How memory changes with time: From bees to humans

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I certify that the work carried out in this thesis is entirely my own and that ideas and quotations from other sources are fully acknowledged.

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Abstract

Memory is crucial for guiding animals as to where, when and on what to forage, whom to mate with and how to detect and evade predators. The contents of memory can change over time; either passively, where details are forgotten, or by reactivating and consolidating memories, in which previously stored and new information effect the final memory. In humans the fallibility of memory is well studied, with many errors known to effect declarative memory. However, little is known about the potential occurrence of such memory errors in non-human animals. In this thesis I investigate how memory changes over time using key model organisms of memory; the bumblebee and the honeybee. Additionally, I explore errors in human memory.

In Chapter two I explore memory degradation for colour patterns over time in bumblebees. I find no difference in memory decay if patterns are symmetrical around a vertical axis (an arrangement innately preferred) or not. However, not all information is forgotten over time: information about the colour contained in the pattern is retained, whilst the details of the overall configuration of the target flower are lost. In Chapter three I show for the first time in a non-human animal 'merging' of long-term memories. Bumblebees trained to two artificial flower types show a preference for a previously unseen hybrid of the two. This is similar to the memory conjunction error shown by humans. In Chapter four I find no biasing effect of postevent cues, akin to the misinformation effect in humans, in either bumblebees or honeybees. However I note the methodological difficulties in examining this type of memory error in an insect model. Finally, in Chapter five I look at a known error in human memory and show how semantic false memories may be an inevitable by-product of the adaptive cognitive process of categorisation.

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Chapter 1: Introduction

1.1 The fallibility of human memory

1.11 In the beginning: The misinformation effect and the DRM paradigm

Human memory, for all its intricacies and adaptive processes that enable us to function efficiently in our daily lives, is surprisingly fallible. After the seminal first formal exploration of false memories (Bartlett, 1932), research progressed relatively slowly, and some important findings were overlooked at the time of discovery, for example the demonstration that false recollections in a wordlist learning paradigm are due to the associations between the words in the lists and those falsely recalled (Deese, 1959). For much of the 20th century, research into memory failure focused on the effects of interference, i.e. cases when memories compete for representational space, and thus interfere with one other (Keppel and Underwood, 1962, Müller and Pilzecker, 1900, Tulving and Arbuckle, 1966). But it was not until the 1970s when a plethora of studies based on the effect of misleading information, inspired by the 'leading question law' in the judicial system, that the formal discovery and labelling of the 'misinformation effect' occurred and the field of false memory research expanded rapidly (Loftus and Palmer, 1974, Loftus, 2005).

Declarative memory is people's consciously accessible memory for facts and events (Squire et al., 1993) and this is the memory system that false memory research probes. Declarative memory is sub-divided into two further memory types: semantic memory and episodic memory (Squire et al., 1993). Semantic memory is our general knowledge about the world, more specifically factual information, for example dates of important historical events, or chemical symbols (Colman, 2009, Tulving et al., 1972). Semantic

memory does not include personal episodes and the spatial and temporal information among them (Colman, 2009, Tulving et al., 1972). Episodic memory can be considered as our autobiographical memory, covering our personal experiences of events, for example getting married three years ago or having cereal for breakfast this morning (Colman, 2009). Episodic memory includes the spatial and temporal aspects of these personally experienced events (Tulving et al., 1972). The two most commonly used methodologies for studying false memory each deal with one of these.

Studies into episodic false memory use the 'misinformation paradigm'. In this paradigm, information given after an event, or the way in which a question is asked can mislead, with memory being biased in the direction of the information (Loftus, 2005). Memory can be distorted for just small parts or specific features of events (Loftus and Palmer, 1974, Loftus, 1975), or entire events (Bernstein et al., 2005, Loftus and Pickrell, 1995), which are termed 'rich' false memories. The false memories produced are episodic, as participants can often not only 'remember' the event occurring in their life, but also when and where it occurred, with a mental reliving of it upon 'remembering' (Braun et al., 2002, Ost et al., 2005).

Semantic false memory is often studied using the Deese-Roediger-McDermott (DRM) paradigm (Deese, 1959, Roediger and McDermott, 1995). In this type of experiment, participants are required to study lists of words each composed of associates of one non-presented word. During subsequent recall and/or recognition participants 'remember' the non-presented words both with high frequency and high confidence levels (Roediger and McDermott, 1995, Stadler et al., 1999). Thus, semantic false memories are elicited. The creation of these false memories is ascribed to the strength of the associations

between the words presented in the lists and those falsely remembered, i.e. the non-presented words (Deese, 1959).

Whilst episodic and semantic false memories are elicited using different techniques, they are often not distinguished in the literature, with all incorrect recalls and/or recognitions simply termed 'false memories', regardless of the testing paradigm used or type of memory they refer to.

1.12 A new classification: The seven 'sins' of memory

More recently Schacter (1999) re-classified the known transgressions of human memory into seven distinct types, labelling them 'sins', akin to the seven deadly sins present in the bible. The first three 'sins': 'transience', 'absentmindedness' and 'blocking' are placed within the subdivision 'sins of omission', which can more simply be viewed as types of forgetting (Schacter, 1999, Schacter, 2001). 'Transience' describes the general process of memory weakening or loss over time, often generically called 'forgetting', whilst 'absentmindedness' specifically portrays lapses in attention at either encoding or retrieval, which results in either a failure to remember information that was never encoded, or the act of overlooking the information when trying to retrieve it, one example being misplacing one's car keys (Schacter, 1999, Schacter, 2001). Conversely, 'blocking' entails the inability to retrieve information despite a high level of attention, the most common example being the tip-of-the-tongue phenomenon (Schacter, 1999, Schacter, 2001).

The final four 'sins': 'misattribution', 'suggestibility', 'bias' and 'persistence' are placed within the subdivision 'sins of commission', the first three of which can more simply be viewed as types of distortion (Schacter, 1999, Schacter, 2001). 'Misattribution' is where memories are attributed to the wrong source, for example mistakenly confusing something read in a book with a real life occurrence (Schacter, 1999, Schacter, 2001). The semantic false memories elicited by the DRM paradigm and described above fall under this label. With 'suggestibility' misleading information from external sources is incorporated into personal recollections; this is the classification into which the above described episodic false memories fall (Schacter, 1999, Schacter, 2001). 'Bias' describes the influence of our own knowledge and experiences on memory. For example, our current beliefs can distort our memory for past events, such that they are realigned with our current attitudes about the world (Schacter, 2001). Finally, 'persistence' describes repeated intrusive recollections, most commonly this is seen in the inability to forget a traumatic or emotionally negative experience (Schacter, 1999).

1.13 Memory error: An adaptive perspective?

Further to this novel classification system, Schacter (1999) proposed that whilst these 'sins' are generally viewed as negative errors, they should in fact be viewed as potentially inevitable by-products of the many adaptive features of human memory. Schacter (1999, 2001) is not the first to propose such an explanation. Many scholars have long argued that forgetting (known as 'transience' in the seven sins) could actually be adaptive in itself. Anderson and Schooler (1991) proposed that human memory is adapted to environmental structure, such that memories are variable in their current need, with a system that attempts to optimise itself, and thus the most relevant

memories are made available, with past history used to assess whether a memory is currently needed. Bjork and Bjork (1988) further argued that our ability to efficiently retrieve information currently relevant is aided by the fact that we lose access to information no longer required. Therefore, in their view it is this plasticity of memory retention that enables us to successfully adapt to a changing environment. Similarly with 'absent-mindedness', our ability to function at an abstract level, induced by the non-coding of the details of certain items, enables us to perform routine activities on 'autopilot' (Schacter, 2001). As such we can better attend to things we consider more important, but the result is that we sometimes fail to encode important information. A prime example of the consequence of the failure of this adaptive feature of memory can be found in the famous study of the Russian journalist and mnemonist Solomon Shereshevski (Luria, 1968). Shereshevski encoded every fact, figure and experience he encountered with absolute detail, but yet could not grasp abstract concepts. Likewise with 'blocking', whilst occasionally inhibitory memory processes prevent a required piece of information from being recalled, they primarily act to stop an overwhelming amount of information coming to mind whenever we try and retrieve a memory. If numerous memory traces of every detail of information linked to what we are trying to achieve are recalled at once, then confusion would reign (Bjork, 1989).

'Misattribution' is attributed to assigning information to the incorrect source. One specific example is the semantic memory errors elicited using the DRM paradigm (Roediger and McDermott, 1995), which could be considered as the inevitable by-product of our ability to generalise and form categories and concepts (Schacter, 1999). Categorising is seen as an adaptive memory process as it economises memory, allowing us to, rather than encode every detail about every item we encounter, recall a large

number of items based on just a few criteria (Chittka and Niven, 2009, Merritt et al., 2010). However, as a result we may often falsely recognise or recall members of a category, which were not presented, when their exemplars were. The least is known about the potential cause of 'misinformation', in which secondary information biases an existing memory. As with 'misattribution' it is likely caused at least in part by the failure to attribute the memory to the correct source (Schacter, 1999). Similarly to 'transience', applying Anderson and Schooler's (1991) theory of a memory system adapted by the environment, we rarely need to know the specific source details of all memories, just the more general information pertaining to the memories. As such, it is easy to see how we may inadvertently 'remember' information given by others but mistakenly label it as coming from our own knowledge and subsequently combine it with an existing memory. 'Bias' comes in many forms and as such can distort memory in many ways. Stereotypical bias, in which memory is distorted by our stereotypes, may occur as a by-product of these generalisations, e.g. our ability to group people and or objects based on past experiences (Schacter, 2001). As stated previously, categorising is adaptive as it allows efficiency of memory, enabling an item to be placed correctly based on just a few rules rather than a large amount of very specific detail (Chittka and Niven, 2009). Egocentric bias is also common. This is where memories about oneself are distorted in order to enhance the perception of 'the self', for example through exaggerating the difficulties of past experiences to inflate the appearance of current achievements (Schacter, 2001). Whilst it was once thought that accurate perceptions of 'the self' were crucial for maintaining mental health, Taylor and Brown (1988, 1994) have shown that not only do people commonly exhibit what they term 'positive illusions', in which 'the self' is in some way viewed in a more enhanced way, but that these illusions can promote aspects of mental health such as the ability to be happy and contented. Finally with 'persistence', the robustness of traumatic memories as

controlled by the amygdala (LeDoux, 1996) may at best be an annoyance and at worst

be hugely impactful upon everyday functioning (Brewin, 2003). However, the strong

retention and persistent replaying of such information may be crucial if the memory is

deemed to be useful for future survival (Schacter, 1999).

1.2 Memory fallibility in animal models

1.21 Comparative cognitive neuroscience

Our current knowledge as to the workings of human learning and memory owes in large part to the plethora of work with animal models undertaken over the last century. From classical conditioning in the dog *Canis lupus familiaris* (Pavlov and Anrep, 1927) to operant conditioning in the rat *Rattus norvegicus* (Skinner, 1938) and habituation studies with the sea slug *Aplysia californica* (Pinsker et al., 1970), we have learnt much about the behavioural and neuronal aspects of human cognition. Comparative cognitive neuroscience, in which animal models are utilised, in the hope of gaining a better understanding about aspects of the human mind, is now an extremely well established scientific field. Theory states that mechanisms underlying many aspects of human cognition are also present, potentially in a more basic form, in non-human animals, due to the evolutionary connection between species (Menzel, 2008). So why, given the vast number of studies into human memory fallibility, have so few been undertaken in non-human animals? Firstly many of the classic human studies rely on verbal communication (Loftus and Palmer, 1974, Roediger and McDermott, 1995), which would be impossible to reproduce with non-human species. Secondly there is still some argument as to whether non-human animals utilise one of the key memory systems that humans do, which in turn prevents them from producing false memories from that system. The memory system in question is episodic memory.

1.22 Episodic memory in non-human animals?

The eminent psychologist and neuroscientist Endel Tulving (2002) argues that non-human animals are incapable of utilising episodic memory in the way that humans do. For him the ability to utilise episodic memory requires 'mental time travel'; a re-experiencing of the event when recalling it, which in turn requires both a sense of self and that of time passing, neither of which he argues have been widely shown to occur in non-human animals (Suddendorf, 2013, Tulving, 2002). This view is not universally shared, with much research now indicating that non-human animals can utilise a type of memory that involves not only specific events, but information pertaining to where and when they occurred. For example, Clayton and Dickinson (1998) showed that not only do scrub jays *Aphelocoma coerulescens* remember the spatial location and contents of food caches, but also, crucially, when the food items were cached. When both wax worms, which degrade over time and peanuts, which do not, were cached, jays preferentially recovered caches containing wax worms if they had been cached relatively recently, but chose not to if a long period of time had passed. Conversely jays preferentially recovered caches containing peanuts only after a significant period of time had passed. Thus jays fulfil the majority of the criteria of the 'what', 'where' and 'when' definition of episodic memory. Additionally, research with a gorilla *Gorilla gorilla gorilla* (Schwartz et al., 2002, 2004) and the bottlenose dolphin *Tursiops truncatus* (Mercado et al., 1998) has shown some elements of episodic memory utilisation, but none of these studies truly investigated all three of the 'what', 'where' and 'when' criteria simultaneously. Furthermore as none of the non-human animal research proves the 'mental time travel' component of episodic memory has taken place, the term 'episodic-like memory' is used for non-human animals.

