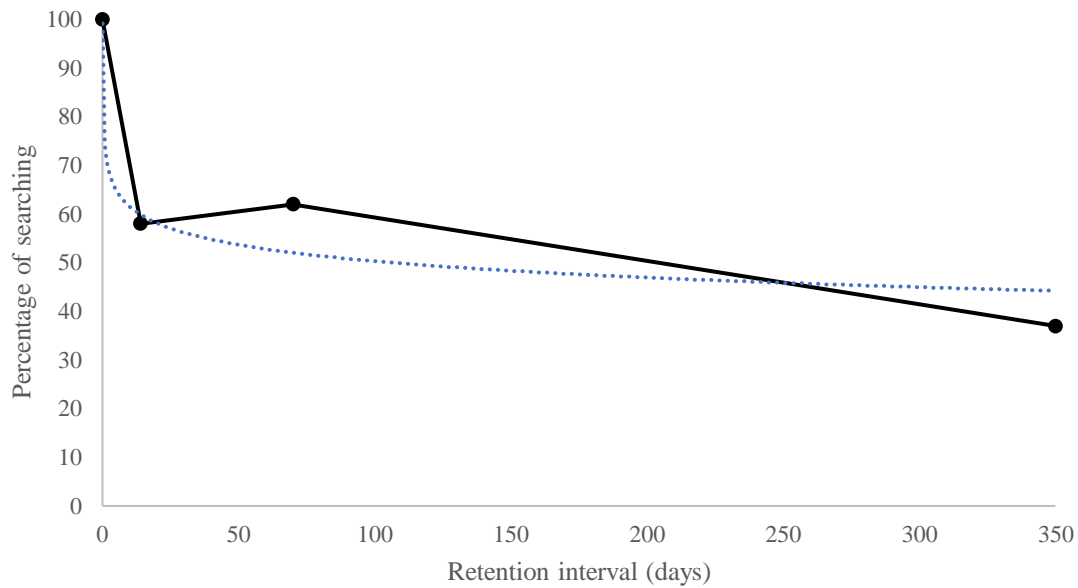


Figure 4.4. Percentage of searching as a function of days since exposure to the hiding event (estimating the first delay to 5 minutes = .003 days). Solid black line shows the forgetting rate across the 2, 10 and 50 week delays. Dotted blue line shows forgetting as a logarithmic function. Figure reproduced from Lewis et al. (2017b).

With regards to search time, the average (median) latency in the experimental condition was 9 seconds ($N=31$, Median = 9, $Q1=6$, $Q3=35$), and for the subjects that completed the control condition second, the average latency was 12 seconds ($N=11$, Median = 12, $Q1=5$, $Q3=26$), indicating that subjects immediately searched the location. There was no change in search time from Retrieval 1 ($M=38.38$, $SD=65.23$) to Retrieval 2 ($M=21.38$, $SD=30.39$) in the experimental condition, $t(12)=1.20$, $p=0.25$, suggesting that even though the apes found no food in the previous session, they were just as quick to search the hiding location again. The results of the two-way ANOVA revealed no difference in search time in the three delay conditions, $F(2,12)=1.51$,

$p=0.26$, nor the two food types $F(1,12)=0.03$, $p=0.86$. Thus, subjects search times in the experimental condition were not influenced by retrieval session, exposure food, or delay.

4.3.4 Discussion

The purpose of this study was to investigate whether apes show evidence of the involuntary form of episodic memory. Apes were exposed to a distinctive food hiding event that occurred once, and after a delay period tested whether they could recall the event when presented with distinct cues that overlapped with the event. A non-goal directed test was used at retrieval to reduce the likelihood that the apes would strategically recall the past event in order to achieve a current goal. Likewise, a specific, single occurring event was used, as such events are often retrieved involuntarily, and unlike repeated events, are less likely to be semantically encoded. Single occurring events were also the standard definition of episodic memory in Tulving (1983)'s original theory. Unlike previous studies, this experiment directly assessed the influence of distinctiveness and the encoding-retrieval match on recall success, and also memory performance over time.

The results showed that the apes successfully recalled the event after two, ten, and fifty weeks, replicating the findings by Martin-Ordas et al. (2013), but using a non-goal directed task, and extending the findings by Kano and Hirata (2015) to show recall over delays much longer than twenty-four hours. Interestingly, the performance of the apes after the two-week retention period was worse than the apes (chimpanzees and orangutans) in the Martin-Ordas et al. (2013) study. This discrepancy may be due to the inclusion of bonobos in this experiment; although statistically speaking there was no

difference between species, numerically the bonobos searched less than the chimpanzees and orangutans (0%, 60% and 100% respectively) in the two-week experimental condition. Due to the many variables in the statistical model, and the relatively small sample of bonobos ($N=7$), it's possible that species differences were not detected. For instance, cognitive differences have been found between bonobos and chimpanzees (Herrmann, Hare, Call, & Tomasello, 2010), with delayed cognitive development compared to chimpanzees (Rosati & Hare, 2012; Wobber, Wrangham, & Hare, 2010).

Additionally, retention showed a marked decline from the exposure (the hiding event) to the two week delay, then levelled, consistent with the classic forgetting curve observed in human memory (Ebbinghaus, 1964; Rubin & Wenzel, 1996). The inclusion of overlapping social information at encoding and retrieval did not improve recall relative to when the information was absent, and the highly distinctive event was not recalled more than the less distinctive event; these findings are discussed below.

The average search time from finding the food on the ground to reaching the hiding location was less than twelve seconds (and only nine in the experimental condition). As the apes needed to climb to the hiding location, this search time reflects a fast and instantaneous response, consistent with involuntary recall (Berntsen et al., 2013; Schlagman & Kvavilashvili, 2008). This fast response was consistent across the three delay periods, and retrieval sessions, suggesting apes spontaneously recalled the event regardless of how long ago it occurred, and when it was last recalled (i.e., if they recalled the event in retrieval session one, they were just as quick to recall it again one week later in the second retrieval). Although fast response times are consistent with involuntary recall, due to not having a comparison group completing the same action

using voluntary recall, it cannot be said for certain that the fast response was due to involuntary, as opposed to voluntary, recall.

Additionally, it was found that subjects that completed the experimental condition first, followed by the control condition, were more likely to search the hiding location during the control retrievals, than those who completed the control condition first (of which none searched). That is, some subjects who witnessed the hiding event and searched in the two retrieval sessions (after two, ten or fifty weeks), subsequently searched six months later when finding a different type of food was on the ground. This is despite having not found food in the hiding location the previous two sessions. Due to the long durations involved, the lack of reinforcement for searching in any retrieval session, and a cue that did not directly match the food at the hiding event, it was not expected that subjects would search. The finding that apes did search, and thus overcame all these difficulties, is a remarkable testament to the robustness of their memory for distinctive events in response to contextual cueing.

The willingness to continue searching despite finding no food goes strongly against any potential critique that the apes used associative learning to encode and recall the hiding location. The apes experienced an absence of food in the hiding location more often than they experienced food (which occurred only once), thus any association with this location and food would have been weakened. This was further supported by the lack of difference in recall between retrieval sessions 1 and 2 of the experimental condition; that is, subjects that searched in Retrieval 1 continued to search in Retrieval 2, despite finding no food. Indeed, only one subject who searched in Retrieval 1 of the experimental condition subsequently failed to search in Retrieval 2. What is perhaps more surprising is that the apes who recalled the event in the control

condition did so even when the cues did not directly overlap. Here, the food on the ground was not the same as the food that had been hidden during the event. Although the overlapping of features at encoding and retrieval is often found to trigger involuntary memories, it is not the extent of the overlap that is important, rather it is the uniqueness of the overlap (see Chapter 1 and introduction to this chapter). As the apes enter this enclosure daily for testing, the absence of any obvious testing apparatus and task may have made the context particularly distinctive. Additionally, the uniqueness of the location of the food (directly below the hiding location), and the presence of uncommon food, may have resulted in a unique enough overlap to trigger recall of the event, without the need for the food to be the same food as was previously hidden.

The uniqueness of the overlap between encoding and retrieval may also explain why the addition of a social cue made no difference to recall, as evidenced by no difference between Retrieval 1 and Retrieval 2 in which the experimenter identity differed. This was further evidenced by the fact that only two subjects who did not search in Retrieval 1 went on to search in Retrieval 2. As the experimenters have both tested the apes on other tasks, their identity may be associated with other memories of past experiences, and thus the identity of the experimenter may be an overloaded cue and as such, not effective as a retrieval cue. Another possibility is that the apes simply did not pay attention to the experimenter; the apes participate in many studies with many experimenters, and more often than not, the experimenter's identity is not important to the task. As such, the apes may have paid more attention to other aspects of the hiding event, resulting in the identity of the experimenter being overshadowed at encoding. These are also possible explanations for the results in Experiment 2 of Chapter 3. Additionally, in this case, it is also possible that the identity of the

experimenter was outshined. As the experimenter identity was more prominent in this design (i.e., the experimenter entered the enclosure carrying a large amount of food), the identity of the experimenter may well have been salient enough to be initially encoded, but was not effective at retrieval because other more salient cues were the focus of attention, in this case the food on the ground and the testing room.

Alternately, it may be that the experimenter identity was confounded with the order of retrieval sessions¹⁸. As the experimenter that hid the food was always in Retrieval 2, which occurred one week after Retrieval 1, it could be performance was enhanced by the social cue but hindered by the additional retention period, resulting in no difference in performance overall. However, due to not finding a significant decline in recall from the two-week to the fifty-week delay, this is unlikely. As such, the results here, and from Chapter 3, suggest that using an experimenter identity as a social cue may be of limited effect at retrieval, especially in the presence of other more salient and diagnostic cues.

With regards to the two exposure foods, no difference in memory recall was found. This was unexpected, as it was predicted that the novelty of the flavoured pellet would enhance memory recall relative to the bread condition. Although it is unclear why this was not the case, I propose two potential explanations. First, the hiding event was very distinctive regardless of which food type was hidden; a human entering the enclosure and hiding a large cache of food in an unusual location is a unique event to all the apes. Additionally, the bread was fairly distinctive in itself - it was not a common food type, and thus finding a large cache of it was a rather rare occurrence.

¹⁸ This suggestion was provided by an anonymous reviewer.

Consequently, the memorability of the event may not have been dependent upon which food was hidden. Second, cardamom was a completely novel flavour for the apes, and so it was possible that not all the apes liked it. During the hiding event, two of the apes (Frodo and Luiza) did not eat the flavoured pellets, with Frodo returning the pellets to the experimenter by pushing them through the enclosure meshing. As such, the reason why more apes did not search in this condition could be that the apes simply did not like the food, and thus were not motivated to search for it.

In terms of the delay periods, there was no evidence of a significant difference between performance from two to fifty weeks, suggesting the event was remembered regardless of how long ago it had been seen. In the previous chapter, the apes successfully recalled a distinctive event for two weeks, these findings therefore replicate and extend those findings. Furthermore, the findings replicate and extend previous findings that show recall of specific events after two weeks (Martin-Ordas et al., 2013), and recall in a non-goal directed task after twenty-four hours (Kano & Hirata, 2015), providing further evidence that suggests apes can recall specific, non-goal directed events after long delays. Although recall performance did not differ between the delay periods, a marked decrease from the time of the witnessing the event and retrieving the food, to the two-week retention period, was observed. This decline in performance levelled over time, showing a pattern consistent with the forgetting curve in humans (Ebbinghaus, 1964; Rubin & Wenzel, 1996). As far as I am aware, this is the first study to show similarities with the human forgetting curve using long retention periods, and is consistent with findings that show a similar forgetting curve in animal working memory retention (see White, 2013).

4.4 Experiment 2 | Cue saliency

The results from Experiment 1 suggest that apes can spontaneously recall a distinctive past event after long delays, when presented with distinct cues that overlap with the memory trace, consistent with involuntary retrieval in humans. Although enhanced performance was not found in the event intended to be more distinctive (the flavoured pellet condition), the results from Chapter 3 suggest that distinctiveness does indeed lead to improved memory recall when compared to an event that is completely lacking in any distinct features. These findings highlight the importance of distinctiveness for successful recall of past events.

Although these findings both converge on the importance distinctiveness in successful recall, both studies share a common element that may have confounded the results; the presence of a large amount of food. Whilst potential reinforcement explanations for performance in Chapter 3 were ruled out, it was not assessed whether the mere presence of a large amount of food may have led to successful memory retrieval. Large food amounts are salient to the apes, and saliency captures attention (Theeuwes, 1991), thus the apes' successful performance may have resulted from increased attention in events involving large amounts of food, rather than as a result of processing the event as distinctive. This could explain why the apes were only successful at recalling events that involved large caches of food, and never successful in events that involved small caches, regardless of whether the food was subsequently received or not (although note that in Chapter 3, Experiment 3, the large cache of food in the reinforced condition was not successfully remembered).

Additionally, in Experiment 1 of this chapter, it was not possible to determine whether the apes' memory of the hiding event was solely cued by the presence of the

food on the floor, or whether other contextual cues were used, such as the set-up of the enclosure (e.g., returning to the same enclosure with the absence of any apparatus). Just as food may have captured attention during encoding, the presence of food at retrieval may also have captured attention above and beyond the other contextual cues. Subsequently, the food may have overshadowed other information during encoding, or outshined other cues during retrieval.

4.4.1 Aims

This second experiment aimed to resolve these issues, that is: to establish whether a distinctive event would be well remembered when the saliency of the food was reduced (by reducing the quantity), and to see whether recall could be triggered by the presence of overlapping contextual cues at retrieval, but in the absence of any food cue.

Additionally, this experiment presented the apes with a distinctive event that shared many features with the event from Experiment 1, such as occurring in the same testing room, with the same experimenter, and also involving the hiding of food, but differing in one unique aspect (access to a restricted enclosure; see procedure). This provided an opportunity to assess whether apes that were successful in Experiment 1 (N=10) would again spontaneously search the hiding location from Experiment 1 (here after: old location) given the high degree of overlapping cues¹⁹. This would be particularly remarkable, given the long retention period since originally witnessing the old hiding event, and multiple searches in which no food was discovered in the old location. As not all apes witnessed this new hiding event (i.e., some participated in only

¹⁹ Given the small sample size, no statistical analysis was conducted on this data.

a control condition), it was predicted that the apes in the control condition would be more likely to search the old location, than apes that witnessed the new hiding event. This is because the apes that witnessed the new hiding event should be more likely to recall the new event than the old one, given that the uniqueness of the overlap between encoding and retrieval is greater in the new event (access to a restricted enclosure is unique to the new event), and the event is the most recent.

4.4.2 Methods

4.4.2.1 *Subjects*

All of the orangutans and A-chimpanzees that took part in Experiment 1 took part here, with the exception of Kara and Ulla who were no longer at the zoo, Swela who had just given birth, and Tanna who did not want to separate from her mother. In addition, three chimpanzees that did not take part in Experiment 1 took part here (Kofi, Robert and Bangolo). The B-chimpanzees and bonobos were not tested due to restrictions imposed by the testing room dimensions. In total, six orangutans and thirteen chimpanzees were tested, all but three chimpanzees had taken part in Experiment 1 (see Table 4.3) Subjects were tested between October 2016 and January 2017.

Table 4.3 Demographics of the subjects, including condition and search results of Experiment 1. Age shows the age at the start of this experiment.

Subject	Species	Sex	Age (years)	Condition	Searched in Experiment 1
<i>Bangolo</i>	Chimpanzee	Male	7	Control	N/A
<i>Raja</i>	Orangutan	Female	12	Control	Yes
<i>Tai</i>	Chimpanzee	Female	13	Control	Yes*
<i>Pini</i>	Orangutan	Female	28	Control	Yes
<i>Bimbo</i>	Orangutan	Male	35	Control	Yes
<i>Natascha</i>	Chimpanzee	Female	36	Control	Yes*
<i>Corrie</i>	Chimpanzee	Female	39	Control	No
<i>Fraukje</i>	Chimpanzee	Female	40	Control	No
<i>Robert</i>	Chimpanzee	Male	40	Control	N/A
<i>Suaq</i>	Orangutan	Male	7	Experimental	No
<i>Kofi</i>	Chimpanzee	Male	11	Experimental	N/A
<i>Lobo</i>	Chimpanzee	Male	12	Experimental	Yes*
<i>Lome</i>	Chimpanzee	Male	14	Experimental	Yes*
<i>Padana</i>	Orangutan	Female	18	Experimental	Yes
<i>Frodo</i>	Chimpanzee	Male	22	Experimental	No
<i>Sandra</i>	Chimpanzee	Female	23	Experimental	Yes*
<i>Dokana</i>	Orangutan	Female	27	Experimental	Yes
<i>Dorien</i>	Chimpanzee	Female	35	Experimental	No
<i>Riet</i>	Chimpanzee	Female	38	Experimental	Yes

* searched in all retrieval sessions post hiding event

4.4.2.2 Apparatus

A specially designed Plexiglas box was used to mount a go-pro camera inside the apes' enclosure, which enabled any potential searching attempts the apes made at retrieval to be filmed. The box and camera had been used in other tasks with the apes', thus they were familiar with the equipment. One slice of regular banana (an eighth of banana)

was hidden during the event; the apes receive banana on a daily basis, and a single piece is not a large amount of food to the apes. The hiding event took place inside enclosure 1 (see Figure 2.1 and 4.5). This enclosure is normally inaccessible and is rarely used for testing, thus access to this enclosure is novel to the apes and distinctive in comparison to their previous experiences of testing. In Experiment 1 the hiding event took place in enclosure 2.

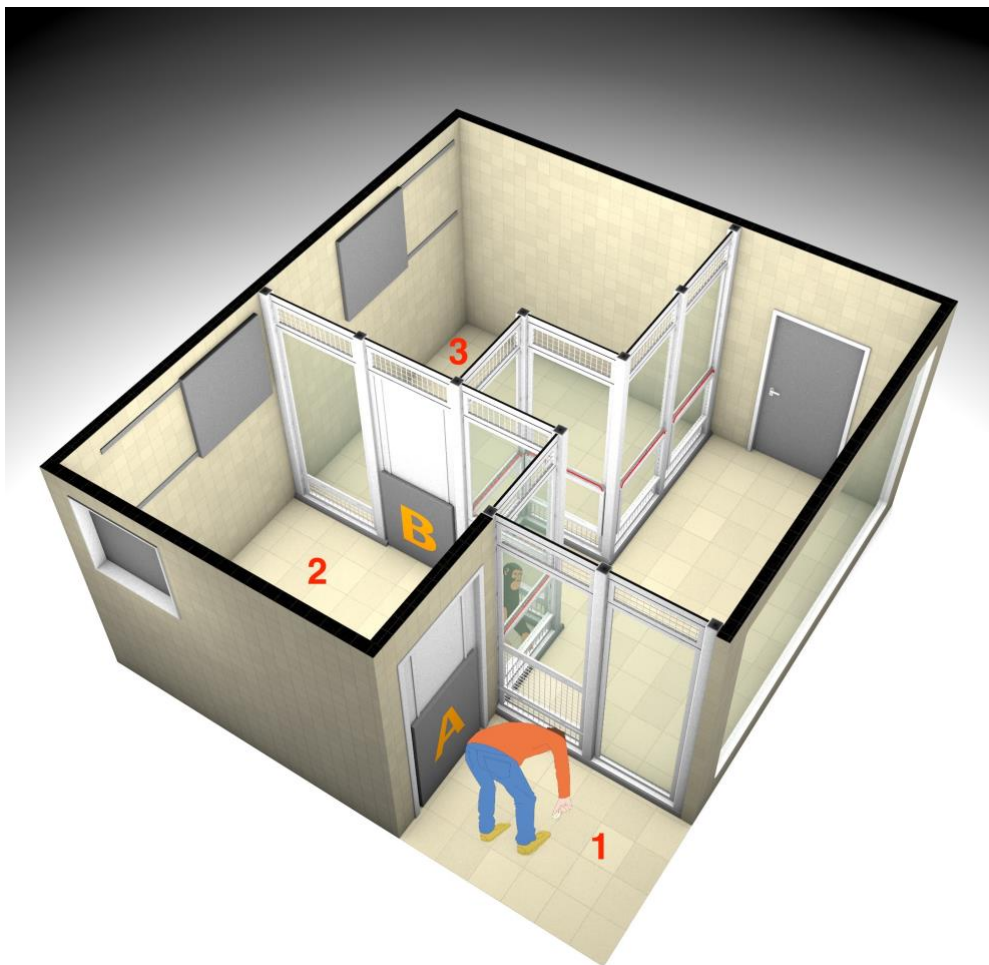


Figure 4.5 Schematic of the testing room. Numbers in red show the enclosure number, letters in orange show the door numbers. The ape watched from enclosure 2 as the experimenter hid banana in enclosure 1. The connecting door A opened once the experimenter left enclosure 1.

4.4.2.3 *Design*

Apes were allocated to either the experimental (N=11) or control condition (N=8; see Table 4.3). In the experimental condition, subjects witnessed a hiding event, followed by a retrieval session two weeks later. In the control condition, subjects only completed a retrieval session. The control condition was used as a baseline to compare the experimental performance to. Unlike Experiment 1, subjects only completed one retrieval session, and E was always the same person during the hiding event and retrieval (as Experiment 1 found no difference between performance when the experimenter identity was manipulated, the variable was not included here).