1.23 Animals and humans: Analogous results

The relatively small amount of research into false memory that has been undertaken in non-human animals has shown results analogous to those seen in humans and has utilised the delayed matching-to-sample (DMTS) paradigm: the commonly used methodology for investigating learning and memory in non-human animals (Blough, 1959). In the paradigm, the subject learns to match a sample with one of two or more comparisons, presented after a delay. As such, the sample is no longer present at the decision point. Subjects are thought to utilise both working memory and long-term memory to successfully learn the paradigm (Blough, 1959). As such, the DMTS paradigm has been utilised in the study of the effect of 'misinformation' in non-human animals. The delay, given after the sample to be remembered, but before the choice test, allows non-verbal postevent cues to be inserted, as 'misinformation' as is in human studies. Harper and Garry (2000) reported that postevent cues bias recognition performance in a visual three-colour delayed matching-to sample (DMTS) task in the pigeon *Columba livia*. When pigeons were shown information after the sample that was consistent with the sample, and as such was consistent with the correct choice in the matching test, their performance was improved (above baseline). Conversely, when shown information after the sample that was inconsistent with the sample and as such was consistent with the incorrect choice in the matching test, their performance was hampered (below baseline) (Harper and Garry, 2000). Thus memory was biased in the direction of the misinformation, just as has been shown to occur in humans. They later furthered this work (Garry and Harper, 2009), showing that the rat is also susceptible to misleading information during a DMTS task involving retractable levers and light cues, again with performance enhanced by consistent misinformation and worsened by inconsistent misinformation. Furthermore human subjects were tested using a methodology back-translated from the pigeon and rat experiments, in which a

computerised DMTS task involving black and white kaleidoscope images were used. The result, that humans are still effected by misinformation in the same way as previously shown in other studies (for example Bernstein et al., 2005, Loftus and Palmer, 1974) provides evidence that the analogous effects of misinformation seen in non-human animal species are not due to the methodological differences created when adapting experiments for non-human subjects (Garry and Harper, 2009).

Additionally Schwartz et al. (2004) reported that misinformation negatively affects event memory in a gorilla. After viewing either a person or an object the gorilla was shown misinformation in the form of a photograph depicting a different person or object. When then given the choice between three photographs, one showing the correct person or object, one showing the incorrect person or object shown in the misinformation and one showing a third irrelevant person or object, the gorilla's selection was biased in the direction of the misinformation and as such performance was decreased (below baseline) (Schwartz et al., 2004). Furthermore, Kraemer and Golding (1997) have argued that adaptive forgetting may also occur in non-human animals. Although these examples seem to mirror results found using humans, it is still unclear to what extent these errors of the mind may occur in non-human species.

1.24 Animal models: A logical choice?

Many species of non-human animal have shown the ability to generalise, categorise and potentially even form genuine concepts, as described in the human literature (Chittka and Jensen, 2011). Non-human species have also demonstrated cognitive bias (Bateson et al., 2011, Harding et al., 2004) and innate or learnt preferences (Giurfa et al., 1996, Kelber, 1997). Furthermore the ability to utilise multiple memories, i.e. the ability to remember how to solve multiple tasks, requiring different answers also occurs in non-human animal models (Avarguès-Weber et al., 2012, Dukas, 1995). As non-human animals therefore use learning and memory systems thought to be responsible for the production of many of the fallibilities of memory, the use of model systems, such as birds, rodents, fish, and bees for exploration into their existence in non-human animals seems logical. To this end, this thesis primarily focuses on the bumblebee *Bombus terrestris* as a model to examine how memory changes over time, with an emphasis on the potential occurrence of memory errors, as shown in humans.

1.3 Bees as a model for learning and memory

Bees have long been used as model systems for the study of neuroethology due to their behavioural richness, ease of laboratory manipulation and accessible central nervous systems (Giurfa, 2003, Menzel, 1968, 1969, Menzel and Giurfa, 2001, Von Frisch, 1967). There is much literature regarding the learning and basic memory capabilities of both honeybees and bumblebees. Honeybees, *Apis mellifera* can learn to associate olfactory stimuli with a reward within only one or two trials, with the learning of colours taking up to five trials and black and white patterns requiring five or more trials (Menzel, 2009). When trained to a single coloured target they continue to correctly choose this stimulus for several days after their initial training (Menzel, 1968). Additionally, the bumblebees *Bombus ternarius*, *Bombus terricola* (Heinrich et al., 1977), *Bombus bimaculatus* (Dukas and Real, 1991), *Bombus impatiens* (Chittka, 1998) and *Bombus terrestris* (Lihoreau et al., 2010) can retain colour, sensorimotor and optimal route information overnight.

The bumblebee *Bombus terrestris* is known to have a preference for bilateral symmetry and it is known that this preference is innate (Rodriguez et al., 2004). Naive individuals, who therefore had no prior visual experience with respect to symmetry, preferentially chose bilaterally symmetric black and white patterned artificial flowers when given the choice between those and asymmetric ones (Rodriguez et al., 2004). It has been inferred that this means that the sensory processing pathways in naive bees' nervous systems are therefore primed to respond to common sensory cues found within their natural environments: symmetrical flowers. The innate preference for symmetry could be considered akin to the preferences and pre-conceptions shown by humans, which are known to cause 'bias' errors in declarative memory (Bartlett, 1932). Additionally,

Giurfa et al. (1996) demonstrated that honeybees can detect and generalise symmetry and asymmetry. Bees trained to discriminate bilaterally symmetric from asymmetric patterns both learn the task, and also transfer the learnt cues to novel artificial flowers (Giurfa et al., 1996, Giurfa and Menzel, 1997). The memory error of 'bias' shown by humans is thought to be caused by our ability generalise, to economise memory (Schacter, 1999, Schacter, 2001), consequently if bees are capable of this generalisation they may be suitable for use as non-human models for the study of such a memory error.

Honeybees have shown the ability to utilise non-elemental learning in which a knowledge as to the relationship between objects, rather than the specific physical features of the objects is needed to solve a task. They can successfully learn DMTS and delayed non-matching-to-sample (DNMTS) tasks using both solid colours and horizontal or vertical striped patterns, thus learning 'same' and 'different', with an ability to transfer these concepts between the sensory modalities olfaction and vision (Giurfa et al., 2001). The bumblebee *Bombus terrestris* has also shown some ability to learn a colour-based DMTS task, but only if spatial cues are also available to locate the rewarded colour (Dale et al., 2005). Modified DMTS paradigms have already been shown to elicit memory errors in the pigeon (Harper and Garry, 2000), rat (Garry and Harper, 2009) and gorilla (Schwartz et al., 2004), analogous to those created by the 'misinformation effect' in humans (Loftus, 2005). It may therefore be appropriate to use bees as animal models in the study of this known human memory error. Moreover, honeybees can categorise objects based on general features, such as 'landscapes', 'plant stems' and 'flower types' (Zhang et al., 2004) and can utilise olfactory (Wright et al., 2008) and number-based visual generalisations (Gross et al., 2009). 'Misinformation' is

thought to cause declarative memory errors due to an inability to attribute memories to the correct source (Schacter and Dodson, 2001). This in turn is considered an unwanted by-product of our ability to group things together, for example by generalising or categorising, to allow a large amount of information to be stored and retrieved, using only a small number of presented items (Chittka and Niven, 2009, Schacter, 1999). As such bees, may be an ideal candidate for the study of the effect of postevent cues ('misinformation') in an animal model.

Additionally, the bumblebee *Bombus occidentalis* can simultaneously hold and alternately retrieve memories for two different colours in order to solve two separately presented colour choice tasks (Dukas, 1995). Furthermore, two concepts can even be utilised simultaneously by the honeybee (Avarguès-Weber et al., 2012). Bees successfully learnt both an abstract concept based on spatial relationships: either above/below or left/right, and an abstract concept based on the perception of difference and successfully transferred this dual-concept to choose unknown targets that were the best match of both concepts: the learnt spatial relationship and different from one another (Avarguès-Weber et al., 2012). Moreover, interference, in which memories compete for representational space, thereby interfering with each other has been shown to occur in several species of bumblebee. Retroactive interference, in which newly learnt information effects the recall of prior learnt information (Müller and Pilzecker, 1900), effects sensorimotor memories, more specifically flower handling times in *Bombus impatiens* (Chittka and Thomson, 1997, Gegear and Laverty, 1995) and *Bombus bimaculatus* (Woodward and Laverty, 1992), and colour memory in *Bombus occidentalis* (Dukas, 1995). This ability of bees to utilise memories for multiple items and/or concepts and the known effects that interference has on them could make them a

suitable candidate to investigate the potential for, in a non-human animal, a known human memory error specific to the integration of multiple memories: the 'memory conjunction error' (Reinitz et al., 1992).

Thus, this thesis uses the bumblebee *Bombus terrestris* and the honeybee *Apis mellifera* to explore the potential use of bees as animal models for the study of known memory errors.

1.4 Structure of thesis

Chapter 2: No influence by the innate preference for bilateral symmetry on memory degradation in the bumblebee

Current knowledge and past experiences are known to strongly bias memory in humans. An innate preference known in bees provides an ideal opportunity to explore this phenomenon in a non-human animal. In this chapter I explore the potential effect of the innate preference for bilateral symmetry on memory degradation in the bumblebee *Bombus terrestris*. I go on to investigate which specific visual features of artificial flowers are retained in long-term memory.

Chapter 3: The merging of long-term memories in the bumblebee

Here, I investigate whether memories for multiple visual items erroneously merge in the bumblebee *Bombus terrestris*. Is a non-human animal susceptible to a misattribution error: the memory-conjunction error, known to occur in humans?

Chapter 4: Postevent cues: Are bees susceptible to the 'misinformation effect'?

This chapter explores the potential for the misinformation effect to occur in non-human animals. I use both the honeybee *Apis mellifera* and bumblebee *Bombus terrestris* to look at the possible biasing effects of postevent cues.

Chapter 5: False memory susceptibility is correlated with categorisation ability in humans

It has been proposed that semantic false memories may be an inevitable by-product of an adaptive feature of human memory: our ability to generalise and form categories and concepts. In chapter five I investigate this possibility using human subjects.

Chapter 6: General discussion

In the final chapter I bring together my findings to readdress whether non-human animals are prone to the types of memory errors shown in humans and whether they are suitable as models for these types of study. I also discuss my findings in relation to the potential adaptive perspective proposed for human memory fallibility.

Chapter 2: No influence by the innate preference for bilateral symmetry on memory degradation in the bumblebee

2.1 Introduction

The reconstructive nature of memory is well-studied in humans, with a plethora of data highlighting the inaccuracies that can occur both during memorising itself or in the acts of recall and recognition (Loftus, 2005, Schacter, 1999). Bartlett's (1932) seminal text *Remembering* was one of the first to demonstrate that memory is not nearly as accurate as we often assume. For one task he instructed participants to read a North American folk-tale and subsequently reproduce the story at various intervals. Bartlett found that the participants rarely recalled all the events in the story with accuracy, but instead 'remembered' details that fitted in with their expectations of the story, akin to their general knowledge and current beliefs about the world. For example the word 'canoe' was replaced by the word 'boat' and the activity of 'hunting seals' was remembered as 'fishing' (Bartlett, 1932). He concluded that memories are therefore highly influenced by the expectations and overall attitude of the person remembering, as well as by the potentially accurately stored memories of the information to be recalled (Schacter, 1996). Additionally, Deese (1959) and Roediger and McDermott (1995) have shown, using simple wordlists, how both memory recall and recognition can be easily distorted by our knowledge of associations between items. Thus, memory is also easily influenced by our pre-existing ideas about how items in the world relate to one another, and what we would expect to happen in a scenario, given certain criteria.

In comparison to the large body of work that exists about memory distortions in human subjects, animal studies have largely neglected the possibility that memory might not just fade with time, but also be subject to similar distortions as those found in humans. This is peculiar, given that there is a vast literature about learning and memory in animals from sea slugs (Pinsker et al., 1970), through insects (Gerber et al., 2004, Menzel, 2008) and mammals (Pavlov and Anrep, 1927, Skinner, 1938), often with important implications for the functioning of human memory.

In this chapter I explore whether a non-human animal, the bumblebee *Bombus terrestris,* is also potentially susceptible to memory inaccuracies, like those shown by humans. More specifically, I investigate the potential for memory to be biased by a known preference, in this case for the symmetry of visual patterns, in a similar way as known stereotypes and pre-conceptions about the world influence human memory during recall and/or recognition.

Several species of insect are known to show a preference for symmetrical flowers (Giurfa et al., 1996, Møller and Sorci, 1998). In bumblebees it is known that this preference is innate. Rodriguez et al. (2004) used naive individuals in their experiments, thus controlling for the test subjects' prior visual experiences, to exclude the possibility that the preference is a simpler by-product of visual object recognition following specific experiences. Their results indicate that the sensory processing pathways in the nervous system of naive bees are primed to respond to relevant sensory cues within their environment, as the majority of flowers are symmetrical (Rodriguez et al., 2004). This innate preference for symmetry may also have a functional significance as symmetrical flowers are thought to be generally more rewarding (Møller and Eriksson,

1995) and there is also some evidence that the asymmetries in plants can be viewed as an index of developmental instability caused by genetic and environmental factors (Møller and Shykoff, 1999, Møller, 2000). Furthermore, Giurfa et al. (1996) demonstrated bees' capacity to detect and generalise symmetry and asymmetry, showing that when trained to discriminate bilaterally symmetric from asymmetric patterns they can not only easily learn the task, but they can appropriately transfer the cues to novel stimuli (Giurfa and Menzel, 1997).