4.4.2.4 *Procedure*

During the hiding event the ape began in enclosure 2. From here, they witnessed E enter enclosure 1 with a slice of banana. E showed the banana to the ape, then hid it in a gap between the floor and metal frame that formed the structure of the enclosure (see Figure 4.5). The subject could only see the banana by putting their head to the floor and looking underneath the frame, but could fit their arm in the gap to reach the banana. After the banana was hidden, E left the enclosure and stood in the experimenter area. The connecting door (door A; see Figure 4.5) between enclosure 1 and 2 was then opened so that the subject could enter enclosure 1 and retrieve the banana. Once the banana had been retrieved and eaten, the session finished. Only the experimental subjects saw this hiding event.

Two weeks later, all subjects completed a retrieval session. Before the subject entered the testing room, the connecting door A was opened; this door is usually closed making enclosure 1 inaccessible. The accessibility to enclosure 1 thus provided a

distinct overlap with the hiding event. Subjects then entered enclosure 3 whilst E stood in the experimenter area in view of the subject. After ten seconds, the connecting door to enclosure 2 was opened (door B; see Figure 4.5). The subject was then given five minutes to explore the area. During this time E remained in the experimenter area and noted any search attempts, taking care not to look at either of the hiding locations to inadvertently cue any searching behaviour. This retrieval session was almost identical to the retrieval session from Experiment 1, except that no food was present on the enclosure floor, and connecting door A was open. Additionally, the identity of E was not manipulated between exposure and retrieval (i.e., E was the same person during exposure and retrieval).

4.4.2.5 *Coding and analysis*

As with Experiment 1, searching of the hiding location (here after: new location) was coded. A search was defined as a subject using their hands/feet/mouth to probe the area, and/or putting their head to the floor and looking underneath the gap.

Additionally, it was coded as to whether subjects who successfully searched in the previous study (N=10; see Table 4.3) searched the old location²⁰. The definition of a search for this location remained the same as first described (see coding and analysis of Experiment 1). Additionally, for every search a latency was calculated, this was the time from when the door to enclosure 1 opened until a search. Twenty percent of the videos were coded by a second coder blinded to conditions (see Appendix B, Table B2). Inter-rater reliability for searching was excellent ($K=1$, $p<0.001$). It was not

²⁰ This total was original 11, however Dokana was later removed from the analysis due to her offspring searching.

possible to calculate reliability for latencies, as only one subject from the twenty-percent sample searched.

For the main analysis, the number of searches and no searches to the new location was compared by condition, using a fisher exact test. Additionally, for the ten subjects that searched in the previous experiment, the number of subjects that searched the new location, the old location, both locations, or neither location, was tallied. It was not possible to statistically compare for any differences between these searches, due to the small sample size, therefore only descriptive statistics are provided.

4.4.3 Results

One subject (Dokana) was dropped from the analysis due to an error with the connecting door and her offspring searching, resulting in a total of 18 subjects. The fisher exact test revealed a significant difference between the control and experimental conditions ($df=1$, $p=0.04$), with more experimental subjects searching ($N=5$) than controls ($N=0$). Additionally, 1 subject in the experimental condition and 1 subject in the control condition searched the old location (see Figure 4.6), these subjects were both subjects that searched in Experiment 1 (see Table 4.4). None of the experimental subjects that took part in Experiment 1 ($N=10$) searched in both locations (see Table 4.4); that is, subjects that searched in Experiment 1 and saw a hiding even in this present experiment did not search both hiding locations. Regarding latency times, the average (median) search time to the new location was 124 seconds ($N=5$, Median = 124; $Q1=59.5$, $Q3=257.5$), and 89 seconds to the old location ($N=2$), compared to just 9 seconds in the experimental group of Experiment 1.

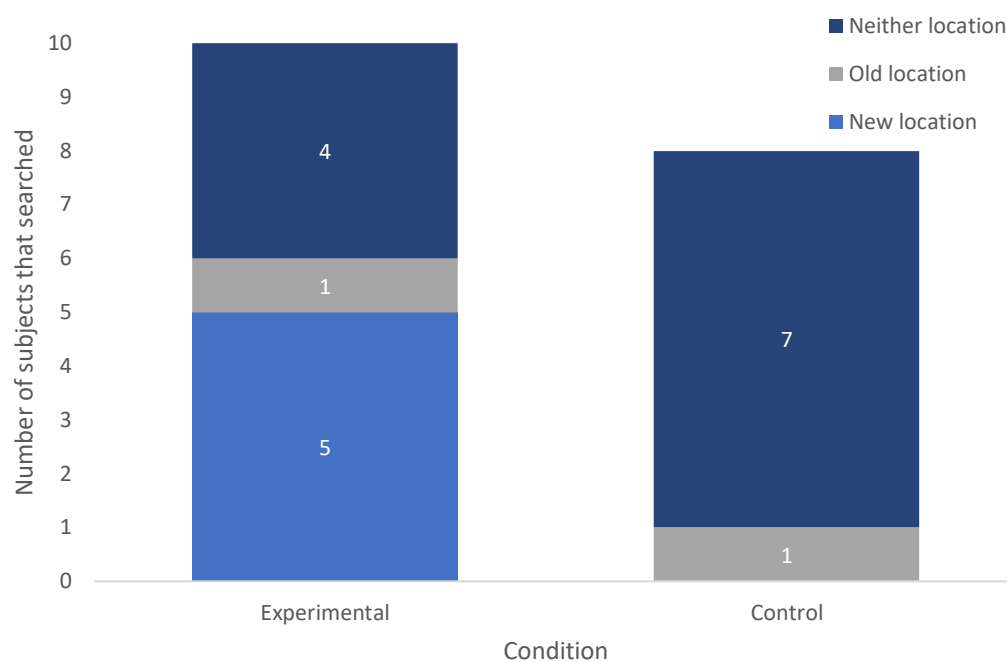


Figure 4.6 Number of subjects that searched the new location, old location, and neither location, by condition.

Table 4.4 Search data for the ten subjects that searched in Experiment 1. Ticks indicate that a subject searched, dashes indicate no searching.

	Subject	New location	Old location
<i>Experimental</i>	Riet	✓	-
	Lome	-	-
	Sandra	✓	-
	Padana	-	-
	Lobo	-	✓
	Pini	✓	-
<i>Control</i>	Natascha	-	-
	Tai	-	✓
	Bimbo	-	-
	Raja	-	-

4.4.4 Discussion

The purpose of this second experiment was to investigate whether the apes could successfully recall a distinctive past event when the saliency of the food was reduced. This was achieved by substantially reducing the quantity of food that was hidden during the event, and by removing the food cue at retrieval. The results showed that half of the apes that witnessed the hiding event subsequently searched the hiding location at retrieval, suggesting that they successfully recalled the event. None of the control subjects searched, indicating that subjects' performance was not a result of randomly searching an area that is often inaccessible.

These results are consistent with the findings from Experiment 1, in which approximately 58% of subjects searched after two weeks. However, they again differ from previous research, in which a higher percent of apes (chimpanzees and orangutans) searched a hiding location after a two-week retention period (Martin-Ordas et al., 2013). The lower search rate observed here may be a result of motivational factors; half of the subjects had participated and searched in Experiment 1, and consequently had experienced finding no food in a hiding location during retrieval, thus they may have lost motivation to search in this current experiment during retrieval.

The finding that subjects were able to successfully recall the hiding event when only a small amount of food was hidden, and no food was present during retrieval, suggests that it is not the food per se that makes the event memorable. Instead, it seems likely that the distinctiveness of the hiding event, and use of distinct cueing at retrieval, is important for recall success. In this case, seeing an experimenter hiding food in a usually inaccessible enclosure, and then finding that enclosure open during retrieval, created a distinct overlap between encoding and retrieval, leading to successful recall of

the event. Interestingly, as retrieval times were slower than in Experiment 1, it may be that the apes voluntarily, rather than involuntarily, recalled the event, as voluntary recall is often slower than involuntary (Berntsen et al., 2013; Schlagman & Kvavilashvili, 2008). Alternately, the slower retrieval times could be due to the reduction of salient cues at retrieval in comparison to Experiment 1 (i.e., no distinctive food on the floor), resulting in the apes taking longer to attend to their surrounds, and subsequently for a memory to be triggered. As it's not possible to ask the apes whether they involuntarily or strategically recalled the event, this is only speculation. Nevertheless, the longer retrieval times in this second experiment emphasise the speed at which subjects searched in Experiment 1, further supporting the notion that retrieval in Experiment 1 was likely involuntary.

Of the subjects that searched in the previous Experiment (N=10), two of them (Tai and Lobo) searched the location from Experiment 1. This suggests that the high degree of overlap between the retrieval session here, and the previous hiding event, triggered their memory of the previous event. This is highly impressive, as the time since Tai first witnessed the event in Experiment 1, to the retrieval session here in Experiment 2, was more than 13 months, and for Lobo was more than two years. Furthermore, both Tai and Lobo searched in all retrieval sessions since witnessing the event in Experiment 1. This means that not only did they successfully recall the event many times, but that they continued to act upon this memory by searching a location in which they had searched and failed to find food multiple times before. Indeed, in a follow-up study, in which the apes were unexpectedly presented with a cardamom flavoured pellet (see Appendix B.2, follow-up, for details), Tai once again

spontaneously searched the location from Experiment 1, along with two other apes (Frederike and Daza), showing remarkable retention of the hiding event.

However, it is surprising that Lobo (the experimental subject in the present experiment) did not search the new hiding location. As this hiding event was more recent, and had a unique overlap with the cues at retrieval (i.e., the open door to enclosure 1), one would predict he would recall this event, rather than the more distant, and less related event from Experiment 1. However, it may be that the hiding event from Experiment 1 was very memorable for this subject (more so than the current hiding event), as this was the first event in which he saw an experimenter enter an enclosure, climb a ladder, and hide an unusual cache of food.

4.5 Conclusions

The results from the two experiments suggest that apes are highly successful at recalling specific, non-goal directed past events, when exposed to distinct cues. Experiment 1 showed that the apes could recall a specific, distinctive event after long delays. Moreover, that they did so instantaneously, and continued to do so in subsequent retrieval sessions, despite finding no food. Such findings are consistent with involuntary retrieval in humans. Additionally, the forgetting rate over time bared a striking resemblance to the forgetting curve in humans, providing further evidence for similarities between human and ape memory. In Experiment 2, apes were also successful at recalling a single, distinctive event when the food amount was reduced, and when food was not the distinct cue at retrieval. These findings suggest that the apes can recall past events that are not highly reinforced with food, and that the contextual environment (i.e., the set-up of the testing room) can be a distinct and effective cue at retrieval. Such findings are particularly important, as they indicate that successful memory performance in the experiments presented so far in this thesis, was not driven by enhanced attention to salient food, but rather due to the processing of distinctiveness.

In the next chapter, the focus of investigation moves away from distinctiveness, and instead turns to the social realm. In the chapters thus far, the identity of the experimenter failed to act as an effective cue during retrieval. Whether this was due to the identity of the experimenter not being encoded, or whether the identity was encoded but was not attended to during retrieval (due to other prominent cues), is unknown. Therefore, the next chapter aims to establish whether social information can be

successfully encoded and integrated to other features in memory, when in the absence of other salient stimuli.

Chapter 5 | Binding of social information

5.1 Introduction

Social cognition in primates has been widely researched (see Anderson, 1998; Tomasello & Call, 1994), not least spurred on by the Machiavellian intelligence hypothesis (also known as the social brain hypothesis), which proposes that social expertise is the driving force of intelligence (Byrne & Whiten, 1989; Dunbar, 1998; Whiten & Byrne, 1997). Research has covered a broad spectrum, including imitation (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007), cooperation (Kappeler & Van Schaik, 2006), and theory of mind (Call & Tomasello, 2008), and has shown that primates can (to varying extents) use social information in a variety of situations for beneficial gain. For example, Mineka, Davidson, Cook, and Keir (1984) found that young rhesus monkeys that observed their mother behaving fearfully towards a snake, also developed a fear of snakes.

Despite the large amount of research on social cognition, social information has been somewhat overlooked by episodic memory research. As discussed in Chapter 1, the majority of research has focused on food as the ‘what’ component of an episodic memory, such as what food was cached, where, and when (or in which context). Consequently, there has been little focus on social information, such as the recall of ‘who’ information from a past event. This is somewhat surprising, given that episodic memory has been proposed to be important for social processing (Cheney et al., 1986; see Chapter 1). Indeed, Schwartz and Evans (2001) draw attention to findings from the human literature, which show that impaired social functioning often jointly occurs with impaired episodic memory. For instance, autistic children often have difficulties with

both social awareness (Baron-Cohen, 2000) and episodic remembering (Klein, Loftus, & Kihlstrom, 2002). Additionally, findings from the autobiographical human literature consistently find that social information (e.g., people) commonly occur in episodic memories (Berntsen, 1996; Berntsen & Hall, 2004; Lee & Dey, 2007).

As such, this chapter aims to specifically address the binding and retrieval of social information (who), from memory. Below I discuss the primate literature that has incorporated social information in the recall of a past event, followed by the specific aims of this chapter²¹.

5.2 Previous research

Research regarding the binding and retrieval of social information from past events has produced rather mixed results. There is some evidence that social information can act as an effective retrieval cue, but the extent to which the social information is bound to other information is unclear. For instance Mendes and Call (2014) found that chimpanzees could recall the locations of hidden food after both a twenty-four hour, and three month retention period, when presented with overlapping social cues. During the initial discovery of the food, the chimpanzees were released into the enclosure in pairs, and an experimenter stood on an observation platform in full view of the subject. During retrieval, the apes were released in the same pairs, and the same experimenter stood on the observation platform; thus, the social information present at encoding was

²¹ The Chapter formed the submission of a manuscript to *Animal behaviour and Cognition* (currently under revision); Lewis, Berntsen and Call (2018), Remembering past exchanges: Apes fail to use social cues. Manuscript submitted for publication. Many of the themes and ideas that are expressed here also feature in the manuscript, with some text and figures reproduced verbatim.

also present at retrieval. They found that the chimpanzees searched the correct hiding location more often than not, and with greater speed than the initial discovery, suggesting they recalled the locations. However, as multiple cues were present at retrieval, it is unknown which cues were driving successful memory retrieval. That is, retrieval may have been cued by the presence of the foraging partner, the presence of the experimenter on the platform, or other non-social cues, such as the spatial environment. Furthermore, the presence of any human experimenter on the platform may have sufficed.

Similar findings by Martin-Ordas et al. (2013, see Chapters 1 and 4 for study details) also suggest that social information, in the form of a human experimenter, may have been bound to other non-social information, such as a tool location and task, and acted as a unique cue at retrieval. However, it is again unclear as to whether the experimenter identity was bound to other features, or whether recall would have been successful in the absence of the experimenter. It is also again unclear as to whether any experimenter would have resulted in successful recall, or whether the experimenter needed to be the experimenter that was present during encoding. This point is particularly important, as the findings from the previous two chapters suggest that the identity of the experimenters was not an effective cue.

Findings from Beran (personal communication) also suggest that the identity of an experimenter may not be an effective source of information. Beran found that chimpanzees could not use the identity of an experimenter to determine which opaque container food was located in. In one situation, chimpanzees failed to learn that one experimenter would always carry an empty container, whilst the other experimenter would always carry a container full of food. In another situation, they were unable to

learn that one experimenter always pointed to the container with food inside, whereas the other experimenter always pointed to the empty container. Thus, the chimpanzees were unable to bind information about the identity of the experimenter to the location of food. A similar study by Wobber et al. (2010) found that chimpanzees and bonobos could successfully learn that one experimenter always held food, and another did not. However, in this study, the experimenters always stood in the same location during testing, thus the apes may have used the spatial location of the experimenter, rather than the identity of the experimenter, to determine where the food was (i.e., food is always located with the left experimenter).

The findings from Beran and the previous two chapters could arguably be attributed to apes being unable to distinguish one human from another; if they cannot tell one experimenter apart from another, changing the identity of an experimenter is not going to alter performance. However, such an explanation is unlikely, due to experiments that show primates are capable of recognizing and distinguishing between human faces (Martin-Malivel & Okada, 2007; Sliwa et al., 2011; Tomonaga, 1999). Furthermore, there is some evidence that apes can distinguish between, and remember, which human experimenter gave them food in previous interactions (Bohn et al., 2016). Here, apes requested absent entities (by pointing to an empty plate of food which previously contained food) more often to an experimenter that had previously refilled the plate, than to a novel experimenter who had not. Thus, they were able to distinguish

between the two human experimenters, and recall that one had provided food during previous interactions.²²

Similarly, a study by Schwartz et al. (2002) found that a gorilla named King could remember which human experimenter previously gave him food, and moreover, could recall what food he had been given, suggesting successful binding of ‘who’ and ‘what’. Prior to this experiment, King had been taught to associate objects and people with wooden cards on which drawings of objects and names were written. For example, he learnt to associate a wooden card depicting a drawing of a banana with a banana, and the name of a person with the corresponding person. King was then handed a particular food item by one of three experimenters. After a delay, he was asked what food he had eaten, and who had given him the food. To answer these questions, he was supplied with five food cards; four depicted foods that he had not been given (distractors), and one depicted food he had eaten last. Additionally, he was given two name cards; one of the names corresponded to the experimenter that had given him food most recently, the other was used as a distractor. When asked which food he had eaten last, and who gave him the food, King was able to choose the correct food and experimenter card above chance. Thus, King could distinguish between the two experimenters, and remember who had given him what. In a later experiment (Schwartz et al., 2004), King was also able recognise which unfamiliar person he had previously seen in a novel event, suggesting that he was able to recognise human faces after a very brief exposure.

²² Note that although the apes recalled who gave them food, they did not need to recall ‘what’ food was provided, or ‘where’ the food was located. Thus, the ‘who’ information was not necessarily bound to any other information. However, binding was not the aim of this study.

The successful performance by King seems to run counter to the findings from the previous chapters in this thesis (and the data from Beran), however, this may be due to the task design. King was explicitly questioned as to ‘who’ gave him the food, and had a forced choice option between two people. Consequently, his attention was explicitly drawn to this social information during retrieval. In the studies presented so far in this thesis, although social information was available at retrieval, the apes were not forced to attend to, or comment upon it. As such, other more salient information may have been attended to during retrieval (see outshining, Chapter 1). Moreover, it is unclear as to how King recalled this information. First, although King’s performance is consistent with the binding of ‘who’ information to ‘what’, it is possible that he could have remembered the information independently; that is, the retrieval of ‘what’ he ate may have been answered without recalling ‘who’ gave him the food, and vice versa. Second, King was only required to recognise which person had given him the food (i.e., to select from a sample), consequently he may have used familiarity judgments to make his choice; that is, he may have selected the person and food that was most familiar, rather than recollecting the feeding event. However, the authors claim that because they included a delay period of twenty-four hours, other food had given to him in this time, and thus would have been more familiar (Schwartz et al., 2005). As such, the mixed findings currently make it unclear as to whether primates can bind and retrieve social information, particularly when other salient information is available during encoding and retrieval.

5.3 Aims

The series of experiments presented below aimed to establish whether apes can bind social information (who) to object information (what), and later retrieve this from memory. Due to a lack of clarity of findings from previous studies, apes were presented with a task in which successful performance could only be based on the retrieval of social information, and not on other salient features (e.g., spatial surroundings). Additionally, the social information (who) needed to be jointly recalled with ‘what’ (i.e., a correct response required recalling who *with* what).

The apes were presented with an object exchange discrimination task. Previous research has shown that primates are capable of exchanging objects for rewards (Osvath & Persson, 2013; Pele, Dufour, Thierry, & Call, 2009) and of succeeding in discrimination tasks (Anderson, 1996; Itoh, Izumi, & Kojima, 2001); furthermore, the apes tested here were all familiar with exchanging objects for rewards. The apes were given three different types of objects, and were trained (via reinforcement) to exchange one of the object types with one experimenter, and one of the other types with another different experimenter; the third type was not trained. After a retention period, the apes were assessed on whether they could remember which object type was rewarded with which experimenter. A retention period of two and ten weeks (between subjects) was used, as previous research has shown that apes are capable of remembering information after both these times periods (Lewis et al., 2017b; Martin-Ordas et al., 2013; Mendes & Call, 2014), with no significant decline in performance from two to ten weeks (see Experiment 1, Chapter 4).

Additionally, if the apes show successful binding of a particular object type to a specific person, it was further investigated whether they could use this information to

infer by exclusion. Specifically, if they learn that object type A is bound to Experimenter 1, and object type B is bound to Experimenter 2, would they assume that object type C should be bound to Experimenter 3? We know that primates and other species are able to infer by exclusion using causal and spatial-temporal information (see Völter & Call, 2017), but it is less clear if they can do so with more abstract information, such as social information.

5.4 General methods

I first describe the general methods that are common to the three experiments in this study. Full methodological details for each of the experiments can be found under their respective specific methods.

5.4.1 Subjects

The majority of apes from the WKPRC participated in this study (see Table 5.1).

Additional demographic information about each ape can be found in Table 2.1 (Chapter 2).

Table 5.1 Participation of subjects by experiment (Exp). Ticks indicate that the subject participated, dashes indicate that they did not. Age shown is the age of the subject at the time of their first experiment.