It is not yet known to what extent innate preferences may affect the rate and structure of memory degradation for learnt stimuli. Here I investigate whether the innate preference for symmetry has an effect on memory degradation in the bumblebee *Bombus terrestris*. I hypothesise that, as time passes after learning, an innate preference, in this case for bilateral symmetry with a vertical axis of symmetry, biases memory causing a gradual switch in choices to only those stimuli matching the innate preference. For this purpose I trained bees to differentially oriented artificial flowers and subsequently tested their memories for the learnt flowers at differing time intervals, including a bilaterally symmetrical flower as a critical lure, to potentially bias memory. Additionally, I tested a sub-set of bees with artificial flowers comprising differing elements of the learnt flower, i.e. colours or spatial configuration, to elucidate more specifically what information is held in long-term memory. My findings indicate that the innate preference for symmetry does not bias memory in the bumblebee. Furthermore my results show that the general colours of the learnt flower are held in long-term memory, whilst the specific spatial configuration of the colours within the flower is forgotten.

2.2 Materials and Methods

Subjects

Bees were from eight commercially obtained colonies of *Bombus terrestris* (Syngenta Bioline Bees, Weert, The Netherlands) which were housed in bipartite wooden nest boxes (28cmx16cmx11cm). Bees were individually marked on the thorax with coloured, numbered markers (Opalith tags, Christian Graze KG, Germany) to allow identification. A differing number of bees were used from each colony and each colony was utilised for a different length of time (colony/N/time: KS4/N=9/49 days, KS5/N=9/25 days, KS6/N=2/2 days, KS7/N=4/8 days, KS8/N=7/19 days, KS9/9/18 days, KS10/N=16/23 days, KS11/N=10/11 days). Prior to experimentation bees were kept naive with no exposure to coloured or oriented artificial flowers given in association with food. Colonies were provided *ad libitum* with defrosted pollen (Koppert BV, Berkel en Rodenrijs, The Netherlands) directly into the nest and any extra feeding required in addition to the products of the experimental foraging was with 50% sucrose solution (v/v) provided directly into colonies' honey pots.

Set-up

Experiments were undertaken in a wooden flight arena (l00cmx71cmx71cm), with a transparent UV-transmitting Plexiglas™ lid, into which access was provided by means of a transparent Plexiglas™ tube. Shutters along the length of the tube enabled the traffic of bees into and out of the arena to be controlled. During experimentation, artificial flowers were presented vertically on the far wall of the flight arena (Fig. 2.1), so that their appearance was independent of the bees' approach direction. This also provided ecological relevance as bilaterally symmetrical flowers are mostly presented

vertically, with radially symmetrical flowers mostly presented horizontally (Giurfa et al., 1996).

Artificial flowers

All artificial flowers were circular (Ø=7cm) with transparent Perspex™ landing platforms (1.5cmx1.5cmx1cm) attached beneath the centre. Each platform had a central well (Ø=0.6cm, depth=0.2cm), into which the experimenter could place droplets of sucrose or water (Fig. 2.2). Additionally each circular flower display disk contained a central hole (Ø=0.5cm) positioned directly above the landing platform, which enabled the experimenter to replenish rewards by means of a pipette from outside of the arena.

2.21 Experiment A: Does an innate preference for symmetry bias memory?

Pre-training

Twenty yellow artificial flowers (Table 2.1) were randomly assigned to positions on the presentation wall (Fig. 2.1b) and each was rewarded with a 20μl droplet of 50% sucrose solution (v/v). Bees were allowed to forage freely on the flowers and all rewards were replenished once they had been consumed, and bees had departed from that flower. This allowed bees to become used to the flight arena foraging scenario, familiarise themselves with foraging on the artificial flowers and enable the determination of individuals that would successfully forage for a minimum of three consecutive foraging bouts, who were therefore suitable for further testing.
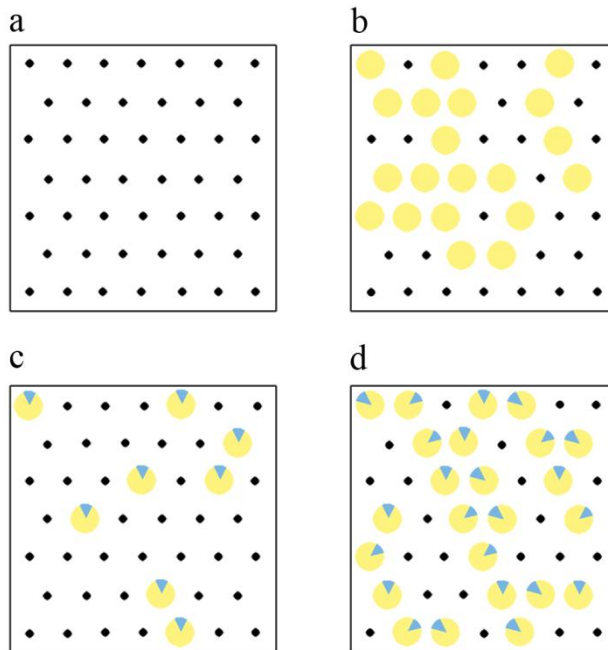
Figure 2.1 Artificial flower presentation wall showing a) all potential flower presentation positions possible, represented by black dots and example flower randomisations showing b) pre-training flowers, c) absolute conditioning (for training group 0^0) and d) differential conditioning/testing (again, for training group 0^0).
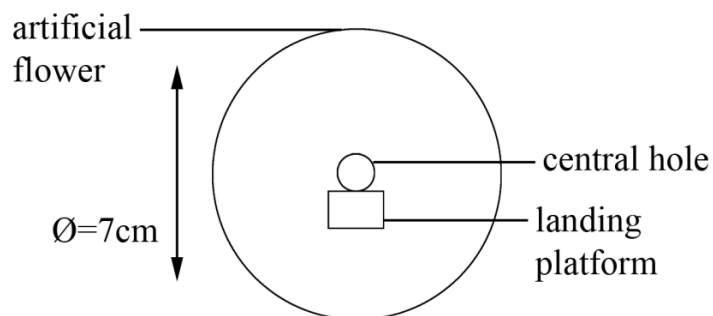
Figure 2.2 Example artificial flower (Ø=7cm), showing central hole (Ø=5cm) to enable the experimenter to insert a reward droplet from outside the arena by means of an electronic pipette. Beneath the hole in front of the artificial flower target, a Perspex™ landing platform (1.5cmx1.5cmx1cm) is attached.

Table 2.1 Artificial flower colour information: Spectrophotometer measurements (hue, brightness, saturation and UV reflectivity) for all artificial flower colours used.

Colour	Hue	Brightness	Saturation	UV Reflectivity
Yellow	Green	0.668	0.261	0.146
Blue	Blue-Green	1.064	0.116	0.282
Red	Uncoloured	0.296	0.054	0.133
Orange	UV	0.559	0.111	0.255

Absolute Conditioning

Eight yellow coloured artificial flowers, with a blue coloured 45^0 sector oriented around a fixed centre (Table 2.1) (Fig. 2.3a) (Chittka et al., 1988) were randomly assigned to positions on the presentation wall (Fig. 2.1c), and each was rewarded with a 20µl droplet of 50% sucrose solution (v/v). The orientation of all eight flowers were either 0^0 (of the sector's midline, with respect to vertical) (bilaterally symmetrical around the vertical axis of symmetry), or $+36^0$ (asymmetrical with respect to a vertical axis) (Fig. 2.3a). Bees were randomly assigned to one of two training groups: 0^0 or $+36^0$ (N=28 per group), which signified which flower orientation was used for training. Three foraging bouts were given and each individual bee's satiation volume was determined from this training phase, to enable the experimenter to administer suitable reward volumes during differential conditioning. Bees were allowed to return to the nest box and empty their crops between foraging bouts, during which time the randomly allocated positions of the flowers were changed to prevent positional learning. Additionally all landing platforms were cleaned with 70% ethanol to remove any scent marks left by the bees. All bees were trained individually.

Differential Conditioning

Twenty-four yellow coloured artificial flowers, with a blue coloured 45^0 sector oriented around a fixed centre were again randomly assigned to positions on the presentation wall (Fig. 2.1d). The twenty-four artificial flowers comprised eight of each of three different orientations. For those bees being trained to 0^0, eight of the flowers were 0^0 which were rewarded with a droplet of 50% sucrose (v/v) (volumes adjusted for each bee, using the satiation volumes determined by absolute conditioning), eight of the flowers were -36^0 and eight of the flowers were $+36^0$, all of which were unrewarded

(empty) (Fig. 2.3a). For those bees being trained to $+36^0$, eight of the flowers were $+36^0$ which were rewarded with a droplet of 50% sucrose (v/v) (again, volumes adjusted for each bee, using the satiation volumes determined by absolute conditioning), eight of the flowers were 0^0 and eight of the flowers were $+72^0$, all of which were unrewarded (empty) (Fig. 2.3a). Thus each of the three orientations had a $\pm36^0$ difference between each other. Each bee was allowed to forage until one hundred and fifty choices had been made. The definition for a 'choice' was the landing of the bee upon the landing platform of a flower. Again, bees were trained individually and allowed to return to the nest box and empty their crops between foraging bouts. While bees were in the nest, the randomly allocated positions of the flowers were changed to prevent positional learning and all landing platforms were cleaned with 70% ethanol to remove any scent marks left by the bees.

Testing

Only bees that successfully completed training were subsequently tested. Individuals were classified as successful if the number of correct choices within their last thirty differential conditioning training choices was statistically greater than chance (χ^2: $p<0.05$). Each bee was randomly assigned to one of four testing time intervals: immediately, twenty-four hours post training, three days post training or five days post training, such that each bee was only tested at one of the four possible time intervals and that an even number of bees from each training group (0^0 and 36^0) were tested at each of the four time intervals (per time interval N=14, per training group and time interval combined N=7). The same twenty-four yellow coloured artificial flowers, with a blue coloured 45^0 sector oriented around a fixed centre used in the absolute conditioning training were again randomly assigned to positions on the presentation wall. All flowers

were unrewarded, but were provided with a 20µl droplet of water to visually encourage

foraging. One foraging bout was given and the first ten choices were recorded.
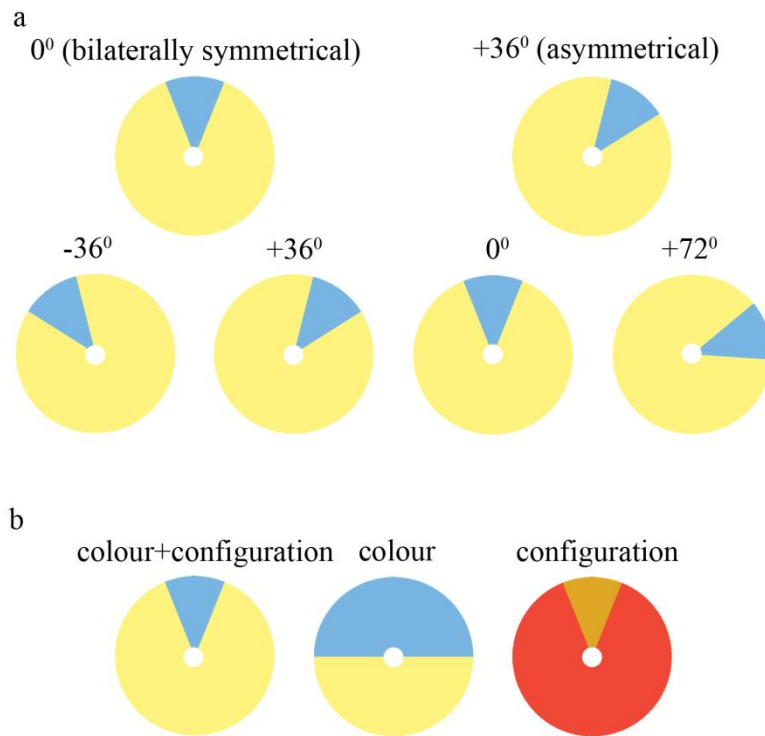
Figure 2.3 Artificial flowers: a) training and testing flower orientations used in each training group: 0^0 (bilaterally symmetrical with respect to vertical): $-36^0/+36^0$ and $+36^0$ (asymmetrical with respect to vertical): $0^0/+72^0$. b) testing flower types used in experiment B: colour+configuration (identical colour combination and spatial configuration as the learnt flower), colour (identical colour combination, but different spatial configuration as the learnt flower) and configuration (different colour combination, but identical spatial configuration as the learnt flower).

2.22 Experiment B: What aspects of a learned artificial flower are retained in long-term memory?

Additionally, to further understand what specific aspects of a learnt flower are retained in long-term memory, bees were tested using artificial flowers comprising of the different elements contained within the learnt flower: colour and configuration.

Pre-training was undertaken in an identical fashion to that described above. The procedures for both absolute and differential conditioning described above were then repeated, with the modification that bees were only trained on artificial flowers in which the blue sector was presented at 0^0 upward (bilaterally symmetrical with respect to vertical) (Fig 2.3).