Subject	Species	Sex	Age (years)	Exp 1	Exp 2	Exp 3
<i>Fimi</i>	Bonobo	Female	7	-	✓	-
<i>Gemena</i>	Bonobo	Female	10	-	✓	-
<i>Luiza</i>	Bonobo	Female	11	-	✓	-
<i>Lexi</i>	Bonobo	Female	16	-	✓	-
<i>Yasa</i>	Bonobo	Female	18	-	✓	-
<i>Kuno</i>	Bonobo	Male	19	-	✓	-
<i>Jasango</i>	Bonobo	Male	25	-	✓	-
<i>Bangolo</i>	Chimpanzee	Male	7	-	✓	-
<i>Kofi</i>	Chimpanzee	Male	11	-	✓	-
<i>Lobo</i>	Chimpanzee	Male	12	-	✓	-
<i>Tai</i>	Chimpanzee	Female	13	-	✓	-
<i>Lome</i>	Chimpanzee	Male	14	-	✓	-
<i>Alex</i>	Chimpanzee	Male	15	-	✓	✓
<i>Annett</i>	Chimpanzee	Female	16	-	✓	-

<i>Frodo</i>	Chimpanzee	Male	22	-	✓	-
<i>Jahaga</i>	Chimpanzee	Female	23	-	✓	-
<i>Zira</i>	Chimpanzee	Female	20	-	-	✓
<i>Hope</i>	Chimpanzee	Female	26	-	-	✓
<i>Dorien</i>	Chimpanzee	Female	35	-	✓	-
<i>Fraukje</i>	Chimpanzee	Female	40	-	✓	-
<i>Frederike</i>	Chimpanzee	Female	42	-	✓	✓
<i>Suaq</i>	Orangutan	Male	5	✓	✓	✓
<i>Raja</i>	Orangutan	Female	10	✓	✓	-
<i>Padana</i>	Orangutan	Female	16	✓	✓	✓
<i>Dokana</i>	Orangutan	Female	27	-	✓	✓
<i>Pini</i>	Orangutan	Female	28	-	✓	✓
<i>Bimbo</i>	Orangutan	Male	33	✓	✓	-

5.4.2 Apparatus

In each experiment, apes were given a number of objects that varied in size, shape, colour, and material. There were at least three objects of the same type (e.g., three blue cubes), and two different object types (e.g., blue cubes and green rectangles; see specific apparatus of each Experiment). In Experiment 1, the objects were placed into the enclosure before the session began, in Experiments 2 and 3, the objects were given to the subject either via a Plexiglas transparent container attached to the meshing (bonobos), or via a food hatch (chimpanzees and orangutans). All objects were replaced when they became damaged (broken or dis-coloured objects), but were not replaced after minor wear and tear.

Apes exchanged the objects with the experimenter through wire meshing, above the wire meshing was a transparent panel, through which the ape could see the experimenter (see Figure 5.1). This panel was replaced by an opaque panel after the ape successfully passed two sessions. The opaque panel blocked the ape's and

experimenter's view of each other, preventing the experimenter from unintentionally cuing the subject to exchange a specific object. However, the apes could still see the identity of the experimenter before the session began, and at the end of each trial, and could see the experimenter's hands and hear their voice during the trials. All exchanged objects were placed into an opaque plastic bucket, and a second identical bucket contained a food reward (grapes).



Figure 5.1 Overview of the procedural set-up. Objects were exchanged through the lower mesh. In Experiments 2 and 3, all objects were placed into the food hatch (to left of the ape) at the start of each trial. The ape could access all objects from the food hatch. In cases where infants were not separated from their mothers, the infant was fed raisins at the far side of the enclosure by the keeper (pictured far left). Photo printed with permission from MPI-EVA

5.4.3 Design

Each object type was assigned a letter (e.g., blue cubes were assigned ‘A’ and the green rectangles assigned ‘B’); the number of different object types varied between experiments (see specific methods), but always included a type A and type B. During training, apes were rewarded for exchanging type A with Experimenter 1 (E1), and only E1, and type B with Experimenter 2 (E2), and only E2. The reward was one grape. Subjects trained separately with each experimenter; that is, E1 and E2 were never present in the same session. All training began with the transparent panel, and switched to the opaque panel after subjects passed two sessions. The criteria to pass a session differed slightly between experiments (see specific methods).

Experiments 1 and 2 included a test after training. This test took place after a two or ten-week retention period, during which the apes received no additional training. The apes were non-differentially rewarded, meaning that they were rewarded for exchanging any object type. This was to ensure the apes’ performance was based on their memory of what they had previously learnt, and not a result of learning during the test. All testing took place with the opaque panel. For full design details see specific methods of each Experiment.

5.4.4 Procedure

Training

At the start of a trial, the ape was given access to all the objects: in Experiment 1, the objects were put into the testing room before the subject entered, in Experiments 2 and 3, they were given to the apes via a food hatch (see Figure 5.1) or a Plexiglas container. This latter method was introduced to enable all objects to be replaced back into the

enclosure at the end of a trial, without needing to remove the ape from the enclosure first. Once the apes had access to the objects, the experimenter sat in front of the mesh and asked the subject for an object. This was achieved by holding both palms face up next to the mesh; one palm held a grape, the other was empty. If the subject did not pass an object through the mesh, the experimenter verbally encouraged them. If they did not respond after five minutes, the session was cancelled and re-scheduled; this happened with Raja (twice) in Experiment 1, Frodo (six times), Fraukje (once) and Kuno (twice) in Experiment 2, and Suaq (three times), and Dokana and Zira (once) in Experiment 3.

If the subject gave a correct object (i.e., Type A with E1, or type B with E2), the experimenter immediately rewarded them with a grape, and then placed the object into a bucket to the left (here-after: object bucket). If the object was incorrect, no reward was given and the object was placed into the object bucket. In cases where an infant took the objects or stole the food reward, the object was retrieved from the infant and replaced back into the enclosure. If the object could not be retrieved, an additional object (of the same type) was put into the enclosure. A trial ended once all correct objects had been exchanged.

At the start of a new trial, all objects were given to the apes as described above. Sometimes the apes had not exchanged all the objects during a trial (e.g., they exchanged all correct objects without exchanging all the incorrect ones). In these cases, the un-exchanged objects either remained in the food hatch/container (as the subject had not removed them), or were on the enclosure floor. Thus, all the objects were not necessary in the same place at the start of a new trial, but were all accessible to the apes. The number of trials per session varied by Experiment.

Test

The procedure for the tests in Experiments 1 and 2 was the same as training, except that the apes were rewarded for every exchange (regardless of whether they were correct), and a trial ended after four exchanges in Experiment 1 (as opposed to after all correct objects had been exchanged).

5.4.5 Analysis

The dependent variable at training was the number of sessions taken to reach criterion. The dependent variable at test was the number of correct exchanges (Experiment 1), or the number of exchanges required to exchange all correct objects (Experiment 2). For details of the statistical analyses, see the specific analyses of each experiment.

5.5 Experiment 1 | Pilot

5.5.1 Aims

The purpose of the first study was to pilot the experimental design on a limited number of subjects. Any subsequent design issues were then rectified in Experiment 2.

5.5.2 Methods

5.5.2.1 *Subjects*

Four orangutans took part in this experiment: two males (Bimbo and Suaq), and two females (Raja and Padana). Their ages ranged from 5-33 years ($M = 16$; see Table 5.1), and all were familiar with exchanging objects for rewards. Subjects were tested between October 2014 and December 2014.

5.5.2.2 *Apparatus*

There were four different types of objects: two of the types were made of wood and two of Plexiglas. For the wooden types, one was circular shaped with a hole in the centre (H:3.8cm x L:3.8cm x D:1.0cm), and the other was cylindrical (H:4.8cm x L:1.5cm x D:1.5cm). For the Plexiglas types, one was a light coloured rectangle (H:2.8cm x L:1.9cm x D:1.6cm), and the other a dark coloured triangle (H:2.9cm x L:2.9cm x D:1.0cm; see Figure 5.2). There were six objects of each type (i.e., 6 objects x 4 types). Different materials and shapes were used so that it was easy for the orangutans to distinguish between the four object types.

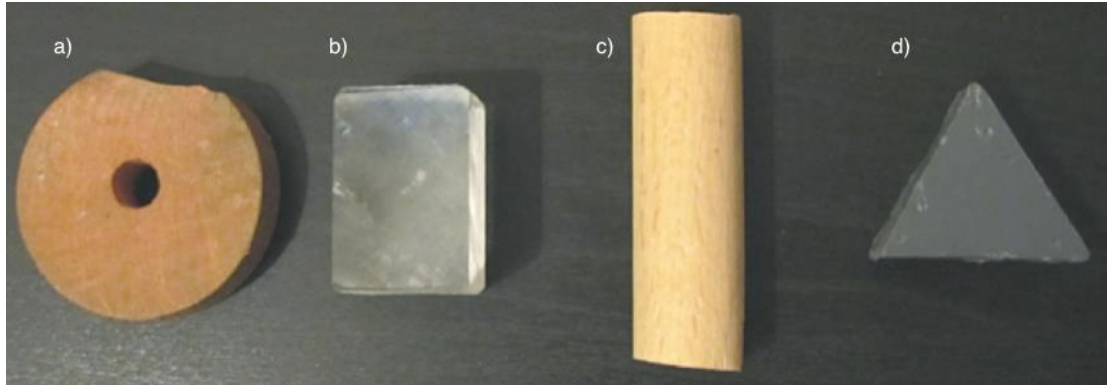


Figure 5.2 The four object types. a) wooden circle, b) Plexiglas rectangle, c) wooden cylinder, d) Plexiglas triangle. Objects a) and b) were present during training with E1. Objects c) and d) were present during training with E2.

5.5.2.3 Design

Training

Each object type was assigned to one of four letters (A, B, C¹, C²). The wooden circle and the Plexiglas rectangle were always assigned to either A or C¹, and were presented with E1 during training. The wooden cylinder and Plexiglas triangle were always assigned either to B or C², and were presented with E2 at training; thus, each pair contained object types made from different materials to help the orangutans to distinguish between the object types. Types A and B were always the correct types, and types C were always incorrect. The assignment of objects to a letter within a pair was counterbalanced between subjects, to control for any preference an orangutan may have for a particular material (e.g., for some subjects the wooden circle was A, and for others

it was C¹).²³

The training sessions alternated between experimenters (i.e., session one was with E1 and session two with E2, and so forth), with one session per day, and two trials per session. All subjects began training with E1. During training with E1, all six A type objects and six C¹ objects were present (C² type and B type were not present), and only type A was rewarded. With E2, type C² and B type objects were present (A types and C¹ types were not present), and only type B was rewarded. This meant that there were six correct exchanges per trial (and six incorrect), with a total of 12 correct exchanges per session (and 12 incorrect).

The C type objects were never rewarded, and served to aid the apes in understanding that only one object type was rewarded by one experimenter. Furthermore, at test, the type C objects established whether the apes remembered which object types were reinforced (i.e., A and B) and which were not (i.e., C¹ and C²), even if they fail to remember which type belonged to which experimenter.

To pass a session, the subject needed to exchange the correct object a minimum of five times in the first six exchanges of each of the two trials (10/12 correct exchanges); that is, in the first six exchanges of both trials they needed to exchange the correct object at least 83% of the time. Training began with the transparent panel, and switched to the opaque panel after two successful sessions. After two successful sessions with the opaque panel, training was completed.

In short, E1 trained with A and C¹ type objects (one of which was the wooden

²³ It was not possible to counterbalance the assignment of object types to experimenters, as there were only four subjects (i.e., the wooden circle and Plexiglas rectangle were only present with E1, and the wooden cylinder and Plexiglas triangle were only present with E2).

circle and the other the Plexiglas cube), and only rewarded type A. E2 trained with B and C² objects (one of which was the wooden cylinder and the other the Plexiglas triangle), and only rewarded type B.

Test:

The test began two weeks after completion of training. There were four test sessions, with three trials per session, and each subject had two test sessions with each experimenter, with each test on separate consecutive days. Subjects began with either E1 or E2, the order of which was randomized between-subjects to control for any possible order effects. The tests then alternated between the two experimenters (e.g. E1 on day one and three, and E2 on day two and four).

At test, 12 objects were present: 4 x A type, 4 x B type and 4 x C type (either C¹ or C²). The type C that was presented during the test alternated between trials (e.g., in the first and third trial object type C¹ was used, in the second trial object type C² was used). Both C types were presented an equal number of times with each of the experimenters across the four test sessions. The apes were not presented with all objects of all types in one test, as this would have resulted in four object types (twice as many as at training), and may have made the test unnecessarily complicated. Additionally, the number of objects of each object type was reduced from six to four, so that the total number of objects (12) was the same as during training, and the number of trials increased from two to three, so that the total number of possible correct exchanges per test remained the same as training (12).

A correct object was an object of the type corresponding to the present experimenter (i.e., object type A with E1, and object B with E2). All objects were

rewarded (non-differential reinforcement), and a trial ended when four objects had been exchanged, regardless of whether they were correct. This was because there were only four possible correct exchanges, thus if subjects remembered what they had learned during training, they would only need four exchanges. Subjects completed three trials, resulting in a total of 12 exchanges per test. A score of 12 would indicate perfect performance (i.e., that the subject exchanged the correct object every time).

5.5.2.4 Procedure

Training

At the start of a trial, E1 put all six A objects and six C¹ objects into the testing room. The procedure then followed the procedure described in the general methods, with E1 rewarding only A objects. The procedure with E2 was identical, except that six B and six C² objects were used instead of six A and six C², and only B type exchanges were rewarded. A trial ended after all six correct objects had been exchanged. Before the next trial began, the subject was removed from the testing room so that the experimenter could place all 12 objects back inside the testing room. The session ended after two trials.

Test

At the start of a trial, the experimenter put four A objects, four B objects and four C objects into the subject's enclosure. The type C type object alternated between trials (see design). The procedure then followed that of general procedure. A trial finished after four exchanges, and the test finished after three trials.

5.5.2.5 *Data analysis*

The dependent variable at training was the number of sessions taken to reach criterion (minimum four). It was expected that the mean number of sessions with each experimenter would be similar. The dependent variable at test was the number of correct exchanges (maximum 12). As there were two tests with each experimenter, the average of the two tests was taken to create one score for the test with E1, and one score for the test with E2. Performance was then compared between the two using a paired t-test. A high score in both tests would indicate evidence of binding, whereas a low score in both tests would indicate absence of binding, and, depending on the errors, failure to remember the rewarded object types (if they do not exchange types A and B more than the two type Cs). A low score in one test and a high score in another would indicate memory of one of the rewarded object types (i.e. a preference for one rewarded object type over the other), this would also indicate failure to bind the object types to the experimenters.

5.5.3 Results

5.5.3.1 *Training*

One orangutan (Raja) was excluded from the experiment after failing to pass a single session with E1 after 20 sessions. The results from the remaining three subjects indicated that the number of sessions required to pass training with E1 ($M=13.33$, $SD=7.77$) was not different to E2 ($M=11.33$, $SD=3.79$; see Table 5.2); $t(2)=-.655$, $p=0.58$.

5.5.3.2 Test

The paired sample t-test revealed performance in the tests with E1 and E2 to be significantly different, $t(2)=8.55$, $p=0.01$. Performance in the test with E1 ($M=10.00$, $SD=1.50$) was significantly better than with E2 ($M=1.33$, $SD=0.29$), with subjects making an average of only two errors (83% correct) in the test with E1. Furthermore, the apes exchanged the A object type across all tests 118 times out of 144 exchanges (82%), showing a clear preference for the A object type over the B and C object types. The B and C types were exchanged 17 and 9 times respectively, with Bimbo and Padana only exchanging the C type once.

As the apes were non-differentially rewarded at test (to prevent further learning), it is possible that they adapted their response based on this new contingency, rather on what they had previously learned during training (i.e., they exchanged objects based on their current reward value, rather than their previous one). Due to the small sample size ($N=3$), it was not possible to statistically analyse only the first exchanges of each test; however, the data showed that there was no difference between the first exchanges in the first test with each experimenter (see Table 5.3). This suggests that the apes preferentially gave one object type, regardless of which experimenter was present. Moreover, if the apes changed their behaviour based on the new contingency, it would be expected that they would exchange all objects randomly in later trials once they learnt that all objects were rewarded. This was not the case, with A type objects being exchanged the most by the three subjects in the last trial of the last test (9/12 exchanges).

Table 5.2 Number of sessions needed with E1 and E2 to meet training criterion.

Subject	Experimenter	No. training sessions
<i>Padana</i>	E1	7
	E2	7
<i>Bimbo</i>	E1	22
	E2	14
<i>Suaq</i>	E1	11
	E2	13

Table 5.3 The first object exchanged in the first test with E1 and the first test with E2, by subject

Subject	First object exchanged in test E1	First object exchanged in test E2
<i>Padana</i>	A	A
<i>Bimbo</i>	A	A
<i>Suaq</i>	B	B

5.5.4 Discussion

The findings suggest that the apes remembered which object types were rewarded, but failed to bind the object types to the experimenters. A strong preference was found for the A type object, as shown by the good performance in the test with E1 compared to E2, and the sheer number of A exchanges in comparison to the other types.

Furthermore, Bimbo and Padana clearly avoided exchanging the C type object, suggesting that they remembered this object was never rewarded. These results seem to suggest that the orangutans recalled which object types were rewarded, and which were not, but developed a preference for one of the rewarded types over the other.

It is not clear why the apes preferred the A object type in comparison to the B, since both types had similar reinforcement histories (as shown by lack of statistical difference between the number of training sessions; although see below). Furthermore, the object assigned to A was not the same for all subjects; two had the wooden circle and one (Bimbo) had the Plexiglas rectangle. Additionally, subjects did not all start with E1 at test, nor did they all give an A object as their first exchange. Thus, it's unlikely they exchanged the A object more because it was the first rewarded object at test; however, it was the first rewarded object at training, as all subjects began training with E1. Thus, it could be that this prompted a preference for this object type (i.e. they preferred the object type that was rewarded first). Alternately, as the apes were more familiar with E1 in comparison to E2 (E2 was an intern), the preference for exchanging the object rewarded by E1 may be because of preferring the more familiar experimenter.

As this experiment was conducted as a pilot, the sample size was deliberately very small. It was thus not possible to analyse only the first exchanges during the test,

meaning that the effect of the new task contingences could not be completely ruled out (i.e., non-differential reinforcement) on performance. Furthermore, although the number of training sessions did not statistically differ between experimenters, subjects needed on average two additional sessions with E1 compared to E2, given a larger sample size this may have been significant. This difference may also have explained the preference for A objects, as on average, subjects exchanged the A type objects 24 more times than the B types, meaning that the A type was reinforced more than the B type.

Regardless of why the apes preferred the A type object, the results show that they failed to recall 'who' rewarded 'what'. However, this failure is likely due to the experimental design. During training, the apes were presented with one set of objects (A and C¹) with E1, and another set of objects (B and C²) with E2. To pass training, they need only have learnt that object types A and B were rewarded, and to avoid type C, rather than learning that object type A was rewarded with E1, and object type B was rewarded with E2. To learn that the rewarded object type was dependent upon the experimenter identity, both object types A and B needed to be presented together with both experimenters. The apes would then only be able to determine which object type was rewarded (A or B), by observing which experimenter was present. These issues were addressed in Experiment 2.

5.6 Experiment 2 | 'what' belongs to 'who'

5.6.1 Aims

The aim of this second experiment was to rectify the issues highlighted in experiment 1, and to further assess the ape's ability to bind objects to identities. To do so, the sample size increased from four to twenty-five, and the procedure was adjusted in the following ways: first, at training all object types were presented with both E1 and E2. For example, in the training session with E1, 4 A objects, 4 B objects and 4 C objects were present. This gave the apes the opportunity to experience exchanging B type objects with E1 (and A types with E2), and subsequently to learn that B types were never rewarded with E1 (and A types never rewarded with E2). Second, training was completed with each experimenter in blocks; that is, subjects completed training with E1 before beginning training with E2. The reasoning behind this change was to make the training easier for the apes. Learning a discrimination rule that alternates from one session to the next may make the training unnecessarily difficult for the apes, and as performance was not great in Experiment 1 (as shown by Raja's failure to pass a single session with E1 after 20 sessions), training needed to be as simple as possible. Third, as Experiment 1 found that the apes could easily distinguish between objects of the same material type, all objects in Experiment 2 were made of wood. This meant that only one C type object was needed (as opposed to two types; one wood and one Plexiglas), again making the training simpler for the apes. Fourth, subjects were tested after a delay of two or ten weeks. Including a second delay period enabled memory performance to be assessed over time. Fifth, subjects only completed one test and one trial at test, and a trial ended when all correct objects had been exchanged. The number of trials and tests was reduced to minimize potential learning of the new contingencies at test. A trial

ended after all four correct objects had been exchanged, as opposed to after four exchanges of any object, to see what errors (if any) a subject made. For instance, if a subject exchanged all four correct objects in the first six trials, it could be seen which two incorrect object types they exchanged. Finally, a third experimenter was introduced at test. This experimenter did not complete any training with the apes, and simply conducted one test session. The purpose of the third experimenter was to assess whether the apes would infer by exclusion that the C object (that was unrewarded by E1 and E2) should be given to the new experimenter (E3).

5.6.2 Methods

5.6.2.1 Subjects

Twenty-five apes took part in this experiment, including the four orangutans from Experiment 1 (see Table 5.1). Subjects consisted of 12 chimpanzees, seven bonobos, and six orangutans, aged between 6-42 years ($M = 19.24$). All subjects were tested between September 2015 and September 2016.