Testing

The procedure for testing described above was repeated, but with the following modifications: all bees were tested three days after training. Twenty-four artificial flowers were presented: eight 0^0 flowers (thus, identical colour combination and spatial configuration as the learnt flower), eight 50% yellow and 50% blue flowers, with the colour division line running horizontally through the centre of the flowers with respect to vertical (Fig. 2.3b) (thus, identical colour combination, but different spatial configuration as the learnt flower) and eight orange coloured flowers with a red coloured 45^0 sector oriented at 0^0 of the sector's midline with respect to vertical (Table 2.1) (Fig. 2.3b) (thus, different colour combination, but identical spatial configuration as the learnt flower).

Data Analysis

The numbers of choices for the correct artificial flower orientation during the last thirty differential conditioning training choices were calculated for each individual to analyse learning. A 2-sample t-test was used to check for any potential difference in learning between the two training groups: 0^0 (bilaterally symmetrical with respect to vertical) and $+36^0$ (asymmetrical with respect to vertical). Additionally the numbers of choices for each test flower orientation were calculated for each individual, in each training group, at each testing time interval, to analyse memory retention and the potential influence of the innate preference for symmetry on memory degradation. A generalised linear model with Poisson errors was used to test whether the pooled number of correct choices (N=7) (the dependent variable) could be explained by time and/or training (the independent variables). Model selection and validation using AIC and/or theta values was undertaken and a pseudo-R^2 value was calculated to check the explanatory power of the model. A further generalised linear model with Poisson errors was used to test whether the pooled number of choices for symmetry (N=7) (the dependent variable) could be explained by time and/or training (the independent variables). Again, model selection, validation and an evaluation of the model's power were undertaken. Finally, the numbers of choices for the three flower types comprising different elements contained within the learnt flower were calculated and analysed using a Wilcoxon rank sum test, to determine what aspects of the learned flower were retained in long-term memory. All data were also converted to give average percentages to display graphically. All analyses were carried out using R statistical software (v.2.14.1).

2.3 Results

2.31. Experiment A: Does an innate preference for symmetry bias memory?

Learning

There was no significant difference between learning of the two different artificial flower orientations: 0^0 (bilaterally symmetrical with respect to vertical) and $+36^0$ (asymmetrical with respect to vertical). Discrimination performance is given as the number of correct choices in the last thirty differential conditioning training choices made (2-sample t-test: t=-0.604, df=54, p=0.548, Fig. 2.4a). It was important to establish this, since a significant difference in learning between the two training groups may have influenced subsequent memory retention of the bees for the correct flower orientation between the training groups.

Memory Retention

Memory for the learnt flower orientation remained high both initially and twenty-four hours after training, falling to around chance level at three days post training (retention is given as the number of correct choices out of ten test choices made at one of four time intervals) (Fig. 2.4b). This pattern of memory degradation was shown by both training groups (0^0: bilaterally symmetrical with respect to vertical and $+36^0$: asymmetrical with respect to vertical). The relationship between the number of correct choices and time was significant (GLM, Poisson errors: final model: correct choices~time+training, df=7, AIC=53.819), both at testing time points 'initial' (z=3.583, p<0.001) and '1 day' (z=3.315, p<0.001). Three days after training this relationship was not significant within the model (time '3 days': z=-0.470, p=0.638). No significant relationship between the number of correct choices and training was shown (training 'symmetrical': z=-0.742,

P=0.458). Additionally there was no significant interaction between time and training (initial model: correct choices~time*training, AIC=59.62, Chi backwards stepwise deletion: time:training: AIC=53.819, p=0.977), therefore this was removed from the model. The final model was not over-dispersed (theta<1) and the proportion of variance in the number of correct choices explained by it were high (pseudo-R^2 = 0.991). Overall, there was a general trend of a decrease in the number of correct choices over time, for both training groups, showing that memory decay occurs. Additionally, memory retention was not dependent upon the orientation, and specifically the symmetry of the learnt flower.
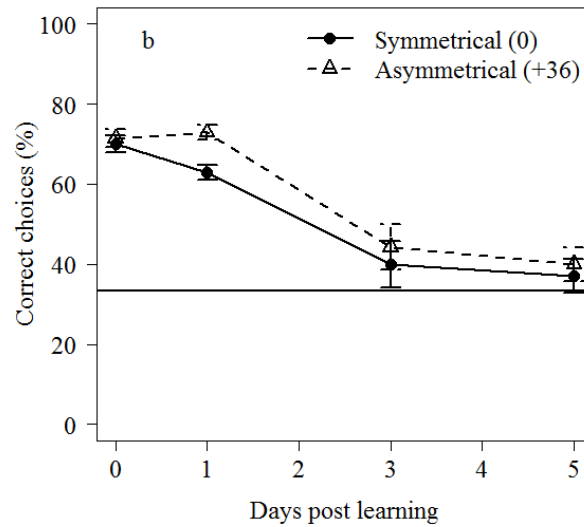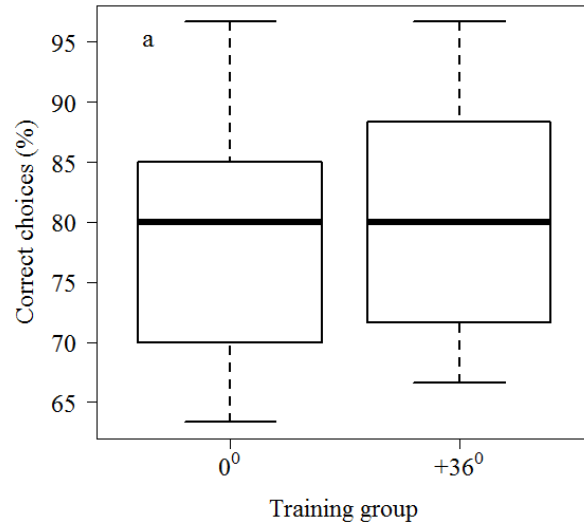
Figure 2.4 a) discrimination performance, given as the percentage of correct choices in the last thirty differential conditioning choices. Black horizontal lines indicate medians (N=28 per training group), boxes delimit the inter-quartile ranges, and whiskers show the ranges. No difference between training groups (2-sample t-test: t=-0.604, df=54, p=0.548). b) memory retention, given as the mean percentage of correct choices made over time ± SE. Solid line indicates chance level. N=56, 7 per time interval/training group. Retention was initially high, then memory degraded over time. (GLM: correct choices~time+training: time 'initial': z=3.583 p<0.001, time '1 day': z=3.315 p<0.001).

Effect of symmetry

Choices for the bilaterally symmetrical flower (0^0) were high both initially and twenty-four hours after training, but only in the group trained to the 0^0 (bilaterally symmetrical) flower (Fig 2.5). The relationship between the number of choices for the bilaterally symmetrical flower and time was significant (GLM, Poisson errors: model: symmetry~time*training, df=7, AIC=55.742), both at testing time points 'initial' (z=-2.962, p<0.001) and '1 day'(z=-3.125, p<0.001), with a significant interaction between training at time at those time points (time 'initial' and training 'symmetrical': z=3.900, p<0.001, time '1 day' and training 'symmetrical': z=3.776, p<0.001). Three days after training, the number of choices for the bilaterally symmetrical flower (0^0) were at approximately chance levels for both training groups: 0^0 (bilaterally symmetrical) and $+36^0$ (asymmetrical) (Fig 2.5) and this was not significant within the model (time '3 days': z=-0.846, p=0.397). No significant relationship between the number of choices for symmetry and training was shown (training 'symmetrical': z=-0.272 p=0.786). Additionally no significant interaction between time and training was shown from three days post learning (time '3 days' and training 'symmetrical': z=0.800, p=0.424). The model was not over-dispersed (theta<1) and the proportion of variance in the number of choices for symmetry explained by it were high. (pseudo-$R^2 \approx 1$).

For the group trained to the 0^0 (bilaterally symmetrical) flower, the average choice percentage for the bilaterally symmetrical flower (0^0) both initially and twenty-four hours after training was much higher than chance at 70% and 63% respectively (Fig. 2.6a). Three days after training, performance fell to near chance level (40%) (Fig 2.6a). For the group trained to the $+36^0$ (asymmetrical) flower, the average choice percentage for the flower bilaterally symmetrical with respect to vertical (0^0), both initially and

twenty-four hours after training was lower than chance at 13% and 11% respectively (Fig. 2.6b). Three days after training this rose to approximately chance level (31%) and then rose again slightly to just above chance level (37%) five days after training (Fig. 2.6b). Thus, any innate preference for symmetry did not in this case bias memory towards the flower bilaterally symmetrical with respect to vertical, with memory degrading such that all flower orientations were chosen at approximately chance levels after three days.
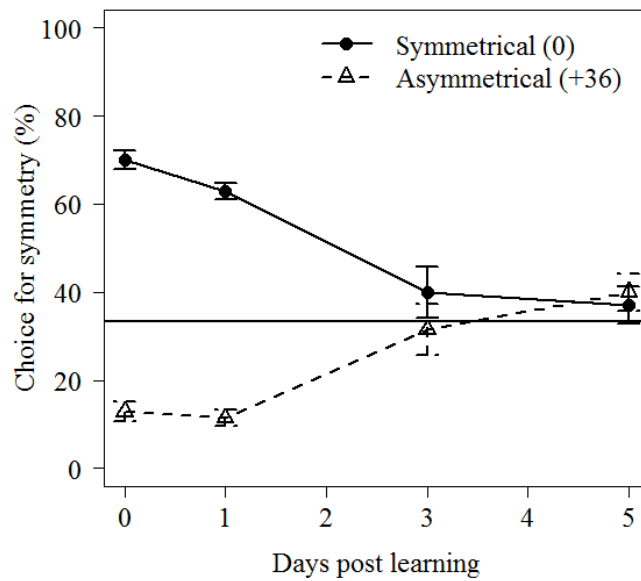
Figure 2.5 Effect of symmetry, given as the mean percentage of choices for the bilaterally symmetrical flower (0^0) made over time $\pm$ SE. Solid line indicates chance level. N=56, 7 per time interval/training group. Choice for symmetry was initially high, but only in bees trained to it, and then memory degraded over time, with no influence by the innate preference for symmetry seen. (GLM: symmetry~time*training: time 'initial' and training 'symmetrical': z=3.900, p<0.001, time '1 day' and training 'symmetrical': z=3.776, p<0.001).
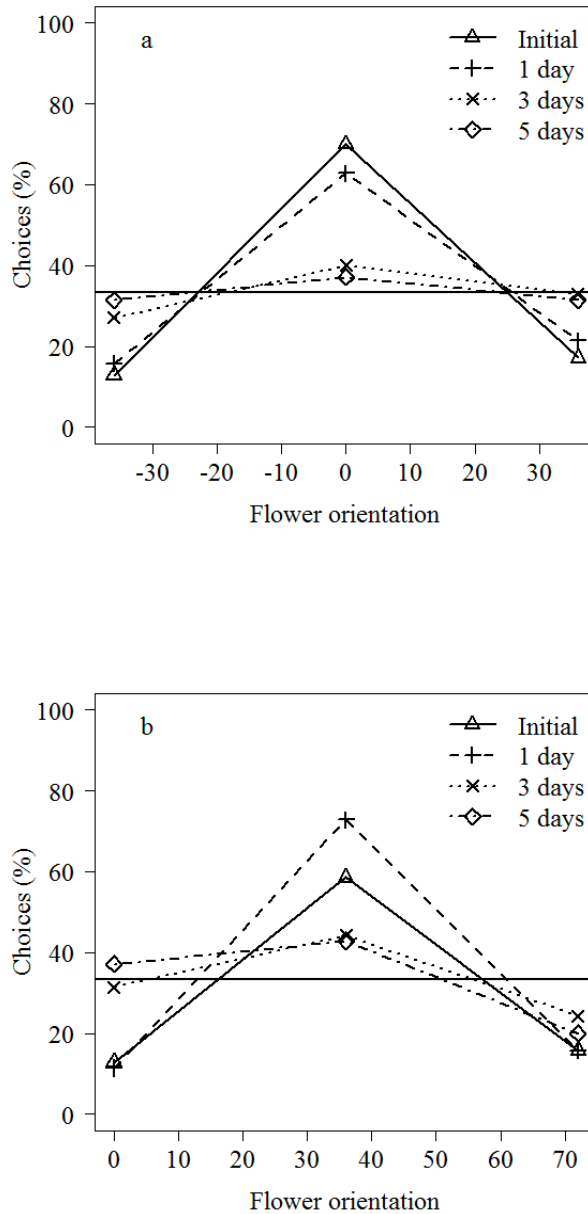
Figure 2.6 Orientation curves showing the mean percentage choices for each differentially oriented flower during the ten choice test at the four different testing time intervals. a) bees trained to 0^0 (bilaterally symmetrical flower) and b) bees trained to $+36^0$ (asymmetrical flower). Solid line indicates chance level. N=56: 7 per time interval/per training group. No influence by the innate preference for symmetry on memory degradation, with choices for all flowers around chance level three days after training.

2.32 Experiment B: What aspects of a learned artificial flower are retained in long-term memory?

No bees made any choices for the 'configuration' flowers during the test, thus this flower type was excluded from the analysis. The 'configuration' flower type was a different colour combination to the learnt flower type, but identical to it in terms of the spatial configuration of the colours within it (Fig. 2.3b).

There was no significant difference between the number of choices made for the learnt flower type: 0^0 (bilaterally symmetrical, with respect to vertical) ('correct') and the 'colour' flower type, which was identical in colour combination, but different in the spatial configuration of the colours presented to the learnt flower type (Wilcoxon rank sum test: w=59.5, p=0.401). 52% of the test ten test choices were for the learnt flower type: 0^0 (bilaterally symmetrical, with respect to vertical) ('correct') and 48% of the ten test choices were for the 'colour' flower type (Fig. 2.7). Thus, bees retain information pertaining to the colours present in a learnt flower type in long-term memory, but information pertaining to the specific configuration of the colours is forgotten more rapidly.
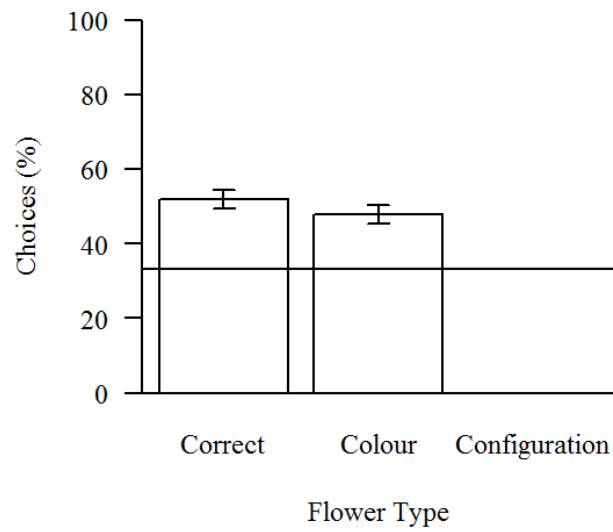
Figure 2.7 Choice accuracy, given as the mean percentage of choices made for each of the three flower types during the ten choice test ± SE, three days post training. Solid line indicates chance level, N=10. Both the learnt flower type ('correct') and the flower type with the learnt colour combination ('colour') were favoured, but with no difference between these two flower types (Wilcoxon rank sum test: w=59.5, p=0.401).

2.4 Discussion

My findings show that in the bumblebee *Bombus terrestris*, the innate preference for bilateral symmetry has no influence on the structure of memory decay. Bees trained on artificial flowers either bilaterally symmetrical or asymmetrical (with respect to vertical) show high levels of memory retention both initially and twenty-four hours after learning. General memory degradation, with all flowers being chosen at around chance level has occurred by the time three days have elapsed after learning.

Bumblebee memory does not therefore seem to be as susceptible to the potential influences/biases of known preferences in the same way as known associations, stereotypes or attitudes and expectations about the world can bias human memory (Bartlett, 1932, Loftus, 2005, Roediger and McDermott, 1995). Here I have shown that when presented with an artificial flower displaying features know to be innately preferred by bees (in this case bilateral symmetry, with respect to vertical), this innate bias does not interfere with the memory process, such that this is not picked with increased frequency, but that all testing flower types are picked with equal frequency, showing that memory simply degrades over time.

Furthermore my results show that different features of a learnt flower appear to be retained in memory for differing lengths of time. Bumblebees retained colour information (in this case yellow and blue) for longer than configurational information about the pattern features within the flower (in this case the specific orientation of the learnt flower and more generally the presence of a differentially coloured 45^0 sector within an otherwise solidly coloured flower). The bumblebees *Bombus ternarius*,

Bombus terricola (Heinrich et al., 1977), *Bombus bimaculatus* (Dukas and Real, 1991), *Bombus impatiens* and *Bombus occidentalis* (Chittka, 1998) have long been known to retain colour information at least overnight, and colour retention is also know to last several days in the honeybee *Apis mellifera* (Menzel, 1968). However there is also evidence that some pollinating insect species may retain configurational information in their long-term memory. The honeybee has been shown to successfully visually recognise and discriminate images of human faces, two days after training has ceased (Dyer et al., 2005). It is known that configural processing is utilised when solving the task (Avarguès-Weber et al., 2010). These studies did not however use both colour and configurational differences, and as such it is still largely unknown whether bees use a 'hierarchy' system when remembering different cues.

Additionally my findings do not show whether it is potentially a combination of colours that bees are able to hold in long-term memory, or whether it is simply the predominant colour of a learnt flower that is remembered. A follow-up study in which artificial flowers which present the colours from the learnt flowers separately during the test would be needed to clarify this point.

In nature, bees are often known to exhibit flower constancy, in which only one flower species (and as such colour and/or morphology) is visited for a period of time (Waser, 1986). It has been hypothesised that this constancy occurs due to temporal limitations on retrieving information from long-term memory compared to short-term memory, and the potential for more errors to occur when retrieving information about multiple items, as opposed to one (Chittka et al., 1999). Thus, flower constancy should increase as bees encounter flowers that are increasingly dissimilar in morphology or colour (Waser,

1986). Additionally bees are known to generalise to colours after learning, with the original test colour having a significant effect on the number of choices for new test colours, such that those most similar in colour to the learnt colour are chosen with the greatest frequency (Gumbert, 2000). Thus my finding that *Bombus terrestris* preferentially chooses test flowers that are the same colour combination as the originally learnt flower, over test flowers that are distinctly different colours, but in the same configuration as the originally learnt flower are not that surprising.

Overall, my result that memory in the bumblebee *Bombus terrestris* is not influenced by its innate preference for bilateral symmetry indicates that it may not be as susceptible to the inaccuracies of memory caused by known preferences in the way that human memory is. However the methodology used in this study is quite different from that administered in the classic human experiments and as such my results are not directly comparable. Conversely, there is some evidence that methodologies adapted from human false memory studies, for use with non-human animals, produce results that may be surprisingly comparable. Garry and Harper (2009) demonstrated that humans when tested using a methodology back-translated from a paradigm created to test the effect of postevent cues (akin to misinformation) in the pigeon *Columbia livia* and rat *Rattus norvegicus*, showed analogous results to those obtained using the classic verbal misinformation paradigms. Additionally, my findings do not exclude the possibility that the bumblebee may be susceptible to other types of memory inaccuracies seen in human memory. Other non-human animals have already been shown to be susceptible to postevent cues, which are akin to the misinformation effect that occurs in humans (Harper and Garry, 2000, Schwartz et al., 2004).

Chapter 3: The merging of long-term memories in the bumblebee

3.1 Introduction

The way in which animals (including humans) process sensory input and the ability to store it in memory and subsequently recall it to enable modification of behaviour appropriate to the current situation, has long been of interest. The degree to which memories for multiple inputs within the same sensory domain affect the recall of one another has been widely studied in humans, with much now known about interference theory (Dewar et al., 2007, Jonides and Nee, 2006), and the use of misinformation (Loftus, 1997, Loftus, 2005). Interference, in which memories compete for representational space, thereby interfering with each other, is known to occur in three forms: proactive, in which prior learnt information inhibits the recall of more recently learnt information (Keppel and Underwood, 1962), retroactive, in which newly learnt information impedes the recall of prior learnt information (Müller and Pilzecker, 1900) and output, in which the act of recalling information itself interferes with further retrieval of that information (Tulving and Arbuckle, 1966).

Such interference effects are known from across the animal kingdom, including in pollinating insects. For example, retroactive interference has been shown in the bumblebees *Bombus bimaculatus* (Woodward and Laverty, 1992), *Bombus impatiens* (Chittka and Thomson, 1997, Gegear and Laverty, 1995) and *Bombus occidentalis* (Chittka, 1998, Dukas, 1995). Additionally, proactive interference effects have been shown in the rat *Rattus norvegicus* (Dunnett and Martel, 1990) and both proactive and

retroactive interference effects shown in the pigeon *Columba livia* (Grant, 1975, Grant and Roberts, 1976).

However, some forms of interference between multiple memories have been studied almost exclusively in humans. One example is the *misinformation effect*, in which information given between memory encoding and recall and/or recognition distorts memory for the original information. Whilst this is similar to retroactive interference, the new information actually biases the previously stored memory, rather than resulting in its suppression (Loftus, 1975, McCloskey and Zaragoza, 1985) . Additionally humans are known to make predictable memory errors specific to the integration of multiple memories. The 'memory conjunction error', in which small pieces of information from multiple memories are combined to create a hybrid 'memory' comprising those pieces, has been shown to occur during the recognition of both nonsense words and pictures of faces and during the recall of simple sentences (Reinitz et al., 1992, Reinitz and Demb, 1994). For example participants who memorised a list of words including *barter* and *valley* subsequently mistakenly recognised the word *barley* (Rubin et al., 1999).

In animals the misinformation effect has been reported in only a handful of species. A gorilla (*Gorilla gorilla gorilla*; Schwartz et al., 2004) exhibited event memory biasing from misleading photographs, whilst postevent cues (akin to misinformation) have been shown to bias colour recognition in the pigeon (Harper and Garry, 2000) and lever selection in the rat (Garry and Harper, 2009).

Thus, compared to the vast knowledge about how multiple inputs affect the recall of one another in human memory, much less is known for non-human animals. In this chapter I explore whether a non-human animal, the bumblebee *Bombus terrestris*, is also potentially susceptible to memory 'merging' as occurs in human subjects. Specifically I ask whether in bumblebees, the memories for multiple leant items are combined, causing the erroneous choice of a hybrid item during recall and or/recognition, akin to the memory conjunction error that occurs in human memory (Reinitz et al., 1992, Reinitz and Demb, 1994, Rubin et al., 1999). I hypothesise that, as time passes after learning, the memory traces for visually distinct flower types may 'merge', such that visual features learnt in distinct training bouts are combined in the mind, so that a flower type that has never been viewed before, but is a combination of the features presented during training is mistakenly chosen. For this purpose I trained bees using a reversal learning paradigm to both a solid coloured artificial flower and a black and white patterned artificial flower and subsequently tested their memories for the learnt flowers at differing time intervals, including a hybrid flower comprised of a combination of both the main features of the learnt flowers: colour and concentric circle patterning, as a critical lure to potentially bias memory. Additionally, I tested a sub-set of bees that had been trained to a black and white patterned artificial flower, whose pattern was different to the pattern presented in the hybrid flower, to confirm that any 'merging' is not simply a generalisation to either of the individual training features: colour or pattern. My findings indicate that the bumblebee, when required to utilise its long-term memory, commits an error in which information from multiple memory traces 'merge'. Furthermore my results show that this is a genuine 'merging' of memories and not more simply a generalisation to a single learnt feature.

3.2 Materials and Methods

Subjects

Bees were from four commercially obtained colonies of *Bombus terrestris* (Syngenta Bioline Bees, Weert, The Netherlands), and were housed in bipartite wooden nest boxes (28cmx16cmx11cm). Bees were individually marked on the thorax with coloured, numbered markers (Opalith tags, Christian Graze KG, Germany) to allow identification. A differing number of bees were used from each colony and each colony was utilised for a different length of time (colony/N/time: KM0/N=8/12 days, KM1/N=14/24 days, KM2/N=13/19 days, KM3/N=10/6 days). Prior to experimentation bees were kept naive with no exposure to coloured or patterned artificial flowers given in association with food. Colonies were provided ad libitum with defrosted pollen (Koppert BV, Berkel en Rodenrijs, The Netherlands) directly into the nest and any extra feeding required in addition to the products of the experimental foraging was with 30% sucrose solution (v/v) provided directly into colonies' honey pots.

Set-up

Experiments were undertaken in a wooden flight arena (l00cmx71cmx71cm), with a transparent UV-transmitting Plexiglas™ lid, into which access was provided by means of a transparent Plexiglas™ tube. Shutters along the length of the tube enabled the traffic of bees into and out of the arena to be controlled. During experimentation artificial flowers were presented vertically on the far wall of the flight arena (Fig. 3.1), so that their appearance was independent of the bees' approach direction.

Artificial flowers

All artificial flowers were circular (Ø=7cm) with transparent Perspex™ landing platforms (1.5cmx1.5cmx1cm) connected to and placed directly in from of them. Each platform had a central well (Ø=0.6cm, depth=0.2cm), into which the experimenter could place droplets of sucrose or water (Fig. 3.2). Additionally each artificial flower contained a central hole (Ø=0.5cm) positioned directly above the landing platform, which enabled the experimenter to replenish rewards by means of a pipette from outside of the arena.