5.6.2.2 Apparatus

Three types of wooden objects were used: a green rectangle (H:4.9cm x L: 2.3cm D:1.2cm), a blue cube (H:2.5cm x L:2.5cm x D:2.5cm) and a pink triangle (H:2.1cm x L: 4.5cm x D:2.9cm; see Figure 5.3). There were four objects of each type, resulting in a total of 12 objects. The rest of the apparatus is described in the general procedure.

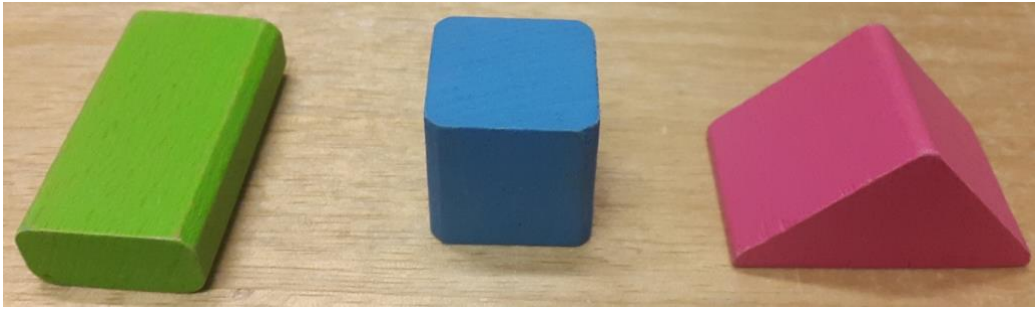


Figure 5.3 The three object types

5.6.2.3 Design

Training:

There were two different experimenters (E1, E2) and three types of objects (see apparatus). The experimenters were all familiar to the apes, and had tested the apes on at least one other study prior to this experiment. Each object type was assigned a letter (A, B or C), for instance, the green rectangle was assigned A, the blue square was assigned B, and the pink triangle was assigned C (assignment was counterbalanced between-subjects). At training, all object types were present with each of the experimenters (i.e., all 12 objects). E1 only rewarded object type A, and E2 only rewarded object type B; type C was never rewarded. Apes trained with one experimenter at a time, and did not begin training with the second experimenter until passing training with the first. This was in contrast to Experiment 1, in which sessions alternated between experiments. The experimenter that they trained with first was randomized between-subjects to control for any potential order effect (i.e. some began with E1, and some with E2).

There were four trials per session, with one session a day. To pass a session, the subject had to exchange the correct object a minimum of 13 (out of 16) times in the

first four exchanges of each of the four trials (81.25% correct); that is, only the first four exchanges per trial were counted, and they had to exchange a minimum of 13 correct objects across the four trials to pass the session. Once subjects had successfully passed two sessions, an opaque panel was inserted into the panel frame above the mesh, just as with Experiment 1. All subjects needed to pass six training sessions (two transparent and four opaque), with both E1 and E2.

Once apes had passed these six sessions, it was checked whether they exchanged the correct object type at least 50% of the time in the first four exchanges of the four opaque passed sessions. As there were sixteen correct exchanges per session, the apes may have learnt which object type was correct *during* a session, rather than learning over sessions which object type was correct. If this were the case, performance would likely be poor in the first few exchanges of a session, whereby the apes exchange the objects randomly until they learn which one was correct. Therefore, it was checked this was not the case by examining whether they exchanged the correct object the majority (at least 50%) of the time in the first four exchanges of the four opaque sessions. If subjects failed to do this, they received additional training sessions until they reached a 50% (or greater) exchange rate in the last four opaque sessions. If subjects failed to complete two consecutive sessions, or did not pass at least one session by the 15th session, they were dropped from the study. This training criteria was increased from Experiment 1 to ensure the apes really learnt which object type was rewarded by which experimenter.

Test:

The test took place two (10-20 days, $M=15$) or ten weeks (68-95 days, $M=76$) after completion of training. There were three test sessions (within-subjects), one with E1 one with E2, and an additional test with a third experimenter (E3). E3 had conducted many other tests with the apes, and was thus familiar to them, but was never present during the training of this Experiment, nor Experiment 1. The tests were conducted on separate consecutive days (with the exception of Fimi, who had a two-day delay between her first and second test), and the order of tests was randomized between-subjects (see Figure 5.4 for an overview of the training and test phases).

During each test session, subjects completed four trials, and were rewarded for passing any object through the meshing (non-differential reinforcement). A trial finished when all four correct objects had been exchanged; a correct object was an object of the type corresponding to the present experimenter (e.g. object type A with E1). If the apes successfully learnt to bind an object type with a specific experimenter at training, they should preferentially give that object type at test when the experimenter is present (e.g., during E1's test the subject should give object type A). If they are able to bind and recall this information perfectly, it will take them four exchanges to give all the correct objects. If the apes are able to show inference by exclusion, in E3's test they should give object type C; object types A and B are rewarded with E1 and E2, and only E1 and E2, respectively, and object type C is not rewarded by either E1 or E2, thus object type C must be rewarded with E3.

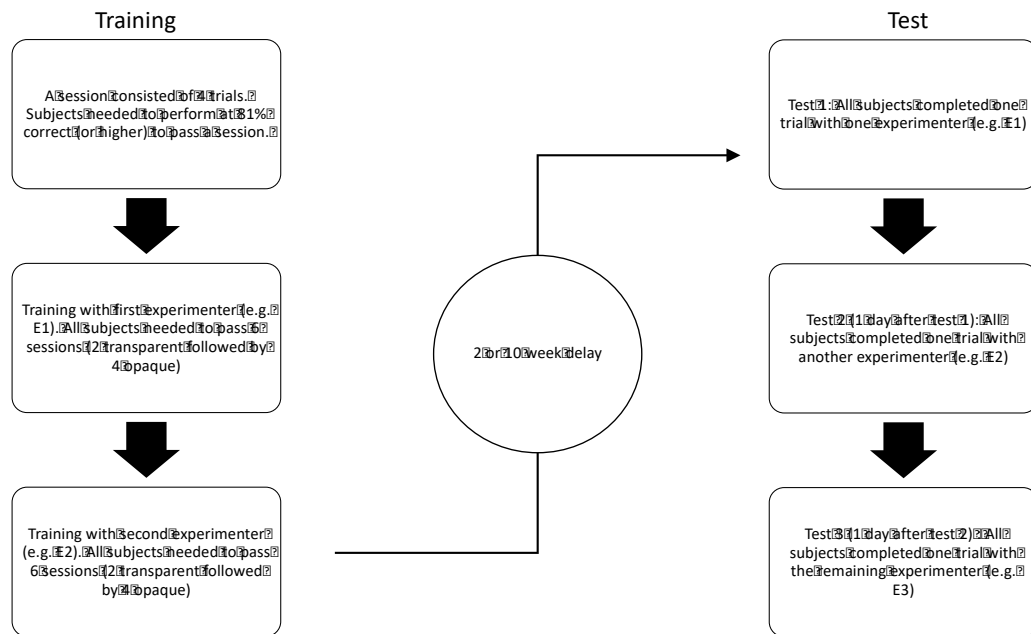


Figure 5.4 Example order of training and test phases.

5.6.2.4 Procedure

Training:

At the start of a session the experimenter put all 12 objects into the food hatch (or container). Some of the apes chose to select one object at a time from the food hatch/container, whereas others emptied all of the objects onto the enclosure floor. Objects were then exchanged and rewarded in the same way as the general procedure, with E1 rewarding A and only A, and E2 rewarding B and only B. There were four possible correct objects per trial, once all four correct objects had been exchanged the trial ended.

Test:

The test followed the test procedure described in the general methods. A session finished once all four correct objects had been exchanged.

5.6.2.5 Data analysis

The analyses described below were conducted on the data from all subjects. An additional analysis was conducted on only the data from the three orangutans from Experiment 1, in order establish whether experience in Experiment 1 may have influenced performance in this experiment; the results suggest that this was not the case (see Appendix C.1, orangutan data). In cases of multiple testing, the alpha level was adjusted using the Bonferroni correction. Greenhouse-Geisser was reported when Mauchly's test of sphericity was significant.

Training:

The dependent variable was the number of sessions taken to reach criterion (minimum 6). To establish whether learning rates differed between species, and whether the apes' performance with the second experimenter was influenced by training with the first experimenter, a 3 (species) x 2 (experimenter; first and second) mixed ANOVA was conducted. The apes may show difficulties with inhibiting the object type that was rewarded with the first experimenter when they begin training with the second experimenter, as has been observed in other studies on inhibition in apes (Beran & Evans, 2009; Uher & Call, 2008; Vlamings, Hare, & Call, 2010; Vlamings et al., 2006). Differences in performance between the first and second experimenter may also be due

to proactive interference²⁴, whereby the apes have difficulties learning new information as a result of previously learnt information (Anderson & Neely, 1996)

Test:

Each subject took part in three tests, one with each experimenter (E1, E2, E3). It was first assessed whether performance differed between the three tests. If the apes successfully bind and recall which object type is rewarded by which experimenter, then performance in tests with E1 and E2 should be better than E3 (as E3 was never associated with any of the object types). However, if the apes also perform well in the test with E3, this would indicate successful inference by exclusion. Performance on the three tests (within-subjects) was tested between species and between delay groups (between-subjects), using a 3 (test) x 3 (species) x 2 (delay) mixed ANOVA. The dependent variable was the number of exchanges needed to exchange all four correct objects (minimum 4, maximum 12), with a low score indicating high levels of performance. Performance between the two delay periods was expected to be similar, but with a possible decrease after ten weeks. Additionally, any errors the apes made in the three tests was assessed, by counting the number of times an A object, a B object and a C object was incorrectly exchanged (i.e., all A errors in tests E2 and E3, all B errors in tests E1 and E3, and all C errors in tests E1 and E2). A repeated measures ANOVA compared the average number of incorrect exchanges between the three object types. It was expected that the previously rewarded types (A and B) would be erroneously exchanged more than type C.

²⁴ This suggestion was provided by an anonymous reviewer

To further test whether the apes successfully bound object type A to E1 and object type B to E2, we ran two paired t-tests; the first assessed whether the apes exchanged more A type objects with E1 compared to E2 in the first four exchanges, and the second assessed whether they exchanged more B type objects with E2 compared to E1 in the first four exchanges. Only the first four exchanges were counted, as there were four correct objects per experimenter. If the apes successfully bound the object types to the experimenters, they should exchange more A type objects with E1 than E2, and more B type objects with E2 than E1. Alpha level was corrected to 0.025 to control for familywise error.

An additional analysis considered whether performance in tests with E1 and E2 was influenced by the experimenter with which they last trained, independent of the delay period. If the apes fail to bind the object type to the experimenter, they may instead preferentially exchange the most recently rewarded object with both experimenters. This was tested using a 2 (test; E1, E2) by 2 (experimenter last trained) by 2 (delay) mixed ANOVA; the dependent variable was the number of exchanges needed to exchange all four correct objects (the same as the first ANOVA described). Test was within-subjects and experimenter last trained and delay were between-subjects. The alpha level for the two ANOVA tests was adjusted to 0.025 to control for familywise error.

Further analyses were also conducted on the first exchanges of each of the three tests. During the first exchanges, the apes can only base their response on previous learning, and not on any feedback received during test. To assess whether performance between the three tests differed, the number of correct and incorrect first exchanges between tests was compared, using an exact Cochran's Q test. It was also investigated

whether performance in tests with E1 and E2 was influenced by the experimenter with whom they last trained. This was achieved by calculating whether the number of apes that trained with E1 last, and gave object A in the first exchange of both tests, was above chance, and likewise, whether the number of apes that trained with E2 last, and gave object B in both tests, was above chance. Chance was calculated as 0.33 (as subjects could exchange A, B or C objects), and alpha level was adjusted to 0.025.

5.6.3 Results

5.6.3.1 Training

One chimpanzee was dropped from the experiment during training with the first experimenter (Dorien), and three with the second experimenter (Annett, Tai, Fraukje), due to failing 15 sessions. In addition, one orangutan (Raja) was dropped with the second experimenter after five sessions, due to failing to complete two consecutive sessions (sessions four and five), resulting in a total of 20 apes. Of the subjects that passed six sessions, all exchanged the correct object type in the first four exchanges of the four opaque sessions more than 50% of the time ($M=87.50\%$, $SD = 14.44\%$), showing that they retained what they had learnt across sessions.

The means and standard deviations by species and experimenter can be seen in Table 5.4. A main effect of experimenter was found, $F(1,17)=26.94$, $p<.001$, $\eta_p^2=.613$, whereby subjects took longer to learn with the second experimenter than the first. This effect was due to the apes continuing to exchange the object rewarded by the first experimenter in the first few sessions with the second experimenter (see Table 5.5). No main effect of species was found, but a trend was observed which suggested that bonobos took longer to complete training than the chimpanzees and orangutans $F(2,17)=3.39$, $p=0.06$, $\eta_p^2=.285$. Additionally, an interaction between species and experimenter was found, $F(2,17)=12.62$, $p<.001$, $\eta_p^2=.598$, which showed that bonobos and orangutans took more sessions to complete training with the second than the first experimenter, but that chimpanzees did not (and were marginally better with the second). However, these results should be taken with caution; 3 of the chimpanzees failed to complete training with the second experimenter after 15 sessions and were dropped from the study (Tai, Fraukje, Annett), thus their data were not included in the

analysis. The failure to pass training shows the difficulty with learning with the second experimenter, and thus there is likely to be no real differences between chimpanzee learning rates as compared to the orangutans and bonobos.

Table 5.4 Mean number of sessions needed to complete training with the first and second experimenter, by species.

		<i>Bonobo (N=7)</i>	<i>Chimpanzee (N=8)</i>	<i>Orangutan (N=5)</i>
First experimenter	<i>M</i>	10.86	11.38	9.40
	<i>SD</i>	2.61	2.50	1.67
Second Experimenter	<i>M</i>	17.14	11.25	12.00
	<i>SD</i>	3.58	2.05	3.54

Table 5.5 Mean number of times (percentages in parentheses) the correct object type for the first experimenter was given to the second experimenter, in the first 3 sessions with the second experimenter. Only the first 4 exchanges per trial were counted, with 4 trials per session, giving a total of 16 exchanges per session.

Species	Session 1	Session 2	Session 3
<i>Bonobo</i>	12.29 (76.81%)	11.14 (69.63%)	8.86 (55.37%)
<i>Chimpanzee</i>	13.5 (84.38%)	12.38 (77.38%)	8.88 (55.50%)
<i>Orangutan</i>	13.6 (85.00%)	10.20 (63.75%)	7.20 (45.00%)

5.6.3.2 Test

One chimpanzee (Frederike) was removed from the analysis due to experimental error, resulting in a total of 19 subjects. A main effect of test was found, $F(1.15, 14.95) = 16.77$, $p = 0.001$, $\eta_p^2 = .563$, but not species or delay (both: $F < .71$, $p > 0.51$; see Figure 5.5). None of the interactions between species, test and delay were significant (all: $F < 2.73$, $p > 0.10$). The main effect of test showed that the apes needed more exchanges to reach four correct objects with E3 (i.e. C type objects; $M = 11.42$, $SD = 1.26$) than they did in tests with E1 ($M = 7.42$, $SD = 2.60$) and E2 ($M = 6.89$, $SD = 2.42$); that is, A and B type objects respectively. Additionally, tests with E1 and E2 were not significantly different $t(18) = .49$, $p = 0.63$, $d = 0.11$, meaning subjects took the same number of exchanges to exchange the correct object in both tests. The greater number of exchanges in the test with E3 suggests subjects were avoiding the non-reinforced object and preferentially selecting the reinforced objects. Although performance was better in tests with E1 and E2 compared to E3, further analysis revealed that the apes were not successfully binding object type A with E1 and object type B with E2, as shown by no difference between the number of times object A was given to E1 ($M = 1.47$, $SD = 1.74$) compared to E2 ($M = 1.47$, $SD = 1.35$); $t(18) = .00$, $p = 1$, nor the number of times object type B was given to E2 ($M = 2.47$, $SD = 1.35$) compared to E1 ($M = 2.47$, $SD = 1.74$), $t(18) = .00$, $p = 1$.

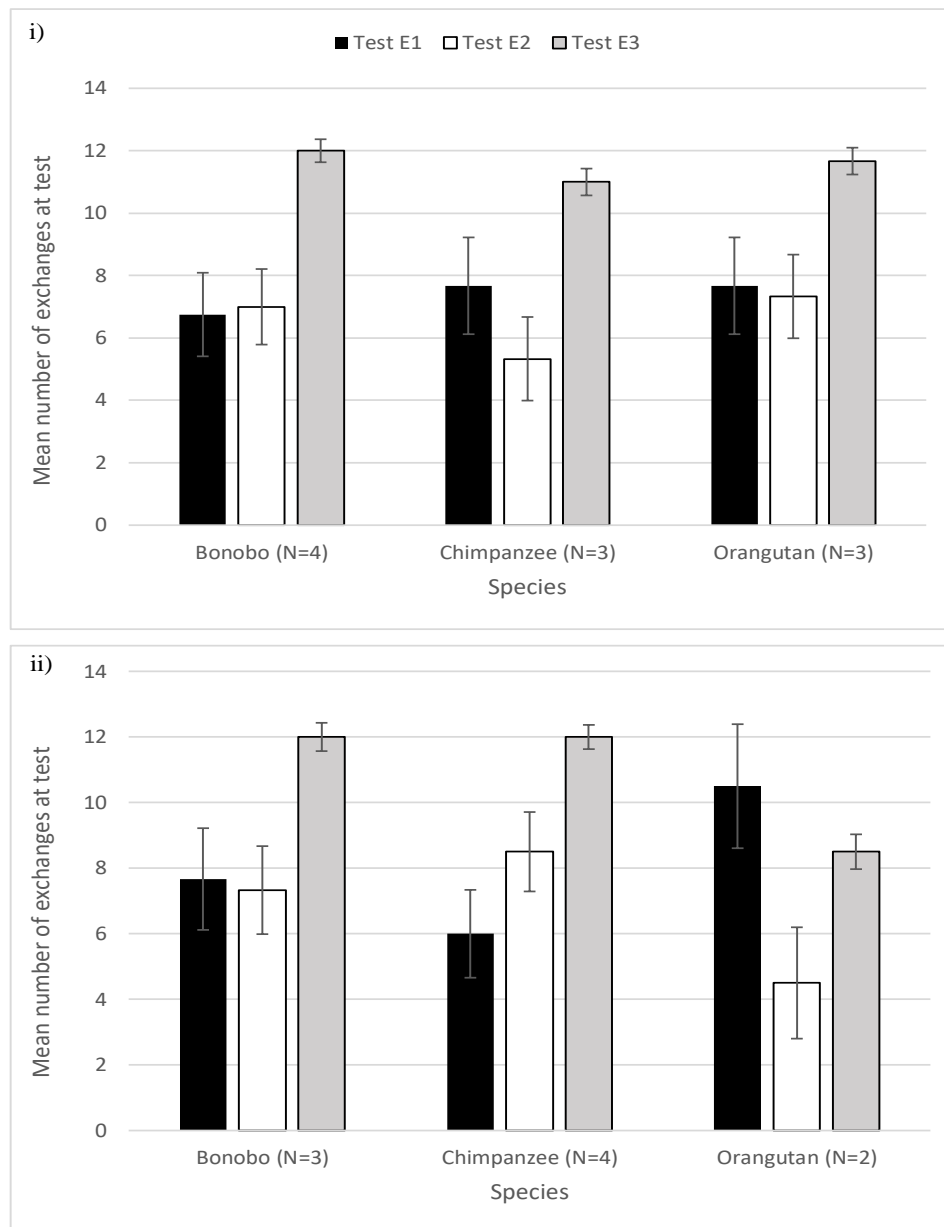


Figure 5.5 Mean number of exchanges needed to exchange all 4 correct objects in each test, by species. i) depicts subjects in the 2 week delay period, ii) depicts subjects in the 10 week delay period. Error bars denote the standard error.

Regarding the number of times an incorrect object type was exchanged, a main effect of object type was found, $F(2,36)=29.81$, $p<0.001$, $\eta_p^2=.624$. This effect showed that the C type object ($M=1.37$, $SD=1.34$) was exchanged less than the A type ($M=6.05$,

$SD=2.17$) and B type ($M=6.26$, $SD=2.17$), indicating that when subjects exchanged the incorrect object, it was more often the object type that has been rewarded during training, rather than the un-rewarded (C) type.

An additional analysis considering only tests with E1 and E2, revealed a significant interaction between test (i.e., between A and B type objects) and the experimenter with whom they trained last, $F(1,15)=17.35$, $p=0.001$, $\eta_p^2=.536$. There was no 3-way interaction when delay was included, $F(1,15)=0.009$, $p=0.93$, $\eta_p^2=.001$. This meant that subjects performed better (had fewer exchanges) in the test in which the correct object type was the type last trained with, independent of delay. For example, if they trained with E2 last (reinforced B type), they had fewer exchanges in the test with E2 (in which object type B was correct) than the test with E1 (in which object type A was correct; see Figure 5.6) Thus, subjects preferentially exchanged the object type that was reinforced last. As subjects took longer to train with the object that was reinforced last (i.e., training data showed greater mean number of sessions with the second experimenter, as mentioned previously, cf. Table 5.4), an additional analysis tested whether this object type was preferred due to being reinforced more; a non-significant correlation between the number of training sessions with the last experimenter and the number of exchanges on the corresponding test showed that apes preferred the last rewarded object type independent of how much it had been reinforced, $r(19) = .09$, $p = 0.72$.