3.21 Experiment A: Do memories for two visually distinct artificial flowers merge?

Pre-training

Eight white coloured, black rimmed artificial flowers (Table 3.1) were randomly assigned to positions on the presentation wall and each was rewarded with a 20µl droplet of 50% sucrose solution (v/v) (Fig. 3.1a). Bees were allowed to forage freely on the flowers and all rewards were replenished once they had been consumed, and bees had departed from that flower. This allowed bees to become used to the flight arena foraging scenario, familiarise themselves with foraging on the artificial flowers and enable the determination of individuals that would successfully forage for a minimum of three consecutive foraging bouts who were therefore suitable for further testing. A reversal learning paradigm was then administered to create conflict between two visually distinct flower types in the bees' memories.
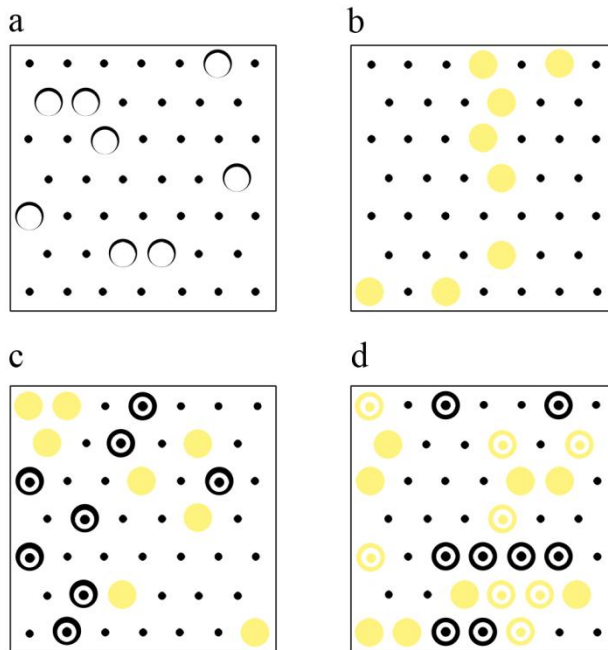
Figure 3.1 Artificial flower presentation wall showing all potential flower presentation positions possible, represented by black dots and example flower randomisations showing a) pre-training flowers, b) absolute conditioning (for training group 'colour'), c) differential conditioning and d) testing.
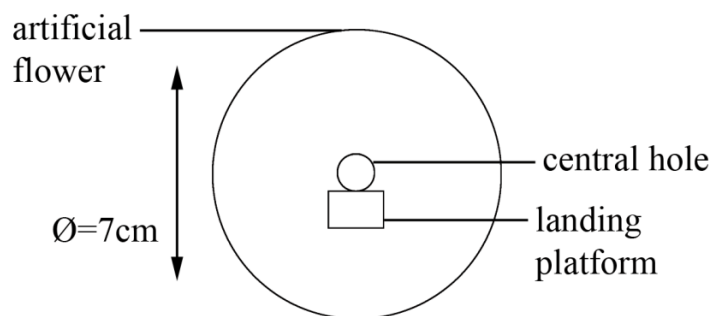
Figure 3.2 Example artificial flower (Ø=7cm), showing central hole (Ø=5cm) to enable the experimenter to insert a reward droplet from outside the arena by means of an electronic pipette. Beneath the hole in front of the artificial flower target, a Perspex™ landing platform (1.5cmx1.5cmx1cm) is attached.

Table 3.1 Artificial flower colour information: Spectrophotometer measurements (hue, brightness, saturation and UV reflectivity) for all artificial flower colours used.

Colour	Hue	Brightness	Saturation	UV Reflectivity
White	Blue-Green	1.679	0.232	0.417
Black	Uncoloured	0.156	0.013	0.048
Yellow	Green	0.571	0.367	0.063

Absolute Conditioning

Either eight yellow coloured artificial flowers (C) (Table 3.1) (Fig. 3.3), or eight black and white artificial flowers patterned with concentric circles (BW-r) (Table 3.1) (Fig. 3.3) were randomly assigned to positions on the presentation wall and each was rewarded with a 20µl droplet of 50% sucrose solution (v/v) (Fig. 3.1b). Bees were randomly assigned to one of two training groups: 'colour' or 'black and white' (N=15 per group), which signified which flower type the bee would be trained to first: C for 'colour' and BW-r for 'black and white'. Three foraging bouts were completed by subjects and each individual bee's satiation volume was determined from this training phase, to enable suitable reward volumes to be administered during differential conditioning. Bees were allowed to return to the nest box and empty their crops between foraging bouts, during which time the randomly allocated positions of the flowers were changed to prevent positional learning. Additionally all landing platforms were cleaned with 70% ethanol to remove any scent marks left by the bees. All bees were trained individually.

Differential Conditioning

Sixteen artificial flowers were again randomly assigned to positions on the presentation wall (Fig. 3.1c). For those bees being trained to 'colour' (C), eight of the flowers were yellow coloured which were rewarded with a droplet of 50% sucrose (v/v) (volumes adjusted for each bee, using the satiation volumes determined by absolute conditioning) and eight of the flowers were black and white patterned with concentric circles (BW-r), which were unrewarded (empty). For those bees being trained to 'black and white' (BW-r), eight of the flowers were black and white patterned with concentric circles which were rewarded with a droplet of 50% sucrose (v/v) (again, volumes adjusted for

each bee, using the satiation volumes determined by absolute conditioning) and eight of the flowers were yellow coloured, which were unrewarded (empty). Each bee was allowed to forage until one hundred choices had been made. The definition for a 'choice' was the landing of the bee upon the landing platform of an artificial flower. Again, bees were trained individually and allowed to return to the nest box and empty their crops between foraging bouts. Whilst bees were in the nest, the randomly allocated positions of the flowers were changed to prevent positional learning and all landing platforms were cleaned with 70% ethanol to remove any scent marks left by the bees.

For those bees showing a number of correct choices within their last twenty differential conditioning training choices statistically greater than chance (χ^2: $p<0.05$), both absolute and differential conditioning were then repeated, but with the rewarded and unrewarded flower types reversed, such that those bees initially trained to and rewarded upon the yellow coloured flowers (C) were then trained to and rewarded upon the black and white flowers patterned with concentric circles (BW-r) and vice versa.
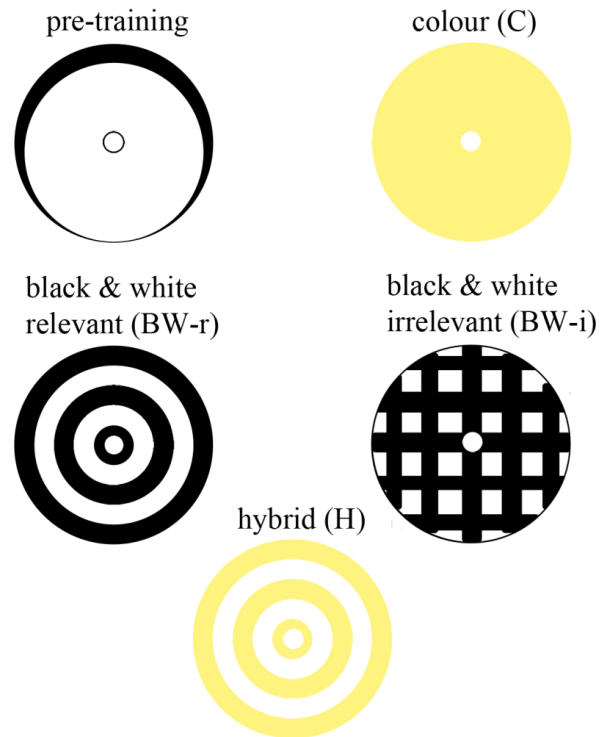
Figure 3.3 Artificial flowers: training and testing flowers. The hybrid flower (H) comprises a combination of the features from the flowers 'colour' (C) and 'black and white relevant' (BW-r), such that both the colour (yellow) and the pattern (concentric circles) are presented in it. The pattern in the 'black and white irrelevant' flower (BW-i) is not presented in the hybrid flower (H).

Testing

Only bees that successfully completed training were subsequently tested. Individuals were classified as successful if the number of correct choices within the last twenty choices of their second differential conditioning training was statistically greater than chance (χ^2: $p<0.05$). Each bee was randomly assigned to one of three testing time intervals: immediately, twenty-four hours post training or three days post training, such that each bee was only tested at one of the three possible time intervals and that an even number of bees from each training group ('colour' and 'black and white') were tested at each of the three time intervals (per time interval N=10, per training group and time interval combined N=5). These testing time intervals allowed both short-term and long-term memory to be studied. The same eight yellow coloured artificial flowers (C) and eight black and white artificial flowers patterned with concentric circles (BW-r) used in the differential conditioning training were again randomly assigned to positions on the presentation wall (Fig. 3.1d), as well as eight of a hybrid flower (H) (Fig. 3.3). The hybrid flowers (H) comprised a combination of the features from the two different flower types presented during differential training: colour (C) and black and white patterned with concentric circles (BW-r), such that both the colour (yellow) and the pattern (concentric circles) were presented in it. All flowers were unrewarded, but were provided with a 20µl droplet of water to visually encourage foraging. One foraging bout was given and the first twenty choices were recorded.

3.22 Experiment B: Does generalisation or merging occur?

To confirm that memory merging really occurs rather than a generalisation to either of the flower features (colour or concentric circle patterning) the experimental procedure was modified to include a training group using a black and white flower showing a pattern irrelevant to that displayed in the hybrid flower. Pre-training was undertaken in an identical fashion to that described above. Again, a reversal learning paradigm was then administered to create conflict between two visually distinct flower types in the bees' memories.

Absolute Conditioning

The procedure for absolute conditioning described above was repeated, but with the following modifications of the artificial flower patterns. Either eight black and white artificial flowers patterned with concentric circles (BW-r), (Fig. 3.3) or eight black and white artificial flowers patterned with horizontal and vertical lines in a grid structure (BW-i) (Fig. 3.3) were presented. Bees were randomly assigned to one of two training groups: 'relevant black and white pattern' or 'irrelevant black and white pattern' (N=10 per group), which signified which flower type the bee would be trained to first: BW-r for 'relevant black and white' and BW-i for 'irrelevant black and white' and also whether the pattern used in the training flower type was relevant to the pattern used in the hybrid flower to be used in testing.

Differential Conditioning

The procedure for differential conditioning described above was repeated, but with the following flower modifications. Sixteen artificial flowers were again randomly assigned to positions on the presentation wall. For those bees being trained to 'relevant black and white pattern' (BW-r), eight of the flowers were black and white patterned with concentric circles which were rewarded with a droplet of 50% sucrose (v/v) (volumes adjusted for each bee, using the satiation volumes determined by absolute conditioning) and eight of the flowers were yellow coloured (C), which were unrewarded (empty). For those bees being trained to 'irrelevant black and white pattern' (BW-i), eight of the flowers were black and white with horizontal and vertical lines in a grid structure (BW-i) which were rewarded with a droplet of 50% sucrose (v/v) (again, volumes adjusted for each bee, using the satiation volumes determined by absolute conditioning) and eight of the flowers were yellow coloured (C), which were unrewarded (empty).

Again, for those bees showing a number of correct choices within their last twenty differential conditioning training choices statistically greater than chance (χ^2: $p<0.05$), both absolute and differential conditioning were then repeated, but with the rewarded and unrewarded flower types reversed, such that those bees initially trained to and rewarded upon both types of black and white patterned flowers (BW-r and BW-i) were then trained to and rewarded upon the yellow coloured flower (C).

Testing

The procedure for testing described above was repeated, but with the following modifications. All bees were tested twenty-four hours post training as Experiment A showed this to be a testing time interval of interest. Twenty-four artificial flowers were presented. For those bees that had been trained to the 'relevant black and white pattern' (BW-r), the same eight yellow coloured flowers (C) and eight black and white flowers patterned with concentric circles (BW-r) used in the differential conditioning training were presented, as well as eight of the hybrid flower (H). In this scenario the hybrid flower type was indeed comprised of a combination of the two features of the training flower types: yellow colour and concentric circles. For those bees that had been trained to the 'irrelevant black and white pattern' (BW-i), the same eight yellow coloured flowers (C) and eight black and white flowers patterned with horizontal and vertical lines in a grid structure (BW-r) used in the differential conditioning training were presented, as well as eight of the hybrid flower (H). In this scenario the hybrid flower type was not comprised of a combination of the two features of the training flower types, but only one: yellow colour.

Data Analysis

The numbers of choices for all different flower types displayed during testing were calculated for each individual, in training group, at each testing time interval, to analyse memory retention and the potential occurrence of memory merging. A generalised linear model with Poisson errors was used to test whether the pooled number of choices for the last rewarded flower type (N=5) (the dependent variable) could be explained by time and/or training (the independent variables). Model selection and validation using AIC and/or theta values was undertaken and a pseudo-R^2 value was calculated to check the explanatory power of the model. A further generalised linear model with Poisson errors was used to test whether the pooled number of choices for the hybrid flower type (N=5) (the dependent variable) could be explained by time and/or training (the independent variables). Again, model selection, validation and an evaluation of the model's power were undertaken. Additionally the data were separated into the numbers of choices for all flower types made during the first half of the test (first ten choices) and the second half of the test (second ten choices), as the test length was over double the number of possible 'correct' choices that could be made. These data were used to analyse genuine memory 'merging' over generalisation. Two 2-sample t-tests were used to test whether the numbers of choices for both the last rewarded flower type and the hybrid flower type were significantly different between the group trained to the relevant black and white pattern and the group trained to the irrelevant black and white pattern. A further 2-sample t-test was used to test whether the difference in the number of choices for the hybrid flower type, between the first ten and second ten choices of the twenty choice test, was significantly different between these too training groups. All data were also converted to give average percentages to display graphically. All analyses were carried out using R statistical software (v.2.14.1).

3.3 Results

3.31 Experiment A: Do memories for two visually distinct artificial flowers merge?

Memory Retention

Memory for the last rewarded flower type was initially high for both training groups (C then BW-r and BW-r then C). Twenty-four hours after training it then fell considerably, again in both training groups, followed by a slight rise again at three days post training (retention is given as the number of choices for the last rewarded flower type out of twenty test choices made at one of three time intervals) (Fig. 3.4). The relationship between the number of choices for the last rewarded flower type and time was significant (GLM, Poisson errors: final model: choice for last rewarded~time+training, df=5, AIC=42.586), both at testing time points '1 day' (z=-4.045, p<0.001) and '3 days' (z=-4.045, p<0.001). No significant relationship between the number of choices for the last rewarded flower type and training was shown (training 'C then BW-r' z=0.410, p=0.682). Additionally there was no significant interaction between time and training (initial model: choice for last rewarded~time*training, AIC=46.097, Chi backwards stepwise deletion: time:training: AIC=42.586, p=0.783), therefore this was removed from the model. The final model was not over-dispersed (theta<1) and the proportion of variance in the number of choices for the last rewarded flower type explained by it were high (pseudo-R^2=0.980). Overall, there was a general trend of a decrease in the number of choices for the last rewarded flower type over time, for both training groups, showing that memory decay occurs. However the amount of memory decay was different between the training groups, with a greater decay shown by those bees trained to the relevant black and white flower type (BW-r) first and greater memory retention shown by those bees trained to the colour flower type (C) first (Fig 3.4).