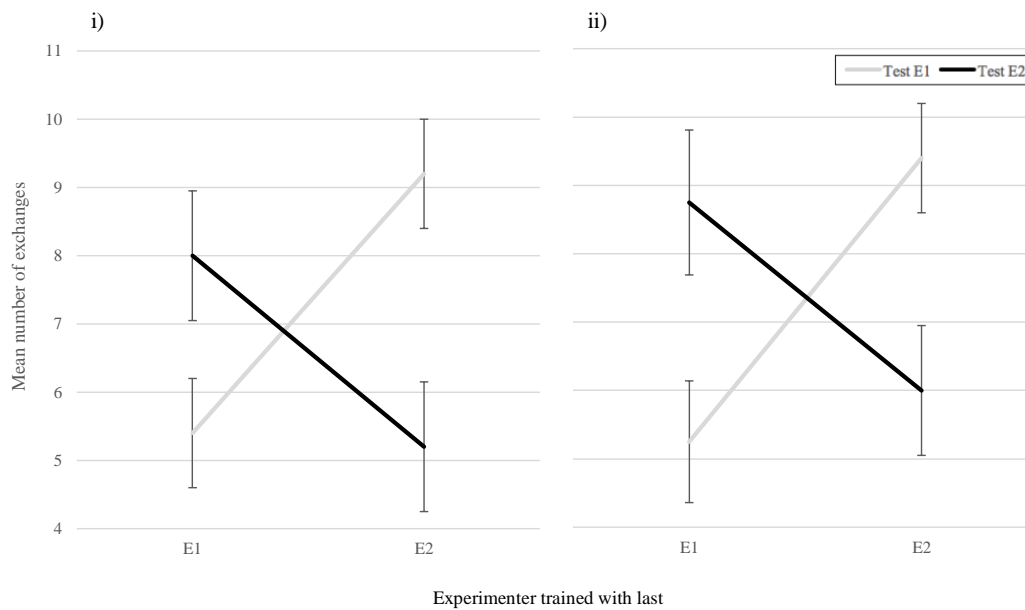


Figure 5.6. Mean number of exchanges in tests E1 and E2 by experimenter with whom they last trained. i) Depicts subjects in the 2 week delay period, ii) depicts subjects in the 10 week delay period. Error bars denote standard error.

When analysing just the first exchanges in each test, results indicated that performance in the three tests was significantly different, $Q(2) = 10.33$, $p = 0.005$, with worse performance with E3 (0% correct exchanges) compared to E1 and E2 (37% and 58% correct first exchanges respectively). An exact McNemar test revealed no difference between performance in tests with E1 and E2 ($p = 0.48$). These results replicate the main analysis, with subjects performing significantly worse in the test with E3 compared to tests with E1 and E2, and with comparable performance between tests with E1 and E2.

Binomial tests revealed that of the apes that trained with E1 last ($n = 9$), 78% gave object A in the test with E1, which was significantly above chance ($p < 0.008$, CI [0.40, 0.97]), and 89% gave A in the test with E2 ($p < 0.001$, CI [0.52, 1.00]). Of those

who trained with E2 last, all ten subjects gave object B in both tests, which was significantly greater than chance ($p < 0.001$, CI [0.69, 1.00]). Furthermore, 79% of all subjects (15 of 19) exchanged the object type rewarded last at training first across all three tests. Again, results are consistent with the main analysis, in which apes preferentially exchange the object type that belonged to the experimenter they last trained with, regardless of test condition.

5.6.4 Discussion

The results show that the apes successfully remembered which object types were rewarded two and ten weeks previously, but that they failed to recall which type was rewarded by who. Additionally, they were unable to infer that object type C should be exchanged with E3. Although no evidence of binding was found, the apes did not perform randomly at test, as shown by a significantly worse performance with E3 as opposed to E1 and E2, and significantly more incorrect exchanges of A and B type objects than C type objects. These results suggest that subjects avoided the previously non-rewarded object (type C), and preferentially exchanged the rewarded types. Furthermore, they preferentially gave the object type that was rewarded with the experimenter with whom they trained with last. This effect was not explained by a greater number of training sessions with the last experimenter (i.e., more reinforcement), as shown by a lack of correlation between the number of training sessions with the last experimenter, and the number of exchanges required at test with the same experimenter (e.g., a greater number of training sessions with E1 did not correlate with fewer errors in the test with E1). Thus, these findings suggest that the apes did not simply forget what they had previously learnt, but rather, they successfully

recalled which object was rewarded last, and which object was never rewarded at all. This effect cannot be explained by familiarity (i.e., selecting an object based on memory strength), as all three object types were presented the same number of times, and were thus equally familiar to the apes. These findings are consistent with the previous experiment, and with other studies that show apes can learn and remember abstract relations between objects and rewards (Osvath & Persson, 2013; Vlamings et al., 2006). In the present study, this effect was independent of having a two-versus ten-week delay.

A potential reason why the apes failed to bind the object types to the experimenters is that the apes failed to interpret the training in the way that was intended. During training, the apes were trained with each experimenter in blocks; that is, they passed training with one experimenter before moving on to the next. As such, to pass training the apes may simply have learnt that one object type was rewarded, and that the rewarded object type arbitrarily changed once during training, without interpreting the identity of experimenter as the signal of the change in rewarded object type. This rule learning is much simpler than a conditional discriminative task, as it simply requires that the apes learn that the rewarded object type changes (similar to a reverse discrimination task), rather than that the rewarded object type is dependent upon the experimenter identity (a conditional discrimination task). Such an interpretation is supported by the finding that the last rewarded object type was the preferred object type; if the apes believe that the rewarded object type changed (as opposed to being dependent upon the present experimenter), they should preferentially give the last rewarded object type. To fully ensure that the apes had understood the nature of the task, the experimenters needed to be randomized between sessions,

meaning that the correct object type would have changed between sessions. This was rectified in Experiment 3 (see below).

The poor performance with E3 is likely due to the failure to infer by exclusion that object C should be given to E3. If the apes failed to learn the relationship between object type A and E1, and object type B and E2, it is not possible to infer by exclusion that the remaining object must go with E3. However, it's possible that the apes may have failed to make this inference even if binding was successful, and instead may have chosen to avoid object C due to it never being reinforced.

With regards to the other findings, a trend was found in which bonobos took longer to complete training than the chimpanzees and orangutans. This was mainly driven by the high average number of sessions needed to complete training with E2 (see Table 5.4). Such performance may reflect increased difficulty for bonobos with inhibiting a previously successful action. These findings can be seen as consistent with Wobber et al. (2010), who found that bonobos were just as quick as chimpanzees to learn a discrimination rule, but were slower to learn the reversal rule, in which the incorrect and correct response swapped. This was particularly true for younger bonobos. However, the findings of this current experiment should be taken with caution, due to the non-significant trend and the relatively small sample size of bonobos ($N=7$). Additionally, although chimpanzees were significantly quicker at completing training with the second experimenter compared to the other species, these results are unlikely to reflect any true species differences due to three chimpanzees who failed training with the second experimenter and were removed from the analysis.

Regarding delay, no difference was found between the two and ten week conditions, thus all subjects showed long-term memory of reinforced objects for up to

ten weeks. This adds to the growing literature on long-term memory in primates, which has already shown primates ability to remember events and spatial locations (Kano & Hirata, 2015; MacDonald, 1994; Martin-Ordas et al., 2013; Mendes & Call, 2014; Menzel, 1999), to recognize people and places (Murai, Tanaka, Tomonaga, & Sakagami, 2011), and to retain knowledge over long periods of time (Beran, 2004; Beran & Heimbauer, 2015; Fagot & Cook, 2006; Laska, Alicke, & Hudson, 1996; Martin-Ordas et al., 2013; Vale et al., 2016).

5.7 Experiment 3 | Conditional discrimination

5.7.1 Aims

The purpose of this final Experiment was to resolve the recency issue that likely lead to successful performance during training in Experiment 2. In Experiment 2, the apes may have learnt a reversal discrimination, in which at first one object type was rewarded (e.g., A) and then a previously unrewarded object type was rewarded instead (e.g., B). At test, they then preferentially exchanged the last rewarded object type (a recency effect). As such, this experiment ensured successful performance could only be achieved by learning that the rewarded object is dependent upon the identity of the experimenter.

The design remained very similar to Experiment 2, except for three important changes. First, no object type C was used. The purpose of the C object in the previous Experiment was to see whether the apes would remember at test which object types were reinforced and which types were not, and to see if the apes could infer by exclusion. The data from both Experiment 1 and 2 showed that the apes remembered the rewarded object types, thus there was no need to establish this again, and as there was no evidence of binding in Experiment 2, the additional complex element of inference by exclusion was removed here. Second, training with E1 and E2 was randomized between sessions. This meant the apes could not initially learn that one object type was always rewarded, and that this then then switched once during training. Neither could they learn a new rule, such as the rewarded object type changed each session, as the randomisation of sessions meant that there was no pattern or order to the sessions. As such, in order to determine which object type was rewarded in a session, the apes needed to attend to the identity of the experimenter. Third, no test was

included. The test in the previous experiment enabled memory assessment after a long delay. Although the apes did not learn what was intended, they did remember the information after both two and ten weeks delay, thus it was not necessary to test for this again. In short, the sole aim Experiment 3 was to see whether the apes could learn which object should be exchanged with whom.

5.7.2 Methods

5.7.2.1 Subjects

Four chimpanzees (aged 16–43, $M=26.25$) and four orangutans (aged 8–29, $M=21$) took part. All but two of the chimpanzees had participated in Experiment 1 (see Table 5.1). All subjects were tested during September 2017.

5.7.2.2 Apparatus

Two different types of wooden objects were used: an orange rectangle and a yellow cube (the same dimensions as Experiment 2; see Figure 5.7). There were four objects of each type, resulting in a total of eight objects. The rest of the apparatus is described in the general procedure, and remained the same as Experiment 2.

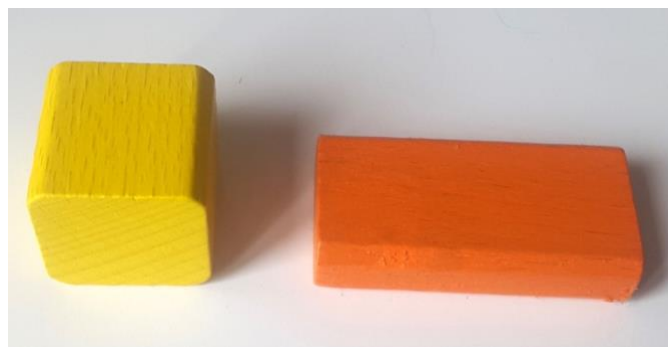


Figure 5.7 The two object types.

5.7.2.3 Design

The design remained the same as Experiment 2, except for the following important changes: there were only two types of objects (4 x A and 4 x B), training with E1 and E2 was randomized between sessions (with the stipulation that neither experimenter conducted more than two consecutive sessions), and there was no test (for reasoning behind the changes, see above). All subjects received the same order of sessions, except for cases in which a subject did not want to participate/could not participate on a given day. In these cases, sessions were rearranged for another day (this occurred four times with Suaq, twice with Dokana and once with Pini and Padana). All subjects began their first session with E2. Additionally, E1 remained as the same Experimenter from Experiment 1, however E2 changed. This was due to the former E2 from Experiment 1 being unable to participate. The E2 in this current experiment had conducted one other test with the apes previously. Although this meant that E1 was more familiar to the apes than E2, and had participated in a previous exchange task (Experiment 1), the results suggest that performance as a group did not differ between E1 and E2 (see results).

The criteria to pass a session remained the same as Experiment 2; however, the number of sessions the subjects completed changed slightly. All subjects received a minimum of eleven sessions with each experimenter. Once eleven sessions had been completed, subjects that had passed at least one of the eleven sessions with each experimenter received additional sessions to enable them to have the opportunity to pass training (the minimum number of sessions was set to eleven, because by session eleven with E1 and E2 in Experiment 2, all subjects participating in this current experiment had passed at least two sessions ($M=5.67$, $SD=1.16$), and on average had

completed training within ten sessions (range 8-14; $M=9.67$, $SD=1.78$), with the exception of Zira and Hope who did not take part in Experiment 2. The number of additional sessions was dependent upon performance; for every additional session a subject passed with E1 and E2, they received another session each with E1 and E2 until six sessions were passed with each experimenter. If they failed one of the additional sessions with either experimenter, training ended and it was counted as failed (e.g., if they passed session 12 with E1 but failed with E2, training was failed). If subjects passed training with one experimenter before the other, training still continued with both experimenters until the subject either passed with both experimenters or failed training.

As with Experiment 2, once six sessions had been passed it was checked whether the correct object type was exchanged the majority of the time in the first four exchanges of the four passed opaque sessions. As there were only two object types, the correct object needed to be exchanged on average at least three of four times in the first four exchanges (75% of exchanges). If subjects were exchanging randomly, approximately two of four exchanges would be correct in the first trial of each session (50% of exchanges). Subjects that did not exchange the correct object at least 75% of the time received additional training sessions until they reached 75% correct exchanges in the last four opaque sessions.

Failure to pass training would indicate difficulty with binding 'who' to 'what', whereas passing training would suggest the apes are able to successfully do this when there is no other information to guide successful performance (such as a reversal rule in Experiment 2).

5.7.2.4 Procedure

The procedure remained the same as Experiment 2, except only eight objects were present (4xA and 4xB), and there were no test sessions.

5.7.2.5 Data analysis

The dependent variable was fail or pass (i.e., subjects either passed training or did not). The number of subjects that failed and passed was compared to chance using a two-tailed exact binomial test. As there were only two possible outcomes (fail or pass), chance was set to 0.5. Additionally, performance was assessed for improvement over time by comparing whether the average number of correct exchanges in the first four exchanges of the four trials of a session (max. number of correct exchanges = 16) was greater in the last five sessions, compared to the first five sessions. For each subject, a single score was calculated, based on the average of the combined scores of the first five sessions with E1 and E2 (first 5 score), and an average of the combined scores of the last five sessions with E1 and E2 (last 5 score). The first 5 and last 5 scores were then compared using a paired t-test. As two of the apes (Zira and Hope) had not participated in Experiment 1, this analysis was also repeated with these subjects removed, as prior experience on a similar task may lead to quicker improvement over time.

To assess whether the apes' performance differed between E1 and E2 (as a result of previous experience with E1), we compared the average number of correct exchanges in the first four exchanges of the four trials of a session (max. number of correct exchanges = 16) between E1 (E1 score) and E2 (E2 score). A single score for each subject was calculated as the average score across all completed sessions (e.g., if

the subject completed 12 sessions with E1, the average score across those 12 sessions was the E1 score). We then compared the E1 scores and E2 score using a paired t-test. Zira and Hope were not included in this analysis, as they did not have any prior experience with E1 in Experiment 1.

5.7.3 Results

None of the eight subjects successfully passed training, binomial tests revealed this performance was significantly worse than chance ($p=0.008$). However, three of the apes successfully passed at least one session with both E1 and E2, but then subsequently failed to pass session 12 with both experimenters (see Figure 7, b,e-f). Performance between the first 5 sessions ($M=9.16$, $SD=1.95$) and last 5 sessions ($M=9.93$, $SD=1.35$) did not differ, $t(7)=1.20$, $p=0.27$, $d=0.45$. This result was replicated when Zira and Hope were removed from the analysis, $t(5)=0.98$, $p=0.37$, $d=0.45$, suggesting that prior experience did not aid with learning. Performance between E1 ($M=10.06$, $SD=2.01$) and E2 ($M=9.57$, $SD=1.49$) did not differ, $t(5)=.64$, $p=0.55$, $d=0.27$, suggesting that previous experience with E1 did not influence performance.

On an individual level, the performance of the apes was quite varied. Three of the apes (Pini, Hope and Dokana) exchanged the objects randomly with both E1 and E2, performing roughly at chance levels and showing little improvement over time. As such, they failed to pass a single session with either experimenter (Figure 7; d, g-h). Zira showed a similar pattern, until the last three sessions when her performance improved with E1 but deteriorated with E2 (Figure 7; c), suggesting she preferentially learned to give object type A to both experimenters. Alex's performance with E2 seemed to improve over time, but at the detriment to performance with E1. However, in

the last two sessions his performance with E1 improved whilst his performance with E2 remained good, suggesting he may have begun to understand the conditional discrimination rule. As a result, he was given an additional session each with E1 and E2 (despite not passing a session with E1) to see whether his performance would continue to improve; however, he failed this session with E2 (Figure 7;a). Frederike and Padana passed multiple sessions with both E1 and E2, but failed to reach the criteria of six passed sessions with each experimenter, and failed to pass session 12 with E2 and E1 respectively, suggesting they had not learnt the conditional discrimination rule (Figure 7; b,e). Suaq successfully passed six sessions each with E1 and E2; however, he did not exchange the correct object type above 75% in the first four exchanges of his last four opaque sessions with either experimenter. He instead reached only 68.75% correct, before subsequently failing to pass session 12 with E2, suggesting he too had not learnt the conditional discrimination rule (Figure 7; f).

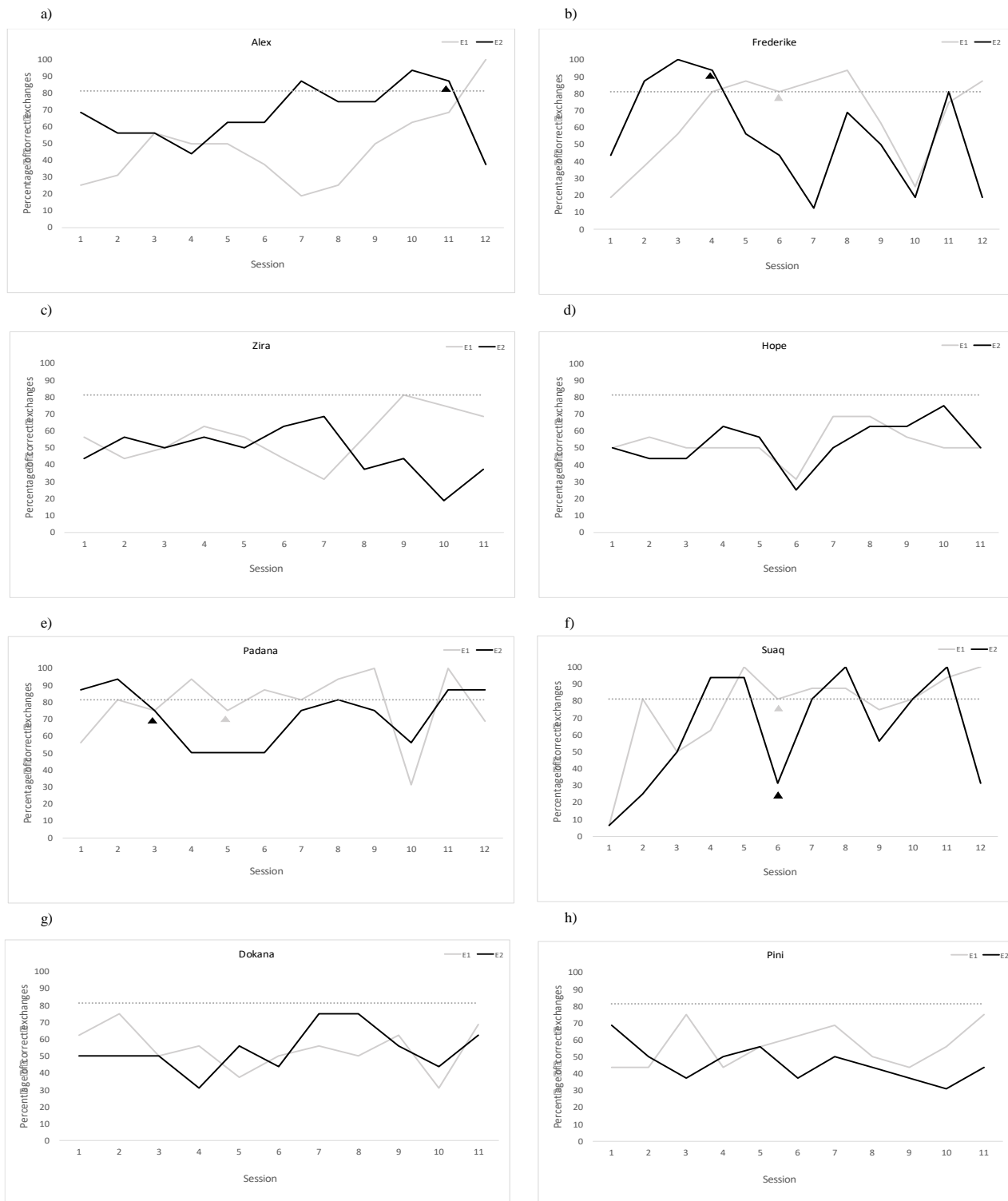


Figure 5.8. Percentage of correct exchanges with E1 and E2 by session, for each subject. Only the first four exchanges of each trial in a session were counted (16 exchanges per session).

Dotted line shows pass criterion (13/16 correct exchanges; 81.25% correct).