For the group trained to the colour flower type (C) first, the average choice percentage was highest for the last rewarded flower type: relevant black and white (BW-r) at all three time intervals – 68% initially, 42% twenty-four hours after training and 49% three days after training (Fig. 3.4). Thus at all three time intervals, memory retention was high and the effects of retroactive interference were seen (secondary information, in this case the black and white relevant flower type (BW-r) impeded the recall of prior learnt information, in this case colour (C)). For the group trained to the relevant black and white flower type (BW-r) first, the average choice percentage was highest for the last rewarded flower type: colour (C), only initially (69%) (Fig. 3.4). Twenty-four hours and three days after training it had fallen to just above chance at 35% and 38% (Fig. 3.4). Thus memory retention was only initially high, again with the effects of retroactive interference seen.

Figure 3.4 Memory retention, given as the mean percentage of choices for the last rewarded flower types made over time ± SE. Solid line indicates chance level. N=30, 5 per time interval/training group. Retention was initially high, and then memory degraded over time. Although decay was greatest in those bees trained to the relevant black and white flower type (BW-r) first, whilst retention was greatest in those bees trained to the colour flower type (C) first (GLM: correct choices for last rewarded~time+training: time '1 day': z=-4.045 p<0.001, time '3 days': z=-4.045 p<0.001).

Memory 'Merging'

Choices for the hybrid flower type were initially low for both training groups (C then BW-r and BW-r then C). Twenty-four hours after training they rose, again in both training groups, but more considerably in those bees trained to the relevant black and white flower type (BW-r) first. Three days post training the rise remained, only in those bees trained to the relevant black and white flower type (BW-r) first, with choices for the hybrid flower type falling again in those bees trained to the colour flower type (C) first (merging is given as the number of choices for the hybrid flower type out of twenty test choices made at one of three time intervals) (Fig. 3.5). The relationship between the number of choices for hybrid flower type and time was significant (GLM, Poisson errors: final model: choice for hybrid~time+training, df=5, AIC=39.713), both at testing time points '1 day' (z=3.382, p<0.001) and '3 days' (z=2.697, p=0.007). Additionally, a significant relationship between the number of choices for the hybrid flower type and training was shown (training 'C then BW-r' z=-2.505, p=0.012). Furthermore, there was no significant interaction between time and training (initial model: choice for hybrid~time*training, AIC=43.563, Chi backwards stepwise deletion: time:training: AIC=39.713, p=0.928), therefore this was removed from the model. The final model was not over-dispersed (theta<1) and the proportion of variance in the number of choices for the last rewarded flower type explained by it were high (pseudo-R^2=0.992). Overall, there was a general trend of an increase in the number of choices for the hybrid flower type over time, for both training groups (Fig 3.5). However memory 'merging' only occurred in those bees trained to the relevant black and white flower type (BW-r) first, and only when long-term memory was utilised (Fig 3.5).
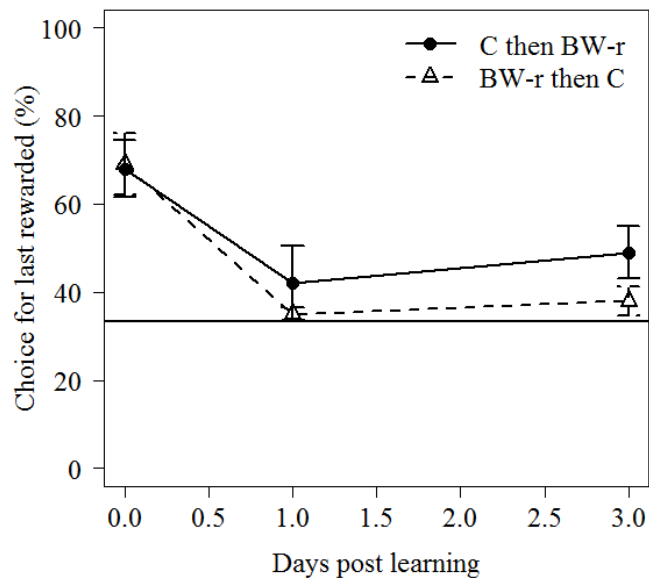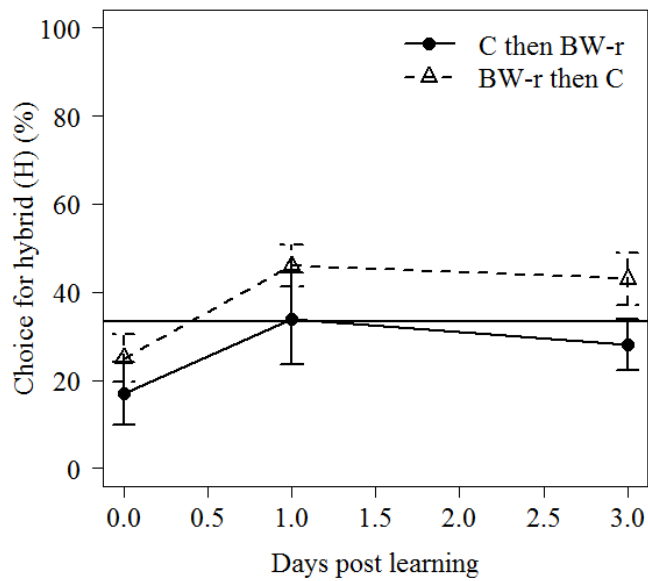
Figure 3.5 Memory 'merging', given as the mean percentage of choices for the hybrid flower type made over time ± SE. Solid line indicates chance level. N=30, 5 per time interval/training group. Merging occurred at 1 day and 3 days post training, but only in those bees trained to the relevant black and white flower type (BW-r) first (GLM: choices for hybrid~time+training: time '1 day': z=-3.382 p<0.001, time '3 days': z=-42.697 p=0.007).

For the group trained to the colour flower type (C) first, twenty four hours after training the mean percentage choice for the last rewarded flower type: relevant black and white (BW-r) was just above chance (36%, where chance expectation would have been 33.33%) for the first half of the test (first ten choices) (Fig. 3.6a), but rose to 64% during the second half of the test (second ten choices) (Fig. 3.6a). The mean percentage choice for the hybrid flower type (H) was at approximately chance level (34%) during the first half of the test (first ten choices) (Fig. 3.6a), and fell to below chance 18% for the second half of the test (second ten choices) (Fig. 3.6a). Three days after training, the mean choice percentage for the last rewarded flower type: relevant black and white (BW-r) was above chance level throughout the test (mean = 42% & 56%) (Fig. 3.7a). Conversely, the mean percentage choice for the hybrid flower type (H) was below chance level throughout the test (mean = 23% & 30%) (Fig. 3.7a).

For the group trained to the relevant black and white pattern flower type (BW-r) first, twenty four hours after training the mean percentage choice for the last rewarded flower type: colour (C) was above chance (48%) for the first half of the test (first ten choices) (Fig 3.6b) but below chance (22%) during the second half of the test (second ten choices) (Fig. 3.6b). Conversely, the mean percentage choice for the hybrid flower type (H) was at approximately chance level (32%) during the first half of the test (first ten choices) (Fig. 3.6b), but above chance (52%) for the second half of the test (second ten choices) (Fig. 3.6b). Three days after training the same trend was seen: last rewarded flower type: colour (C): mean = 52% & 24% (Fig. 3.7b), hybrid flower type (H): mean = 34% & 52% (Fig. 3.7b). Thus the above result of the occurrence of memory 'merging' stemmed from the switch in choices from the last reward flower type to the hybrid flower type over the course of the test.
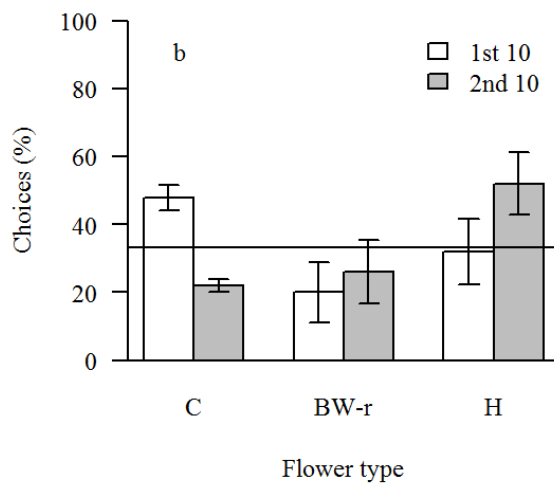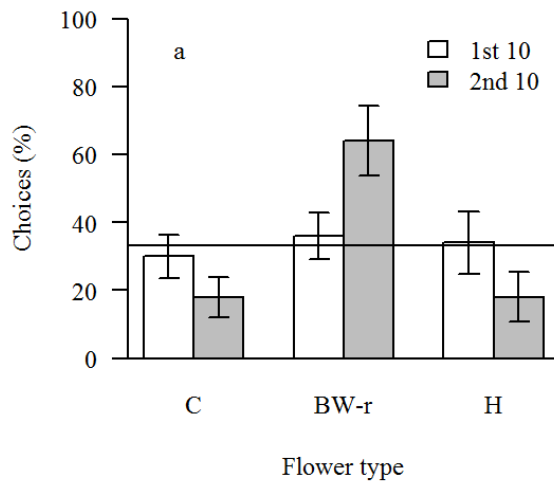
Figure 3.6 Mean choice percentages ± SE twenty-four hours after training, split for the first ten and second ten choices of the twenty choice test for a) bees trained to the colour flower type (C) first and b) bees trained to the relevant black and white flower type (BW-r) first. N=5, solid line indicates chance level. Bees switched choices from for the last rewarded flower type: colour (C) to the hybrid flower type (H), but only bees trained to the relevant black and white flower type (BW-r) first.
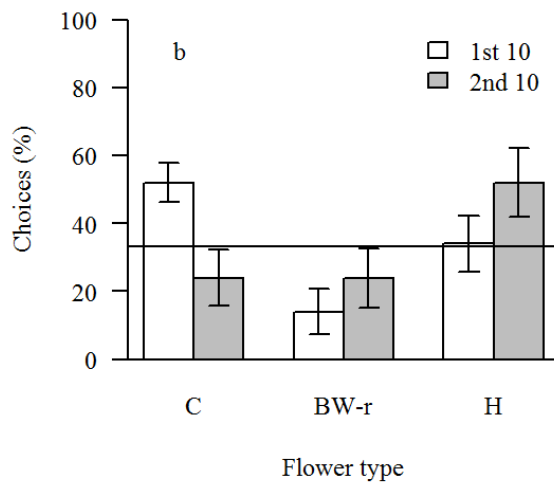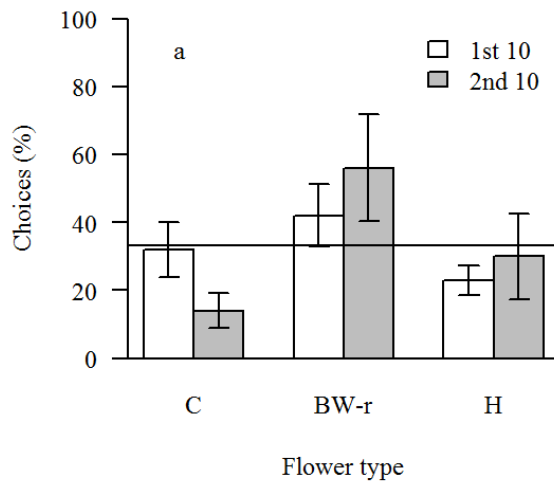
Figure 3.7 Mean choice percentages ± SE three days after training, split for the first ten and second ten choices of the twenty choice test for a) bees trained to the colour flower type (C) first and b) bees trained to relevant black and white flower type (BW-r) first. N=5, solid line indicates chance level. Bees switched choices from for the last rewarded flower type: colour (C) to the hybrid flower type (H), but only bees trained to the relevant black and white flower type (BW-r) first.

3.32 Experiment B: Does generalisation or merging occur?

There was a significant difference in the number of choices made for the last rewarded flower type: colour (C), between the two training groups: relevant black and white pattern (BW-r) and irrelevant black and white pattern (BW-i) (Welch 2-sample t-test: t=-3.881, df=10.378, p=0.003). Additionally, there was a significant difference in the number of choices made for the hybrid flower type (H) between the two training groups: relevant black and white pattern (BW-r) and irrelevant black and white pattern (BW-i) (2-sample t-test: t=2.416, df=18, p=0.027).