▲ Opaque panel used from this session onwards with E1

▲ Opaque panel used from this session onwards with E2

5.7.4 Discussion

The results show that all of the apes failed to pass training, meaning that they did not learn to exchange one object type with one experimenter, and the other object type with the other experimenter. Furthermore, their performance did not improve over time, as shown by no difference in the number of correct exchanges between the first and last five sessions. These results suggest that given more sessions, the apes would still have failed to learn that the correct object type was dependent upon the experimenter present.

Although all the apes failed training, some of the individuals did surprisingly well, despite not seemingly learning the conditional rule. This was likely due to some apes developing various strategies, as opposed to exchanging the objects randomly. For instance, Frederike and Alex seemed to develop a preferred object type; Frederike preferred the B type object in the first few sessions, successfully passing sessions two through four with E2, but then switched her preference to the A type object in sessions five through eight (see Figure 5.8; b). Likewise, Alex developed a preference for the B type object from session six; however, this preference was lost from session nine, as his performance with E1 gradually improved (see Figure 5.8;a). These performances likely reflect confusion by the apes as to which object was correct, but interestingly, they show that the apes did not resort to exchanging randomly, rather they chose one object type and persisted with it for a few sessions, and then switched and tried the other object type. Similarly, although Zira originally exchanged the objects randomly, in session nine she began to preferentially exchange the A object type and successfully passed a session with E1. The following sessions with E2 were her worst, whilst

performance with E1 remained good, suggesting she developed a preference for exchanging the A type object (see Figure 5.8; c).

The two most successful apes, Suaq and Padana, seemed to use a different strategy. These subjects were able to learn within a session which object type was rewarded. That is, in the first trial they would often exchange both object types randomly, then in the next three trials they would change their response to reflect the object that was currently being rewarded. This strategy approximates a win-stay, lose-shift strategy, which has been evidenced in rats and monkeys (Rayburn-Reeves, James, & Beran, 2017; Rayburn-Reeves, Stagner, Kirk, & Zentall, 2013). By using this strategy, they were able to pass many sessions, but performed poorly in the first few exchanges, in which they learnt which object type was correct (see Table 5.6). This was also reflected by Suaq passing seven sessions with E1, and six with E2, but only reaching an average of 68.75% correct exchanges in his first four exchanges of his last four passed sessions.

Despite failing to pass training, this performance shows an impressive ability to quickly update a response to reflect current reward contingencies. This is consistent with the finding that monkeys, with practice, improve on a reversal task using short inter-trial intervals, but not long intervals. Improvement in only the short delays suggested that the monkeys used working memory to determine which stimulus had been most recently rewarded, and updated their response accordingly (Hassett & Hampton, 2017). Thus, it's likely Suaq and Padana's successful performance was a result of using working memory to remember which object was rewarded in a given trial.

Table 5.6 Number of correct exchanges in the first four exchanges of each trial, for each passed session. Numbers in red indicate chance (or below) performance.

	Session	Experimenter	<i>Trial 1</i>	<i>Trial 2</i>	<i>Trial 3</i>	<i>Trial 4</i>
<i>Suaq</i>	2	E1	2	3	4	4
	5	E1	4	4	4	4
	6	E1	2	4	3	4
	8	E1	3	4	4	3
	10	E1	1	4	4	4
	11	E1	3	4	4	4
	12	E1	4	4	4	4
	4	E2	3	4	4	4
	5	E2	4	4	4	3
	7	E2	2	4	4	4
	8	E2	4	4	4	4
	10	E2	1	4	4	4
	11	E2	4	4	4	4
<i>Padana</i>	2	E1	1	4	4	4
	4	E1	3	4	4	4
	6	E1	3	3	4	4
	7	E1	2	4	3	4
	8	E1	4	4	3	4
	9	E1	4	4	4	4
	11	E1	4	4	4	4
	1	E2	3	3	4	4
	2	E2	3	4	4	4
	8	E2	2	4	3	4
	11	E2	2	4	4	4
	12	E2	2	4	4	4

5.8 General discussion

The purpose of the three Experiments was to investigate whether apes can bind and recall social information. Using an object exchange paradigm, apes were taught to exchange a particular object type with a specific person. After a delay of two (Experiment 1 and 2) or ten weeks (Experiment 2), the apes' memory of which object type belonged to which person was assessed. Additionally, their ability to use inference by exclusion was tested by introducing a third person at test (Experiment 2), with whom they should give object type C, the type that did not belong to either of the other two experimenters.

The results from the three experiments combined show that the apes failed to bind and recall which object type was rewarded with which experimenter. In Experiments 1 and 2, the apes clearly remembered which objects were rewarded, and could remember this information after long periods of time. However, they did not alter their response depending on which experimenter was present at test. The reason why the apes failed in Experiment 1, may be due to the objects never being presented together during training. In Experiment 2, this problem was resolved, yet the apes still failed, likely due to learning a reversal discrimination rule during training. Crucially, the results from Experiment 3 suggest that the apes still failed to learn to exchange a particular object with a particular experimenter, even when there was no other obvious pattern or rule to guide their response during training.

Consequently, it seems that the apes simply did not readily encode, or attend to, which experimenter was present, even in the absence of other more salient information. This failure to use social information may be specific to social information in the form of human experimenters (as evidenced by the repeated negative findings found

throughout this thesis), and is likely due to the lack of saliency of such information (as a result of repeated occurrences in other tasks, and the experimenter not often being integral to the task; see discussion in Chapters 3 and 4). Indeed, Martinez and Matsuzawa (2009) found that chimpanzees were able to perform above chance in a conditional discrimination task when the social stimuli were a male human and a female chimpanzee. Contrasting a human experimenter with a conspecific in this way, likely made the experimenter a more salient stimulus. Likewise, there are cases in which chimpanzees and bonobos have learnt to successfully distinguish between the actions of different experimenters. For instance, Subiaul, Vonk, Okamoto-Barth, and Barth (2008)²⁵ found that five of seven chimpanzees were able to learn that one individual would act selfishly (by turning away from the ape and keeping food for themselves), and that another would act generously (by giving the food to the ape). Four of these chimpanzees were then able to successfully select a novel ‘generous’ experimenter after observing them acting generously (see also Russell, Call, & Dunbar, 2008). Similarly, Wobber et al. (2010, Experiment 3) found that chimpanzees and bonobos could successfully learn that one experimenter always held concealed food, and another did not. However, the success of the apes in these experiments may be a result of learning which actions/behaviours to respond to (e.g., learning to avoid any experimenter that turned away), rather than which specific person did what. As such, the present finding that apes seem unable to readily encode the identity of humans, at least when the information is not salient, warrants further research using other task designs and ape populations to clarify the robustness of this finding. For example, it is

²⁵ I thank an anonymous reviewer for drawing my attention to these papers.

possible that with more or different training, the apes may have learned that the experimenter was crucial to the task.

Although the apes failed to use the experimenter identity in this task, they did not resort to exchanging objects randomly. Instead, they performed in a consistent manner, choosing to exchange an object type that was rewarded most recently (Experiment 2), or by developing individual strategies that varied in success (Experiment 3; see previous discussion). Such performance was unexpected, but was logical and sensible if the identity of the experimenter was not encoded or attended to. These findings can be said to be “meaningful failures”, a term coined by Breland and Breland (1961), in which non-human animals respond in unexpected but meaningful ways.

A potential future avenue would be to conduct a similar test with conspecifics, due to previous research suggesting that conspecifics may be more salient as cues (Martinez & Matsuzawa, 2009). Indeed, early research concerning theory of mind suggested that apes were unable to adjust their behavior based on what a human experimenter could, or could not, see (Povinelli & Eddy, 1996), but were successful with conspecifics (Hare, Call, Agnetta, & Tomasello, 2000). Likewise, it may be worthwhile to compare children’s performance on a similar task, as there is evidence that humans may rely more on social information than apes (van Leeuwen, Call, & Haun, 2014). Alternatively, the apes may learn to attend to the identity of the experimenter if provided with more support. As the apes’ previous testing experiences have likely predisposed them to ignore who it is that is testing them, and to fail to consider the experimenter as a stimulus in a task, they may require additional support to

learn to encode this information. For instance, in this task, the experimenters could initially be made salient in some way (such as by wearing unusual clothing), so that the apes pay attention to who is exchanging objects with them. The saliency of the experimenters could then be reduced once the apes understand that the experimenter is an important element of the task. Furthermore, the apes' performance may be improved by training with additional experimenters and objects (i.e., more than two experimenters and two objects)²⁶. This would make learning a reversal rule or updating within a session more complex (as there would be multiple alternative choices), and as such, may prompt the apes to look for alternative information (such as the identity of the experimenter). Likewise, the apes may have benefited from training with both experimenters in the same session, that is, having E1 present in one area of the testing room, and E2 in another area (counterbalanced between sessions). This would require the apes to adapt their response within a session, as opposed to learning that one object type is consistently rewarded in a session, and again may result in the apes searching for additional information to determine which object is correct.

Performance could also be aided by incorporating differential outcomes (Goeters, Blakely, & Poling, 1992). The differential outcomes effect refers to the improved performance in discrimination tasks when different reinforcers are associated with the different stimulus types. For instance, Trapold (1970) found that rats that learnt to respond to a clicking noise by pressing the left bar, and to tone sounds by pressing the right bar, learnt quicker when the two responses were differentially

²⁶ I thank an anonymous reviewer for drawing my attention to this possibility.

rewarded (one with a pellet and the other with sucrose), than when they were both rewarded with the same food. The same principle applied to this paradigm (e.g., rewarding yellow cubes with apple, and orange rectangles with banana), may aid the apes in learning the discrimination rule.

In summary, the results of this chapter found that apes did not bind and recall which object type belonged to which experimenter, and consequently did not infer by exclusion that an untrained object type belonged to a new experimenter. This failure to bind and recall social information was not a result of forgetting, as the apes clearly showed a preference for the previously rewarded objects types over the non-rewarded object type. Also, this effect was shown after both two and ten weeks, showing that apes can successfully remember information over long time periods. The apes thus seemed to show a “meaningful failure”, whereby in the absence of any salient information, they based their responses on a reinforcement rule (Experiment 2), or used other strategies, such as updating within a trial (Experiment 3).

Chapter 6 | General discussion

Galaxies and stars are born and they die, living creatures are young before they grow old, causes always precede effects, there is no return to yesterday... The singular exception is provided by the human ability to remember past happenings.

(Tulving, 2002, p. 1)

This ‘human’ ability to remember past happenings has been the foundation for this thesis. The episodic memory debate (discussed in Chapter 1) has questioned whether this ability is uniquely human, or whether it may be shared among other animals. This final chapter provides a summary and discussion of my findings on great apes’ ability to remember past events. I begin with an overview of the three experimental chapters and their respective key findings, followed by limitations relating to the experimental designs and broader issues. I then discuss the implications of the findings, before suggesting potential future avenues of investigation.

6.1 Overview and key findings

The aim of this thesis was to further our understanding of the similarities and differences between the way humans and animals recall past events. Such research enables us to better understand which cognitive abilities are unique to humans, and which have a longer evolutionary history. Current comparative research suggests that various species are capable of recalling the content of past experiences, such as what happened, where and when, or in which context. The findings here suggest that the similarity between ape and human recall of past events goes beyond mere content.

Chapter 3 focused on the distinctiveness effect in relation to the recall of a past event, and thus assessed the retrieval of ‘what’ within a context. Apes were presented with a platform task, in which their goal was to remember under which opaque container food was hidden. Across three experiments, performance was consistently poor when no element of the hiding event was distinct, but was greater than chance when a distinctive element was included. Crucially, this effect was independent of reinforcement, indicating that reinforcement was not a predictor of performance. The findings suggest that distinctiveness affects memory in apes and humans similarly.

Chapter 4 continued with the theme of distinctiveness by assessing the involuntary recall of a distinctive past event. Using a paradigm that incorporated the characteristics of human involuntary retrieval, apes showed spontaneous recall of a hiding location after only a single exposure. Additionally, corroborating the results from Chapter 3, they continued to recall the hiding location in the absence of any reward (as shown by no difference in searching between retrieval 1 and retrieval 2), and searched in a similar situation when the initial reward was significantly reduced (Experiment 2), suggesting reinforcement was not the driver of performance.

The findings from Chapters 3 and 4 show that the apes are capable of remembering details from past experiences, provided that some element of the past experience is distinctive. Although such a finding is intuitive, and reflects human memory, it has not been explicitly addressed before. Moreover, the finding that the apes’ memory was not dependent upon reinforcement, as shown by successful recall when negatively punished (Chapter 3) and after multiple absences of reinforcement (Chapter 4), suggests that performance was not a result of associative memory; that is, the apes did not search as a result of stimulus-response learning. Although in Chapter 4,

it could be argued the apes continued to search in the absence of reinforcement because they expected to be reinforced again at some point (intermittent reinforcement), it is unlikely that an association between the location and presence of food was made after only one occurrence, when followed by a lengthy delay interval (minimum 2 weeks), and by multiple instances of no food in the location. There are cases in which associations can be formed in this way, however, these are often survival related, such as taste aversion (Garcia et al., 1955).

An unexpected finding from these two chapters was that providing the identity of an experimenter as a social cue did not aid memory performance. By overlapping the identity of the experimenter at encoding and retrieval, the experimenter should have acted as a cue at retrieval, leading to successful (or improved) memory performance compared to when the cue was absent. Although it's possible that the lack of effect of the social cue may have been because the apes only recalled the location of the food during retrieval (spatial memory), and not the event, the finding of a distinctiveness effect (Chapter 3), and the recall of the location when probed with a specific set-up (Chapter 4), suggests the spatial location was bound to the context (recall of where within a context). The lack of effect of the social cue, therefore, suggests that this cue was not bound to the memory trace, or if it was bound, was not effective at distinguishing one memory from another. In Chapter 4 this may have been because it was outshined or overshadowed by other cues, whereas in Chapter 3 it was likely not unique enough to successfully distinguish the specific event from other similar events, even in combination with other cues (i.e., the combination of cues was not unique to the specific event).

Consequently, Chapter 5 aimed to see whether the apes could use the social information to guide performance in the absence of more salient information. The apes were taught to exchange a particular object type (what) with a specific person (who), and later retrieve this bound information. Although the apes showed retention of which objects were previously rewarded (what), they failed to bind the object types to the respective experimenters (what with who). In a later experiment, this failure was still evident even when there was no other rule or pattern to guide successful performance across sessions. Although, the apes did attempt to employ various strategies, such as updating within a session, none of them used the identity of the experimenter as an indicator for which object to exchange, nor appeared to grasp this concept over time (as evidenced by no improvement in performance). This consistent finding throughout the three chapters suggests that social information in the form of a human identity is not readily encoded or attended to, and thus not an effective cue. However, this finding is likely specific to the apes tested in this thesis (see limitations below).

Another consistent and prominent finding across the three experimental chapters was the apes' remarkable retention of information over long periods of time. This was the case even when exposed to information only once (Chapter 4), and after minimal (or no) reinforcement (Chapter 3). Moreover, when performance was assessed over time, no substantial decrease in retention was found, and a striking resemblance to the forgetting curve in humans was observed.

6.2 Limitations

6.2.1 Criteria

The traditional method used to investigate episodic memory in animals has been to apply a set of criteria based on Tulving (1972)'s content definition; that is, the integrated recall of what, where and when information from a single episode. As a result of critique and scepticism regarding whether this criteria is sufficient to show episodic memory, various other criteria and demands have been added, such as flexibility (Clayton, Yu, et al., 2003) and the unexpected question (Zentall et al., 2001). Fulfilling the many criteria in one paradigm is a tall order, and has hindered the scope of animal episodic memory research. Moreover, the numerous and restrictive criteria used in animal research is not generally applied to episodic memory paradigms in humans (Dere et al., 2006), resulting in imbalanced expectations across taxa. As such, the paradigms presented in this thesis have not adhered to the extensive and restrictive criteria, but have focused on one or two elements of episodic memory. Crucially, these elements have been assessed within areas that have received little attention. As a consequence, the paradigms presented in this thesis are open to many of the criticisms discussed earlier in Chapter 1; below I present some of these limitations.

Chapter 3 incorporated multiple exposures. This may have led the apes to expect a test, and subsequently they may have strategically and semantically encoded the location of the baited container. The location may then have been retrieved in the absence of any contextual details. However, the fact that the apes' performance did not improve from Experiment 1 to Experiment 3 suggests they were not learning to semantically encode where the location of the baited container was in anticipation of a test. Moreover, they only recalled the location above chance when elements of the

event were distinctive. Distinctive processing involves the encoding of an item within its context, as a result of both item-specific processing and relational processing. Item specific processing is the encoding of features unique to an event, in this case, the presence of a mask, or the throwing away of food upon a correct choice. Relational processing is the processing of the commonalities between the event and other events, for instance, the same type of containers and the same sliding table. When both processing occurs (distinctive processing), a particular event will stand out if there are unique features that are not common to other events - the processing of common features between events provides a context in which the unique features of an event stands out. Thus, a distinctiveness effect requires the processing of items within context.

In Chapter 4, the apes only received one exposure in which all food was recovered, thus it's unlikely they anticipated a test. However, they were only required to recall where something had been hidden, and showed no evidence of recalling other elements of the event, such as the experimenter. Thus, they only showed direct evidence of the recall of 'where', akin to spatial memory. Despite this, the spontaneous manner in which they recalled the location upon presentation of diagnostic cues is indicative of involuntary episodic recall (Berntsen, 1996). Furthermore, in the second experiment of Chapter 4, the apes searched even when no food was present near the hiding location (only the context and experimenter were provided as cues), suggesting that the set-up of the enclosure and surroundings prompted them to search. As such, the context must have been encoded with the location, indicating the apes remembered more than simply 'location x contained food'.

As such, although the experimental designs of these chapters leave open alternative interpretations, the findings are largely consistent with the recall of a past event; apes show enhanced performance when distinctive elements are present as opposed to when they are not (evidence of binding), they can retrieve information about the location of food instantaneously, in the absence of task demands, when cued by diagnostic features (consistent with involuntary episodic retrieval), and do so independent of reinforcement, and without the expectation of recalling the information at a later date.

Chapter 5 differed from the previous chapters by using a paradigm that incorporated extensive training. Consequently, it's likely the apes learnt a rule and recalled this rule, as opposed to recalling a specific past episode. However, the aim of this chapter was not to assess whether the apes could recall information from a specific past event, but rather to assess whether the apes could bind and recall social information. In the previous chapters, the apes did not incorporate the social information when presented with it just once, thus this paradigm provided them with a better opportunity to use the information, by presenting the information numerous times and in the absence of other salient and useful information. Despite this, the apes failed to use the social information, suggesting that this information may be equally unlikely to be encoded, or equally ineffective as a cue, in both episodic and semantic tasks. However, as previously suggested (and discussed below), this may be because of the nature of the social information incorporated here. Regardless of the reason why the apes failed to use the social information, this task suggests that the failure to use it is not specific to episodic remembering, and thus tells us indirectly about ape's recall of social information from past events.

6.2.2 Direct human comparison

The experiments in this thesis aimed to investigate if certain phenomena that have been observed in the human recall of past events also occur in apes, namely the distinctiveness effect and involuntary retrieval. With this in mind, the paradigms were designed to replicate the characteristics observed in these phenomena, such as spontaneous non-goal directed recall on presentation of diagnostic cues, and enhanced memory performance for distinctive, in comparison to non-distinct, events. This method resulted in an indirect comparison of human and ape memory, comparing the findings to what has already been observed in the human and animal literature. A more direct way of comparing human and ape memory would have been to test both groups using the same paradigm (i.e., to test humans and apes in the same, modified experiments). As well as providing a more direct comparison, testing humans on non-verbal tasks that are designed to test for episodic memory in animals may tell us whether such tasks recruit episodic recall, or whether they recruit strategic processing or other non-recollective processes. Indeed, recent research has tested this theory, with mixed evidence regarding the extent to which the different episodic paradigms reported in Chapter 1 result in episodic recollection (Cheke & Clayton, 2013; Holland & Smulders, 2011). For instance, only 30% of subjects that were tested using a what-where-when paradigm reported re-experiencing the episode during retrieval, whereas 87% reported using episodic memory in the unexpected question paradigm (Cheke & Clayton, 2013). The inclusion of human subjects in this thesis would thus have provided a more direct comparison between apes and human memory of past events, and helped clarify if the paradigms used here resulted in recollection, or whether they lead to strategic processing and semantic memory.

6.2.3 Stimuli used as social information

As mentioned previously, the identity of the experimenter as a social cue may have been ineffective because the stimulus was overloaded and not salient to the apes, and as a result was overshadowed, outshined, or simply not considered as integral to the task (see discussions of Chapters 3-5). As such, the implication that this social information is not readily encoded or effective as a cue may be limited to the ape population in this thesis. Furthermore, additional clarification could be achieved regarding whether the apes here specifically struggled with this social information. Although the findings from Chapters 3 and 4 suggest that the social information had no enhancement on performance, the results from Chapter 3 also suggested that other features were ineffective if nothing was distinctive about the event (Experiment 2). Moreover, no direct comparison was made between the presence or absence of social stimuli in Chapter 5; although there is evidence primates can succeed in discrimination tasks using non-social stimuli (Burdyn & Thomas, 1984; Warren, 1964), testing the two types within the same paradigm would have provided more direct comparisons. For instance, a non-social condition could have taught the apes to associate the rewarded object type with a particular context (e.g., the orange rectangle is only rewarded if the exchanges take place in the sleeping room, and the yellow cube is only rewarded if they take place in the observation room). If the apes are also poor at learning to associate non-social stimuli with object types, it's likely that the task itself was difficult, regardless of the type of information involved.

Additionally, the social cue in this thesis was a *human*. As previously mentioned, it's possible that the apes may have paid more attention if the cue was a conspecific (see General discussion, Chapter 5). For instance, an ape is more likely to

attend to which ape is present at the time of a hiding event, as the act of retrieving the hidden food may depend on the relationship the ape has with the present ape (i.e., the ape may not retrieve the food if the present ape is of a higher rank). Thus, the finding that apes did not readily attend to or encode social information should be taken with caution, and needs further clarification.

6.2.4 Sampling

A common problem when it comes to testing non-human populations is the limited and select number of individuals available to test. The apes in this thesis were from the Leipzig zoo, and although the population is relatively large in terms of standard ape house populations, each study was limited to around thirty subjects. When taking into account drop-outs and other testing restrictions, the population for a given experiment was very restricted, and thus sometimes resulted in underpowered analyses. This may have led to instances in which potential differences were not detected, particularly in the case of species differences. For instance, in Experiment 1 of Chapter 4, bonobos searched less than orangutans and chimpanzees, but this difference was not statistically significant. Likewise, bonobos took longer to train in Experiment 2 of Chapter 5, with this difference almost reaching significance. These species differences may reflect differences in the cognitive abilities of bonobos in comparison to chimpanzees and orangutans, consistent with other research (Herrmann et al., 2010; Rosati & Hare, 2012; Suda & Call, 2005; Wobber, Herrmann, Hare, Wrangham, & Tomasello, 2014; Wobber et al., 2010). However, the small number of subjects limits any interpretation of potential species differences.

Additionally, testing subjects from a single population meant that they were subject to the same living conditions, stimulation, environment etc. As such, they may have behaved and responded differently in comparison to apes housed in other zoos or sanctuaries. Moreover, captive apes are familiar with cognitive testing, and live their lives in relative ease compared to wild apes (e.g., they do not need to forage for food or fight for territory, and are kept in good health through regular monitoring). These substantial differences between wild and captive apes may result in cognitive differences, limiting the generalisability of the findings from these apes to apes as a whole (see Boesch, 2007). This issue is far from unique to studying apes, but is a concern among human psychological research, with the predominant testing of western, educated, industrialized, rich, and democratic populations, despite variation between cognition and behaviour across populations (Henrich, Heine, & Norenzayan, 2010). Testing for episodic memory in the wild is a difficult task, not least due to a lack of control over many variables, yet there are instances in which wild primates show instances consistent with episodic remembering and future planning (Janmaat, Polansky, Ban, & Boesch, 2014; Noser & Byrne, 2015). Despite potential differences between populations, there is still value in assessing what captive chimps from specific populations can and cannot do; it at least tells us that apes have the capacity for a certain behaviour in a particular context.

6.3 Implications

The finding that apes are able to remember distinctive events for long periods of time is a novel finding in itself, however, it is not particularly surprising. If memory has evolved as an adaptive function, helping us to survive and reproduce, then remembering particular episodes that are different in relation to what we commonly experience seems beneficial. For instance, remembering the details of a foraging experience that led to a substantial bounty of food is more beneficial than remembering multiple foraging experiences that resulted in the same, regular outcome. Likewise, remembering an occasion in which unripe food was consumed is more useful than remembering the many times ripe food was consumed. Such information can aid us in future scenarios, such as returning to the bountiful location, or recalling how the fruit looked when it was not ripe so to not repeat the same bad experience.

Closely related to the distinctiveness effect is emotion. The two often come hand in hand (see Schmidt, 2007; Talmi, Luk, McGarry, & Moscovitch, 2007), and it is likely that emotion may also have been entangled with distinctiveness in this thesis. For instance, in Chapter 4, the mask may have elicited surprise, and the throwing away of food a negative emotion, such as frustration. Likewise, in Chapter 4, the large amount of food may have led to a positive emotion, along with the element of surprise when a well-known food had an unexpected flavour. As such, it may be that the apes remembered these events well because of the added element of emotion. In humans, emotion generally leads to memory enhancement (Mather & Nesmith, 2008; Talarico, Berntsen, & Rubin, 2009), although this effect may be for focal details (Kensinger, 2009). Research with chimpanzees has found that emotion enhances recognition memory (Kano, Tanaka, & Tomonaga, 2008), and also attracts attention (Allritz, Call,

& Borkenau, 2015; Kano & Tomonaga, 2010). As with distinctiveness, emotion is likely to have a benefit to survival and reproductive success, for example, fear in response to survival threatening situations, and the signalling of the receptiveness of a female to mate (Kano et al., 2008). Being able to remember experiences that elicit emotion may therefore be an evolutionary adaptive function, and would be an interesting area within animal episodic memory to research.

The findings from Chapter 4 suggest that apes can use the involuntary retrieval mode to recall past events. This is consistent with the proposal that animals may have the involuntary form of episodic memory (see introduction of Chapter 4). Regarding the episodic memory debate, such a finding may pave the way for an alternative conception; voluntary episodic memory is unique to humans, but the involuntary form is shared among other species. As previously discussed, involuntary retrieval is less cognitively demanding, and likely an evolutionary earlier process than voluntary retrieval (Rasmussen & Berntsen, 2009). Given the many adaptive benefits of episodic memory (see pages 28-29), it seems logical that other animals would also have this cognitive capacity (at least to some extent) and perhaps the retrieval mechanisms used to recall an episode may be one way in which human and animal episodic memory differ. Indeed, as many animal episodic memory paradigms have incorporated cued recall (i.e., they use external cues to prompt memory recall), the retrieval of the episodes may have been involuntary, as opposed to voluntary. For instance, in Clayton and Dickinson (1998)'s what-where-when paradigm, the birds are presented with a unique sand box at retrieval. This sand box is highly diagnostic of a specific caching event, as it's not associated with any other memory. Thus, the unique overlap of this cue at encoding and retrieval may have led to spontaneous, rather than voluntary,

retrieval. However, as discussed previously, although some characteristics are consistent with involuntary retrieval, others are not (such as goal-directed tasks; see Chapter 4). Thus, the crux of the problem is once again the inability to know for certain how an animal remembered, whether it be involuntary or involuntary, episodic or semantic.

Interestingly, findings suggest that young children are able to spontaneously recall a past event when presented with distinct overlapping cues (Krojgaard, Kingo, Dahl, & Berntsen, 2014; Sonne, Kingo, Berntsen, & Krojgaard, 2017), whereas they have difficulty intentionally retrieving a past event (Simcock & Hayne, 2002). Furthermore, recent findings have shown that both 35month and 46month children can spontaneously retrieve a memory of a past event, with no difference in performance as a function of age. In contrast, older children outperform younger children when strategic retrieval is used (Krojgaard, Kingo, Jensen, & Berntsen, 2017). This perhaps reflects developmental differences between involuntary and voluntary memories, with the former occurring before the later. This earlier development of involuntary retrieval is consistent with the potential proposal that the involuntary form exists in animals but that the voluntary does not. Further investigation of involuntary retrieval in other species would shed further light on the potential evolutionary difference between voluntary and involuntary retrieval. Although it can never be certain as to the retrieval mode a non-verbal species may use, by employing simple paradigms that focus on diagnostic overlapping external cues, in non-goal direct tasks, we can attempt to induce involuntary retrieval.

The consistent finding that the identity of the experimenter was not an effective social cue warrants further investigation. As previously mentioned, this result may be

specific to the apes tested in this thesis; they are tested by many experimenters on many tasks, in which the experimenter is not integral to the task. As such, it's not particularly surprising that the apes did not attend to the identity of the experimenter, and although there are similar findings with other ape populations (e.g., Beran, personal communication, see page 166), these are also captive apes that are frequently tested, and thus may be subject to the same biases. However, if the finding does extrapolate to other apes it could be a reflection of the types of information that apes do, or in this case, do not, prioritize. For instance, apes may be attuned to attending to aspects of their environment that are relevant to survival, such as the location of food, water, and shelter, as opposed to which individual was present in a certain situation. This is similar to the survival processing theory advocated by Nairne (2010), which suggests that the retention of information is enhanced if processed in terms of survival relevance. Consequently, it could be that the apes may have encoded and recalled the social information in this thesis if it was processed in terms of survival fitness. Social information in the wild may be processed in this way, as knowing which individuals have access to, or know where food is located, is beneficial to fitness.

6.4 Future directions

By investigating elements of episodic memory that go beyond the content criteria (i.e., an integrated recall of what, where and when/which), we can learn much more about the similarities and differences between humans and animals recall of past events.

Consequently, future research that investigates under explored elements would be fruitful. Below I present some insightful studies that have done just this, and potential future areas to explore.

6.4.1 Source memory

All episodic memories have some aspect of a source, such as the context in which an event took place. Moreover, it has been suggested that source memory and episodic memory should be considered as the same construct (Siedlecki, Salthouse, & Berish, 2005). Source memory refers to the origin (or source) of a memory, and provides us with information such as how and when a memory was acquired. For instance, rats can determine whether chocolate will replenish in a maze, by remembering whether they were placed in the arm containing chocolate, or whether they entered the arm freely (Crystal, 2015; Crystal, Alford, et al., 2013), and rhesus monkeys can correctly recall whether an image was previously touched or classified, but make source memory errors when the two sources are presented in close temporal proximity (Basile & Hampton, 2017). Similar errors have also been reported by Adachi and Hampton (2011), in which the source of a previously heard monkey was confused with a previously seen monkey.

Source memory errors are common in humans, especially children (Lindsay, Johnson, & Kwon, 1991; Roberts & Blades, 1999), but can be improved if the source and content is explicitly pointed out (Roberts, Evans, & Duncanson, 2016). Such a

finding may have relevance to the apes' performance in Chapter 5 of this thesis, in which performance may reflect the apes' difficulty distinguishing the experimenter as the source of the rewarded item, as opposed to difficulties with social information per se. Future source memory research in animals could investigate ways in which source memory could be improved, such as making the source of the information explicit or salient.

6.4.2 Multiple events

Another area that has received some investigation is the recall of multiple events. For instance, rats and apes can distinguish between multiple events through binding (Crystal & Smith, 2014; Martin-Ordas et al., 2013), and can recall items from multiple contexts (Panoz-Brown et al., 2016). An interesting extension of this work would be to investigate if multiple events can be recalled sequentially (i.e., the chaining of events). Involuntary retrieval can result in the recall of multiple events in sequence, termed as involuntary memory chaining (Mace, 2005). That is, the spontaneous retrieval of one memory triggers the retrieval of another, which in turn may trigger another in a chain like effect. This chaining can also occur during voluntary retrieval, with the voluntary recall of one memory leading to spontaneous recall of other memories (Mace, 2009). Investigating if sequential chaining occurs in animals may thus be another way to investigate the presence of involuntary retrieval in animals.

6.4.3 False memories

Memory is a reconstructive process, open to distortion and error (Schacter, 2001). We often recall memories in ways that are consistent with our ideals and beliefs (Bartlett,

1932), and fill in gaps using scripts that represent what typically occurs in a situation (García-Bajos & Migueles, 2003; Holst & Pezdek, 1992). Furthermore, misleading information can influence our memories, resulting in the implantation of false information, known as the misinformation effect (Loftus, 2005). For instance, the infamous study by Loftus and Palmer (1974) found that participants that watched a car crash and then recalled details about the event, reported the crash to be faster when questioned as to how fast were the cars going when they *smashed* into one another, as opposed to hit, collided, contacted or bumped. Furthermore, the verb *smashed* was more likely to lead participants to report seeing broken glass, despite there not being any.

Currently the misinformation effect has been investigated in three non-human animals; a gorilla (Schwartz et al., 2004), pigeons, and rats (Garry & Harper, 2009; Harper & Garry, 2000). These studies found that memory retrieval was worse when interfering information was presented between the encoding and retrieval stage. However, it's not clear as to whether the misinformation simply lead to poorer memory retrieval, or whether the information changed what was remembered (as occurred in the Loftus and Palmer (1974) study). For instance, in the Schwartz et al. (2004) study, a gorilla witnessed an event, and was then asked to report on details of that event by selecting an item that had been present in the event. The gorilla had a choice between a correct, incorrect (misinformed) and incorrect (distractor) item at test, but did not select the misinformed item more than the distractor item. This suggests that the misinformation was not necessarily implanted into the memory, but just caused proactive interference. However, a study with bees found that misinformation can lead to false implanted information (Hunt & Chittka, 2015). Bees incorrectly favored a

flower that was a novel hybrid of two flowers that had previously been rewarded, over flowers that had actually been rewarded. The authors suggested that when the bees were presented with the novel hybrid flower (misinformation) they falsely identified the flower as occurring before, as a result of merging their memory of the two experienced flowers. The findings suggest that bees' memory is also susceptible to similar errors as humans. The fallibility of memory is thus perhaps an evolutionary old trait, and may have beneficial functions. In the case of the bees, it's been suggested this error of merging may aid with foraging, providing a template of what to look for in a potential food source (Reinhard, 2015).

Replicating this finding in apes would support the notion that the fallibility of memory is an evolutionary old trait, and could be assessed as an extension to the exchange paradigm in Chapter 5. For instance, the apes could be given three types of objects, two of which had previously been rewarded (e.g., the A and B type objects from Chapter 5), and a new type that is a combination of the two rewarded objects (e.g., the colour of the A type and the shape of the B type). If the apes create a false memory of the hybrid object, they should preferentially exchange that object over the A and B types.

6.4.4 Memory retention

Throughout this thesis the apes have demonstrated remarkable retention of information over time. They can recall details from past events after a minimum of two weeks, so long as some feature of the event is distinctive. Furthermore, they continue to show good retention after ten and fifty weeks, with little deterioration in performance. It has

already been demonstrated that apes can retain information for extremely long periods of time (Beran, 2004), including past events (Martin-Ordas et al., 2013); however, this is the first time it has been shown that apes memory performance over long time periods resembles the forgetting curve observed in humans (Ebbinghaus, 1964; Rubin & Wenzel, 1996).²⁷ This finding suggests that the ability to retain distinctive information over time is likely an evolutionary adaptation, enabling us to recall events and experiences that may be beneficial in future scenarios. Further research with other species, and using within subjects' paradigms, could clarify if the forgetting curve in apes consistently resembles that shown in humans.

Another interesting observation regarding the retention of past events is the effect of age. In humans, episodic memory begins to develop around the age of three (Hayne & Imuta, 2011; Perner & Ruffman, 1995; Scarf et al., 2013), and steadily improves until adulthood (Craik & Salthouse, 2011), with rapid decline in old age (Singer, Verhaeghen, Ghisletta, Lindenberger, & Baltes, 2003), resulting in an inverted U-shape pattern of performance. Martin-Ordas et al. (2010) found a similar pattern with chimpanzees and bonobos, in which performance on a what-where-when task showed an inverted U-pattern as a function of age, with subjects under seven and over eighteen years of age performing worse than those that fell between the two ages (adolescents and young adults). However, this effect was reduced to a trend when three orangutans were included in the analysis; these subjects performed poorly on the 'when' component of the task. The poor performance of the orangutans, despite being aged between ten and nineteen, could reflect potential species differences in episodic

²⁷ The forgetting curve has been observed in animal working memory, see White (2013).

memory ability. However, given the small sample, differences may be at the individual and not species level. Further research clarifying if episodic memory is influenced by age in other species would thus be an interesting avenue of research.

6.4.5 The testing effect

The testing effect refers to the phenomenon in which testing of to be remembered material results in enhanced long-term memory retention compared to repeated study of the information (Roediger & Karpicke, 2006). Interestingly, this has been evidenced in rats. Crystal, Ketzenberger, and Alford (2013) presented rats with an eight-arm maze, which was baited with food in each arm. During the study phase, rats could enter four of the eight of arms and retrieve the food. After a retention period (in which they remained in a cage), they were placed into a central hub before being given access to all eight arms. In order to retrieve the remaining four pieces of food, they needed to recall which arms they had already visited and avoid those ones. Crucially, accuracy was improved when the rats received an additional placement into the central hub immediately after the study phase, rather being placed in a cage. As the rats expected to be tested after hub placement (due to many experiences of this), the hub placement was introduced to prompt the rats to retrieve their memory of which arms they had visited. Thus, practicing retrieval improved the rats' memory retention of which arms it had visited.

The authors suggest that “memory retrieval of study arms or a representation of to-be-visited arms” (Crystal, Ketzenberger, et al., 2013, P.R709) could be a possible mechanism by which the rats retrieved the information. This would suggest the use of prospective memory, in which the rats recalled details of which arms they had and had

not visited, and generated a mental plan to visit the unvisited arms. This ability to plan for future scenarios is closely tied to episodic remembering (Suddendorf & Corballis, 2010), and as such, the testing effect may have relevance to the recall of past events in animals. Indeed, there is evidence that testing effect can lead to enhanced source memory and feeling of knowing in humans (Chan & McDermott, 2007). Moreover, the testing effect has been found to influence episodic memory in humans, with individuals with low episodic memory ability showing a larger testing effect than those with stronger episodic memory ability (Brewer & Unsworth, 2012). Consequently, it may be worthwhile to investigate the influence of the testing effect on the recall of past events in animals.

6.5 Conclusion

Since Ebbinghaus (1885)'s first experimental investigation of memory, we have learnt much about its capabilities and functions, yet, there is still much to discover and comprehend. The question as to whether episodic memory is unique to humans is perhaps a question that will never be definitely answered. The arguably impossible task of investigating the phenomenological characteristics of episodic memory in non-verbal subjects makes this a question that cannot be asked, and thus cannot be answered. Despite this, we are developing a greater understanding of the ways in which numerous species remember past events by assessing the observable characteristics of episodic memory.

The aim of this thesis was to further our understanding of the commonalities and differences between human and ape recall of past events, by investigating phenomena that occur in humans that have yet to be investigated in animals. The remarkable similarities between the way humans and the apes in this thesis recall details of past events, in combination with the diverse array of research showing elements of episodic memory in apes and other species, suggests that we likely share some form of episodic memory with at least our closest living relatives. This is not to say that differences between human and ape episodic memory do not exist, and indeed, one proposal is that apes (and other animals) may share the evolutionary earlier, and less cognitively demanding, involuntary mode of episodic memory (Berntsen, 2010; Berntsen & Jacobsen, 2008; Clayton, Bussey, et al., 2003; Rasmussen & Berntsen, 2009). The findings of this thesis suggest apes have this involuntary form, and thus provides a starting point for future investigation. Continued research, covering some of the topics discussed above will continue to build upon our understanding of episodic

memory in other species, and inform us about the origins of the ability and the ways in which it may have further evolved in humans.

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Appendices

Appendix A | Chapter 2

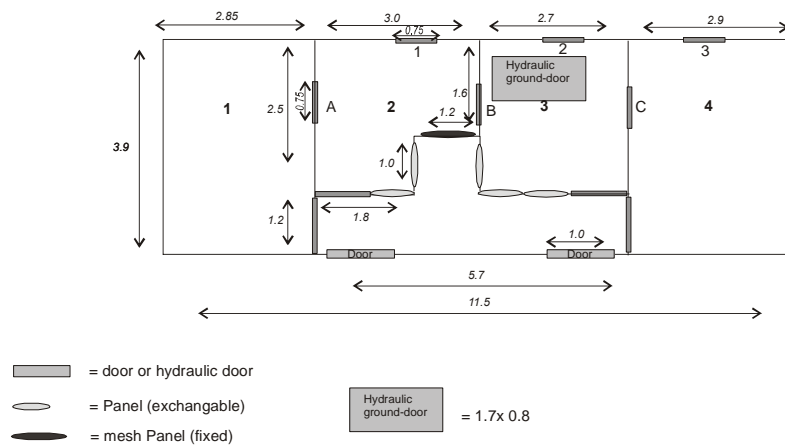


Figure A1 Specifications of the bonobo sleeping room. Measurements in meters.

Figure reproduced with permission from MPI-EVA.

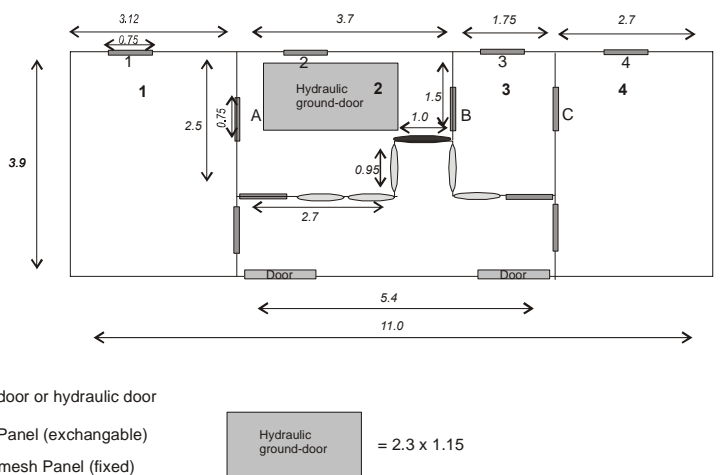


Figure A2 Specifications of the orangutan sleeping room. Measurements in meters.

Figure reproduced with permission from MPI-EVA.

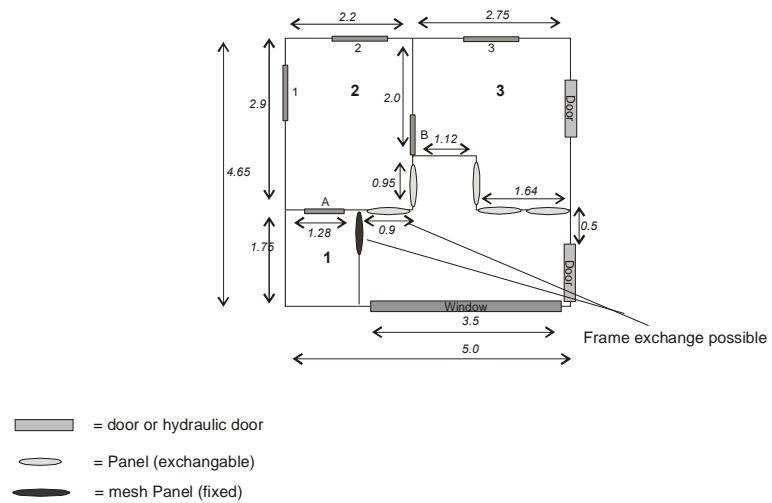


Figure A3. Specifications of the orangutan observation room. Measurements in meters. Figure reproduced with permission from MPI-EVA.

Appendix B | Chapter 4

Table B1. Coding from rater 1

<i>Experiment</i>	Video no.	Search	Time (sec)
<i>1</i>	1	no	
	2	no	
	3	no	
	4	yes	4
	5	no	34
	6	yes	20
	7	yes	14
	8	yes	21
	9	no	
	10	yes	4
	11	no	
	12	no	
	13	no	
	14	no	
	15	no	
	16	no	
	17	no	
	18	yes	2
	19	no	
	20	yes	12
	21	yes	6
	22	no	7 and 23
	23	no	
	24	yes	12
	25	no	
<i>2</i>	1a	no	
	1b	yes	62
	2a	no	
	2b	no	
	3a	no	
	3b	no	
	4a	no	
	4b	no	

a New location

b Old location

Table B2. Coding from rater 2

<i>Experiment</i>	Video no.	Search	Time (sec)
<i>1</i>	1	No	
	2	No	
	3	No	
	4	Yes	3
	5	No	
	6	Yes	10
	7	Yes	12
	8	Yes	20
	9	No	
	10	Yes	4
	11	No	
	12	No	
	13	No	
	14	No	Did not eat pellet
	15	No	
	16	No	
	17	No	
	18	Yes	2
	19	No	
	20	Yes	12
	21	Yes	7
	22	No	
	23	No	
	24	Yes	12
	25	No	
<i>2</i>	1a	No	
	1b	Yes	48
	2a	No	
	2b	No	
	3a	No	
	3b	No	
	4a	No	
	4b	No	

a New location

b Old location

B.1 Model details

Below is the alternative analysis for the data collected in Chapter 4. The Generalized Linear Mixed Model is conducted only on the experimental condition, as the model would not converge when the control condition was also included. As such, to test for differences between the experimental and control condition, separate analyses were run.

Methods

To test for differences in searching between the experimental and control conditions the proportion of searching for each subject in both conditions was calculated (i.e., if a subject searched in 1 of 2 experimental sessions, their proportion was 0.5 for the experimental condition). Differences between conditions was tested using a Wilcoxon exact signed rank test. Subjects that did not complete both a control and experimental condition were removed from the analysis (3 subjects), as well as subjects with tied observations (i.e., the same proportion of searching in both control and experimental conditions; 17 subjects), resulting in 13 subjects. A similar analysis was also conducted using a parametric test. Here the number of times a subject searched in each condition (0-2) was tallied and compared between conditions using a paired sample t-test. Although the data was not completely normally distributed, the t-test is fairly robust to violations of normality (De Winter & Dodou, 2010). Five subjects were not included in the analysis due to missing data (i.e., not completing both retrieval sessions of both the experimental and control conditions), resulting in a total of 28 subjects. This parametric version was conducted because it allowed for the inclusion of more subjects than the non-parametric test (28 compared to 13), and thus was more representative of the data.

To test whether searching would be influenced by the delay period, the exposure food and the retrieval session in the experimental condition, a Generalized Linear Mixed Model with a binomial error distribution (Baayen, 2008) was fitted. Delay, exposure food and retrieval session were fixed effects, species a controlled fixed effect and subject a random effect ($N=31$ individuals, total $n=59$). As a test of the combined effects of delay, exposure food and retrieval session, the full model was compared to a null model comprising only species and the random effect of subject using a likelihood ratio test (Dobson, 2002; Forstmeier & Schielzeth, 2011). The model was fitted in R (version 3.3.1; Team, 2016) using the function `glmer` of the package `lme4` (Bates et al., 2015). Model stability was checked by comparing the estimates from the full model to those obtained from models with the levels of the random effect (each individual subject) excluded one at a time. The stability of the model showed some uncertainty, likely due to only two observations per subject. Variance Inflation Factors (Field, 2005) were obtained from a standard linear model lacking the random effects and the interaction (function `vif` of the R package `car`) to check for absence of collinearity among the predictors, which revealed no issues (maximum Generalized VIF=1.015; Fox & Monette, 1992).

Results

The proportion of searching in the experimental condition was significantly greater than in the control condition (Wilcoxon exact signed-rank test; $W=91$, $N=13$, $p<0.001$), indicating that more apes remembered the hiding event in the experimental condition compared to the control. This was also replicated using a paired t-test, $t(27) 4.12$, $p<0.001$. As a small proportion of subjects in the control condition searched (0.12) further analysis was conducted to see if this was due to the sequence of conditions. (i.e., if the subjects that searched were the ones that had received the

control condition second and subsequently had already completed an experimental condition and witnessed a hiding event). A Mann Whitney-U exact test compared the proportion of searching in the control group by sequence (i.e., control group first, compared to control group second). Results showed a significant difference ($W=4.5$, $N=13$, $p=0.01$), with those in the control sequence second searching more ($M=0.38$) than those in the control sequence first, who never searched ($M=0$). This was also replicated using an independent t-test with Welch-Satterthwaite calculation to correct for a significant Levene's test; control condition second searched significantly more ($M=0.69$, $SD=0.87$) than control condition first ($M=0.0$, $SD=0.0$); $t(15) 3.15$, $p=0.007$.

The full model compared to the null model was non-significant (likelihood ratio test: $\chi^2=0.75$, $df=3$, $p=0.86$), meaning that searching in the experimental condition did not differ as a result of delay, retrieval session or exposure food (see table B3).

Table B3. Results of the full model. Estimate shows estimated coefficient.

Term	Estimate	SE	χ^2	df	<i>p</i>
Intercept	-10.843	5.598			(1)
Delay ⁽²⁾	-2.335	3.870	0.189	1	0.664
Retrieval (session 2) ⁽³⁾	0.748	1.382	0.327	1	0.568
Species (orangutan) ⁽⁴⁾	17.325	8.068	7.308	2	0.026
Species (chimpanzee) ⁽⁵⁾	14.071	8.981			(1)
Exposure food (Pellet) ⁽⁶⁾	1.801	4.863	0.113	1	0.736

⁽¹⁾ not shown because of having limited interpretation

⁽²⁾ z-transformed to mean of 0 and standard deviation of 1; mean and sd of the original variable was 20.322 and 20.911.

⁽³⁾ dummy coded with session 1 as the reference category

⁽⁴⁾ the indicated test refers to the overall effect of species

⁽⁵⁾ dummy coded with bonobo being the reference category

⁽⁶⁾ dummy coded with bread being the reference category

B.2 Follow up

Below is an additional experiment relating to Experiments 1 and 2 in Chapter 4. It was conducted during July 2017. The experiment is presented in brief; additional details about the subjects, testing room, and apparatus can be found in Chapters 2 and 4.

Aims

In Experiment 1 (Chapter 4), some subjects searched the hiding location more than once, despite long retention periods, and finding no food at the location during the search attempts. Additionally, some of the apes also searched the hiding location again in Experiment 2. As such, this experiment was conducted to see whether any of the apes would spontaneously search the hiding location from Experiment 1 again, when unexpectedly presented with a cardamom flavoured pellet (a food associated with Experiment 1) in the same enclosure in which the hiding event took place.

Methods

Subjects

Twelve chimpanzees and five orangutans that took part in Experiment 1 were tested (aged 7-41, $M=17.57$). Additionally, six chimpanzees and one orangutan (aged 7-40, $M=23.77$) that had not previously participated in Experiment 1 took part.

Apparatus

Subjects were tested in the same enclosure in which the hiding event occurred in Experiment 1 (see Chapter 4, Experiment 1 for details). A sliding table was attached to the meshing of the enclosure, and above the mesh was a transparent panel. Two identical blue opaque containers were positioned on the sliding table, one to the right

and one to the left (see figure B1). Cardamom flavoured pellets (as used in Experiment 1) or regular flavoured pellets (received on a daily basis), were placed under the containers.



Figure B1 Procedural set up. Photo printed with permission from MPI-EVA

Design

There were two conditions: experimental (N=17) and control (N=7). The experimental subjects had all witnessed the hiding event in Chapter 4, Experiment 1, whereas none of the control subjects had participated in Experiment 1. All subjects received one session, consisting of five trials, and received identical procedures. Thus, the conditions only differed with regards to experience of a hiding event in Experiment 1. The control condition was used as a comparison in which to compare the experimental performance to.

Procedure

Subjects were presented with two containers face up on a table, one to the left and one to the right. The experimenter (E) showed the subject a regular flavoured pellet, then placed it on the table and put one of the containers face down over the pellet. The other container was placed face down with no pellet underneath it. The sliding table was then pushed towards the subject, and the subject made a choice by pointing through the hole in the panel closest to the container they wanted (see Figure B1). If they chose the correct container, the container was lifted, and the pellet was given to the ape. If they chose the incorrect container, the container was lifted, and no pellet was given to the ape. The pellet was then removed from the correct container. This marked the end of a trial. At the end of a trial, E waited for ten seconds before the next trial began. Crucially, on one of the trials (randomized between subjects, but never the first or second trial) a cardamom flavoured pellet (as opposed to a regular pellet) was placed under the container. After five trials, E left the testing room with any remaining food, and the subject was filmed for five minutes.

Data analysis

Searching was coded in the same way as Chapter 4. It was coded whether subjects searched the hiding location from Experiment 1 (no food was present here). If they searched, it was coded whether they searched immediately after receiving the cardamom flavoured pellet, or whether they searched after all trials had finished and no more food remained (i.e., once E left the testing room with the food). The number of search attempts between the experimental and control condition was compared using a fisher exact test.

Results

Three of 17 experimental subjects searched, compared to zero of the seven control subjects; this difference was not statistically significant; $p = 0.53$.

Of the three subjects that searched, Tai searched immediately after presentation of the cardamom flavoured pellet during trial 3. Whereas Daza and Frederike searched after all trials had finished and E had left the room (at 84s and 234s respectively).

Discussion

Although there was no significant difference between the number of experimental and control subjects that searched, the fact that three experimental subjects did search is an impressive finding, given that the hiding event occurred once many months ago. Moreover, Tai and Frederike not only searched here, but also searched in all retrieval sessions post hiding event in Experiment 1, with Tai also searching again in Experiment 2. This is highly impressive, since both these subjects continued searching despite numerous failed searching attempts (food was never present in any retrieval sessions), and after many months since the hiding event occurred (1year, 10months for Tai, and 2years, 5months for Frederike). Furthermore, during the original hiding event in Experiment 1, Tai saw bread being hidden, and not cardamom flavoured pellets. Thus, the fact she searched in this current experiment when presented with a cardamom flavoured pellet is quite remarkable. To do so, she must recall the hiding event from Experiment 1, which occurred almost two years ago, she must overcome the many search attempts in which she found no food, and finally, she must make a link between the flavoured pellet (which was never hidden in the hiding

location, but was twice found on the enclosure floor underneath the location) and the hiding location.

The reason why more of the experimental subjects did not search may be because many of them received bread during the hiding event in Experiment 1 (N=8). Recalling a hiding event that occurred once many months ago, and then making an inference that cardamom pellets (that were found near the hiding location, but never in the hiding location) may be in the hiding location now, is a tall order, and thus it's not surprising that most of these subjects did not search. However, due to the limited sample size and data, it was not possible to split the experimental and control subjects into two further conditions (one for each food type). Another potential reason why more subjects did not search here, is that a number of subjects never searched in Experiment 1 (N=5), or only searched once (N=2), thus it's not surprising they did not search in this current experiment. Additionally, some of the apes may not have searched due to lack of motivation, having not found food in the hiding location many times previously.

Appendix C | Chapter 5

C.1 Orangutan data

Data analysis

Three of the orangutans in this current experiment (Bimbo, Suaq and Padana) also participated in Experiment 1; this prior participation may have influenced performance. As such, the results obtained from the full set of subjects were compared with results from an analysis conducted on just these three subjects. Due to a sample size of three, the full analysis on the test data could not be run (i.e. delay was not included as a variable, and the first exchanges could not be analysed). Likewise, three tests could not be included in the analysis (E1, E2, E3), as an ANOVA with only three subjects would produce unreliable results. As these subjects had not completed a test with E3 previously (i.e., Experiment 1 did not include E3), the analysis was run on tests E1 and E2 only.

First, it was compared whether training performance with the second experimenter was influenced by training with the first experimenter, using a paired sample t-test. Performance between tests E1 and E2 was then compared using a paired sample t-test. All results, along with the corresponding results from the full sample, are shown in table C1.

Results

There was no difference in the number of sessions taken to complete training with each experimenter, $t(2)=1.31$, $p=0.32$, although training with the second experimenter took marginally longer than with the first (see Table C1). Additionally, tests with E1 and E2 were not significantly different $t(2)=.933$, $p=0.45$, although performance in

test E2 was numerically better. This was likely driven by the performance of Suaq, who performed well in test E2 and poorly in test E1.

Table C1 Mean number of training sessions and exchanges at test by sample.

Reduced sample refers to the sample containing only the 3 orangutans.

		No. Training sessions with 1 st experimenter	No. Training sessions with 2 nd experimenter	No. exchanges in test with E1	No. exchanges in test with E2
Reduced	Mean	9.70	11.70	9.00	6.00
	<i>SD</i>	2.08	4.73	3.00	2.65
Full	Mean	10.70	13.50	7.42	6.89
	<i>SD</i>	2.39	3.98	2.60	2.42

Discussion

The results show that the three orangutans' performance is largely consistent with the results of the full sample. Although the orangutans required slightly less sessions during training, they showed the same pattern of results, in which training with the second experimenter took longer than with the first (although not significantly longer). They did not perform any better during the test with E1 compared to the full sample, and performance with E2 was near identical to the full sample. These results suggest that participation in Experiment 1 may have led to quicker learning during training, but had no obvious benefit to performance during testing.

Appendix D | Publications

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RESEARCH ARTICLE

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Distinctiveness enhances long-term event memory in non-human primates, irrespective of reinforcement

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Non-human primates are capable of recalling events that occurred as long as 3 years ago, and are able to distinguish between similar events; akin to human memory. In humans, distinctiveness enhances memory for events, however, it is unknown whether the same occurs in non-human primates. As such, we tested three great ape species on their ability to remember an event that varied in distinctiveness. Across three experiments, apes witnessed a baiting event in which one of three identical containers was baited with food. After a delay of 2 weeks, we tested their memory for the location of the baited container. Apes failed to recall the baited container when the event was undistinctive (Experiment 1), but were successful when it was distinctive (Experiment 2), although performance was equally good in a less-distinctive condition. A third experiment (Experiment 3) confirmed that distinctiveness, independent of reinforcement, was a consistent predictor of performance. These findings suggest that distinctiveness may enhance memory for events in non-human primates in the same way as in humans, and provides further evidence of basic similarities between the ways apes and humans remember past events.

KEYWORDS

binding, distinctiveness, event memory, long-term memory, primates

1 | INTRODUCTION

Humans remember past events on a regular basis. Such episodic memories serve important social and instrumental functions (e.g., Pillemer, 2003). Until recently, most research on memory of non-human primates (hereafter primates) has focused on short term memory (Beran, Beran, & Menzel, 2005; Fujita & Matsuzawa, 1990; Hoffman & Beran, 2006; Inoue & Matsuzawa, 2007; MacDonald & Agnes, 1999; Menzel, 1973; Mishkin & Delacour, 1975; Robbins & Bush, 1973; Rodriguez, Zurcher, Bartlett, Nathanielsz, & Nijland, 2011), with primate episodic memory research coming into fruition over the past decade (Dekleva, Dufour, de Vries, Spruijt, & Sterck, 2011; Hoffman, Beran, & Washburn, 2009; Martin-Ordas, Haun, Colmenares, & Call, 2010; Menzel, 1999; Noser & Byrne, 2015; Schwartz & Evans, 2001; Schwartz, Colon, Sanchez, Rodriguez, & Evans, 2002; Schwartz, Hoffman, & Evans, 2005). However, comparative studies on episodic memory have been hampered by the definition of the phenomenon (Tulving, 1972, 2001), in terms of the recollection of personal past events involving autonoetic consciousness; self awareness that the event happened in one's own personal past. Since such awareness is hard, if not impossible, to

test in animals, researchers have turned to other more objective operationalizations (see Clayton, Griffiths, et al., 2001; Crystal, 2009; Dere, Kart-Teke, Huston, & De Souza Silva, 2006; Templer & Hampton, 2013 for reviews).

Despite the progress being made here, there is still controversy over what "counts" as episodic memory (Basile, 2015; Suddendorf, 2007; Suddendorf & Busby, 2003), due in part to the many stringent, as well as changing, criteria that arise from Tulving's (1972, 1983, 1984, 1985, 2002, 2005) definitions. In an attempt to overcome some of these conceptual problems, Rubin and Umanath (2015) recently proposed an alternative conceptualization for memory for events, which removes some of the restrictive criteria imposed by the consciousness based conception of episodic memory, and enables researchers to have simpler and more measureable criteria that can also be applied to non-human animals. Rubin and Umanath (2015) refer to memory for events as "event memory," which is defined as "the mental construction of a scene, real or imagined, for the past or the future" (p.1). Unlike episodic memory, autonoetic consciousness is not required. The only criteria required is the construction of a scene from an egocentric vantage point. As such, event memory involves fewer requirements than episodic memory, but still involves the process of

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PROCEEDINGS B

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Research



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Non-goal-directed recall of specific events in apes after long delays

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We examined if apes spontaneously remember one-time, distinctive events across long delays when probed by discriminant cues. Apes witnessed an experimenter hide a cache of food, which they could then retrieve. They retrieved one of two food types; one more distinctive than the other. Two, 10 or 50 weeks later, the apes returned to the same enclosure and found a piece of the previously hidden food on the ground. An experimenter who had not hidden the food was also present. Apes immediately searched the location where the food was previously hidden (no food was here), showing recall of the event. One week later, apes returned to the same enclosure, with the same food on the ground, but now the experimenter that had hidden the food was present. Again, apes immediately searched the hiding location. Apes that had not witnessed the hiding event did not search. There was no significant effect of food type, and retention declined from exposure to the two-week delay, then levelled, consistent with the forgetting curve in humans (Ebbinghaus, H. 1964 *Memory: a contribution to experimental psychology* (transl. H.A. Ruger & C.E. Bussenis). New York, NY: Dover. (Original work published 1885.)). This is the first study to show apes can recall a one-time, non-goal-directed event longer than two weeks ago and that apes' recall declines in accordance with a standard retention function.

1. Introduction

Ebbinghaus [1] was the first to divide memory into three distinct types: voluntary, involuntary and unconscious. Involuntary memory refers to the spontaneous recollection of personal past events, often triggered by cues in the present environment (cued recall) [2]. One of the most famous examples of an involuntary memory comes from the French author Marcel Proust [3], who described the taste of a madeleine cookie dipped in lime tea eliciting his childhood memory of visiting his aunt on Sunday mornings. Involuntary memories are a frequent occurrence in our day-to-day lives [2,4,5]. They are often triggered by features of the present situation that match parts of the remembered event [6,7]. Unlike voluntary memories, they are not goal-directed and strategically retrieved, rather they reflect a bottom-up, stimulus-driven associative process, resulting in significantly faster retrieval times for involuntary over voluntary memories [8,9].

Numerous studies have shown that non-human animals (hereafter animals) can recall past events [10–18], however, only recently has it been proposed that animals may also recall past events spontaneously (i.e. involuntarily) [6,19–21]. Because involuntary memories occur spontaneously, with little effort, and are non-goal-directed, they do not rely on executive control processes or recruit pre-frontal brain regions as much as voluntary memories [22,23]. Consequently, they are considered to be the more basic mode of remembering that proceeds the evolutionary development of voluntary memory [6,19]. As such, if animals are capable of recalling past events strategically (voluntarily), then it follows that they should also be able to recall events via the more basic, and evolutionary earlier, involuntary counterpart.

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Figure D2 Publication based on Chapter 4. Full citation: Lewis, A., Call, J., & Berntsen, D. (2017). Non-goal-directed recall of specific events in apes after long delays. *Proceedings of the Royal Society B: Biological Sciences*, 284(1858), <http://dx.doi.org/10.1098/rspb.2017.0518>