For the group trained to the irrelevant black and white flower type (BW-i), the average choice percentage was highest for the last rewarded flower type: colour (C) (57%), with choices for the hybrid flower type (H) being low (27.5%) (Fig 3.8a). For the group trained to the relevant black and white flower type (BW-r), the average choice percentage was similar for both the hybrid flower type (H) (38.5%) and the last rewarded flower type: colour (C) (37.5%) (Fig 3.8b). Thus, memory 'merging' only occurred in those bees trained to the relevant black and white flower type (BW-r) when long-term memory was utilised. This result therefore supports a genuine 'merging' of information (also found in Experiment A), rather than a generalisation to a single visual feature.
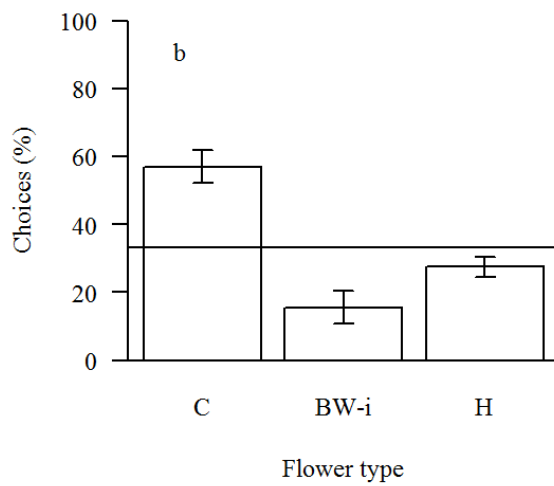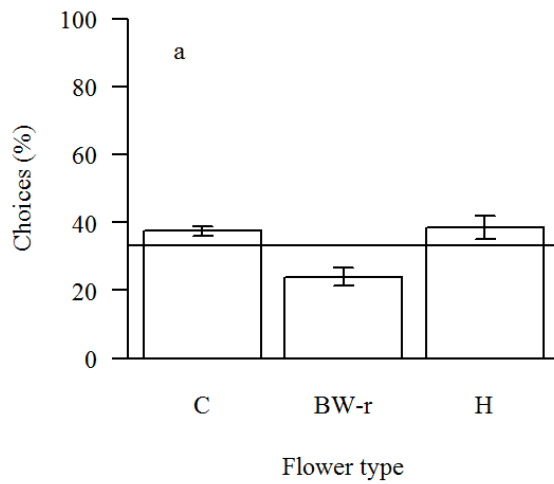
Figure 3.8 Mean choice percentages ± SE twenty-four hours after training for a) bees trained to the relevant black and white flower type (BW-r) first and b) bees trained to the irrelevant black and white flower type (BW-i) first. N=10, solid line indicates chance level. Memory merging, not generalisation occurred as bees favoured the 'hybrid' (H) flower type but only bees trained to the relevant black and white flower type (BW-r) first.

There was a significant difference in the number of choices made for the hybrid flower type (H) between the first ten and second ten choices of the twenty choice test, between the two training groups: relevant black and white (BW-r) and irrelevant black and white (BW-i) (2-sample t-test: t=-2.689, df=18, p=0.015, Fig 3.9). The median choice percentage difference (first ten choices– second ten choices) for the hybrid flower type (H), for the relevant black and white (BW-r) training group was -20% (Fig. 3.9). This was due to an increase in choices for the hybrid flower type (H), at the expense of the number of choices for the last rewarded flower type: colour (C) over the course of the test (Fig 3.10a). Conversely, the median percentage choice difference (first ten choices– second ten choices) for the hybrid flower type (H), for the irrelevant black and white (BW-i) training group was 0 (Fig. 3.9), thus no increase in choices for the hybrid flower type (H) occurred over the course of the test (Fig. 3.10b). As such, the results again support the earlier findings of the occurrence of memory 'merging' when long-term memory is utilised, rather than a generalisation and that the merging stemmed from a switch in choices from the last rewarded flower type to the hybrid flower type over the course of the test.
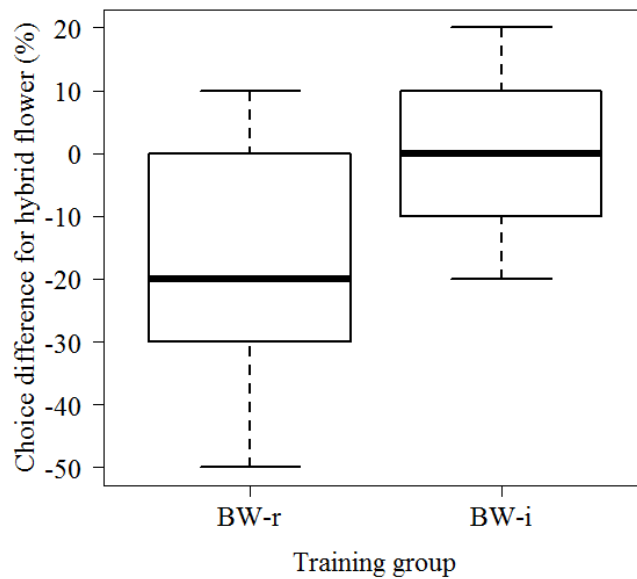
Figure 3.9 Difference in choice percentages for the hybrid flower (H) (first ten test choices − second ten test choices), split by the relevance of the training pattern (BW-r or BW-i) to the hybrid flower (H). Thick black horizontal lines indicate medians (N=10 per training group), boxes delimit the inter-quartile ranges, and whiskers show the ranges. A significant difference between training groups was found (2-sample t-test: t=-2.689, df=18, p=0.015). Bees trained to the relevant black and white flower type (BW-r) increased their choices for the hybrid flower type (H) over the test, whilst bees trained to irrelevant black and white flower type (BW-i) showed few choices for the hybrid flower type (H) throughout the test.
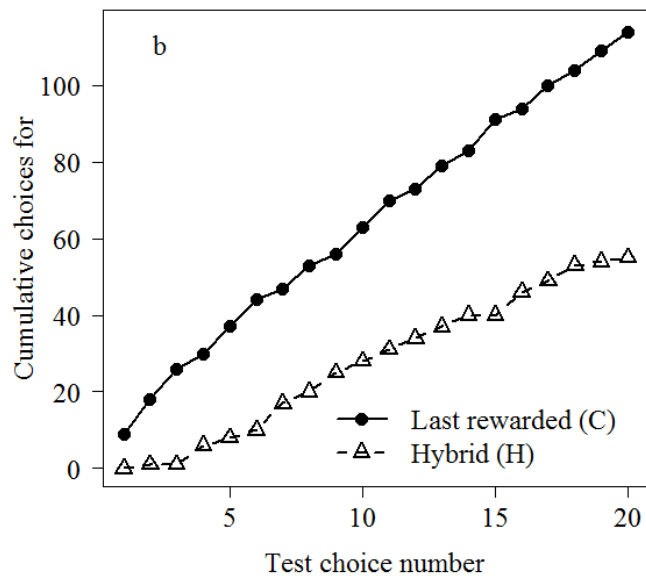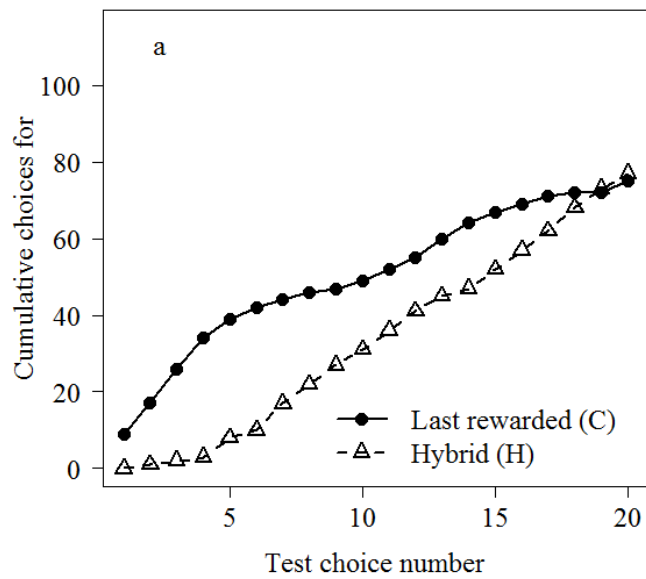
Figure 3.10 Pooled cumulative choices (N=10) for both the last rewarded flower type (C) and the hybrid flower type (H) over the course of the twenty choice test. a) bees trained to the relevant black and white flower type (BW-r) first and b) bees trained to the irrelevant black and white flower type (BW-i) first. Only bees trained to the relevant black and white flower type (BW-r) increased their choices for the hybrid flower type (H) at the expense of their choices for the last rewarded flower type, over the test.

3.4 Discussion

My findings show that in the bumblebee *Bombus terrestris* memory 'merging' occurs, whereby multiple memory traces combine, causing inaccuracy of memory. Bees trained on two visually distinct artificial flower types, solid colour and black and white patterned, show high levels of memory retention initially, but twenty-four hours after learning erroneously choose a hybrid flower that comprises a combination of the two learnt visual features: colour and pattern.

Bumblebee memory therefore seems to be susceptible to an error specific to the integration of multiple memories in a similar way as human memory does in certain experimental settings. The 'memory conjunction error' in which partial information from multiple memories are combined to create a 'hybrid memory' containing elements of multiple memories is known to effect human memory for pictures of faces, nonsense words and simple sentences (Reinitz et al., 1992, Reinitz and Demb, 1994). Here I have shown that, when presented with an artificial flower displaying a combination of features previously learnt, bees mistakenly select this, rather than either memory retention remaining high with the learnt flower types being selected above chance, or memory simply degrading over time with all flower types picked equally.

Additionally, my results show that this 'merging' is the result of a genuine confusion of the information from the memory traces of both training flower types and not just due to a generalisation to the training colour. When a different, non-relevant black and white pattern was used in training, but the original hybrid flower type was displayed in the test, bees selected only the last rewarded stimulus: colour with the highest frequency.

However, this 'merging' also appears dependent upon the order in which the different artificial flower types are learnt. When a black and white patterned flower is last rewarded, this is remembered at the expense of the first rewarded flower type: solid colour, and is retained in memory for three days after learning. This is an expected outcome when retroactive interference is in effect (Müller and Pilzecker, 1900). In retroactive interference, newly learnt information impedes the recall of prior learnt information and it is thought that this occurs due to competition between the two memories, rather than the overwriting of the original memory by the new one (Briggs, 1954). As a result retroactive interference increases when both the stimuli to be learnt and both the responses required to solve the tasks show similarity (Anderson and Myrow, 1971). Recently it has been shown that in the honeybee *Apis mellifera* retroactive interference does indeed occur in landmark learning tasks due to response competition. Cheng and Wignall (2006) found that if the two learnt tasks had conflicting response requirements, in which task one required the bee to turn right at a green landmark and task two required the bee to turn left at a blue landmark, then the effect of retroactive interference when re-attempting task one were pronounced. In opposition they found that when response competition was minimised during either training and/or testing the effect of retroactive interference were either greatly diminished, or even completely eradicated (Cheng and Wignall, 2006).

Conversely, when a solid coloured flower is last rewarded, twenty-four hours after learning, memory 'merging' occurs. This is a curious finding and highlights the potential importance of the order of artificial flower presentation in a reversal learning paradigm for both experimental design and data interpretation. Additionally, it may have implications about the strengths of memory traces for differing artificial flower types: colours vs. patterns. In the honeybees, it is known that colour learning takes

fewer trials (1-5) than does the learning of black and white patterns (5+ trials) (Menzel, 2009). It may be that the memory traces for the black and white patterned flower type were stronger than for the colour flower type, and as such were more resistant to both degradation and manipulation. In humans it is known that stronger memory traces are less prone to the effects of suggestibility (Pezdek and Roe, 1995). However memory strength is known to increase with the frequency of the presentation of the item to be remembered (Ebbinghaus, 1964). In this study all bees made the same number of learning choices for both the black and white patterned flower type and the colour flower type, thus although the absolute number of 'looks' at both the flower types during learning, nor the absolute time taken to learn the two flower types were recorded, all bees would have encountered each of the two flower types with approximately the same frequency.

Furthermore, memory 'merging' appears to occur as a result of a switching of choices from the last rewarded flower, to the hybrid flower type, over the course of the test. Thus, once bees discover that the last rewarded flower type is no longer rewarded, 'merging' occurs. It is therefore possible that such 'merging' may occur as cognitive demand increases, when bees are forced to recall an earlier memory almost concurrently to the more recently formed memory, due to a change in a previously learnt 'rule'. Specifically in this study the test was twenty choices in length, but only eight flowers of the last rewarded flower type were presented. Thus, after eight previously 'correct' choices, a bee will have discovered that the once 'correct' flower type is no longer so, and may try to adjust its behaviour accordingly, incurring increased cognitive demands.

One potential explanation for the formation of the memory conjunction error is that the failure occurs at retrieval (Rubin et al., 1999) and involves '*processing fluency*' (Jacoby, 1991). In this argument, during recall or recognition source monitoring, which is the set of processes that make attributions about memory origins (Johnson, 1988, Johnson et al., 1993) is low and as a result a misattribution occurs due to 'remembering' on the basis of the feeling of familiarity (Rubin et al., 1999). These 'memories' are therefore based not on the recollections of the specific details of items to be recalled/recognised, but on a more general feature that not only applies to the items to be recalled but also to other items, which results in their erroneous retrieval. It is known that human memory utilises the cognitive processes of categorisation and generalisation, in which a large number or items can be stored and recalled based on just a few exemplars, in order to economise and gain efficiency (Chittka and Niven, 2009, McClelland, 1995). Schacter (1999, 2001) proposed that memory errors caused by misattribution (one of which is the memory conjunction error) may therefore simply be inevitable by-products of this adaptive cognitive ability to form general concepts. Many non-human animal species can also generalise, categorise and potentially even form concepts (Chittka and Jensen, 2011), with much research showing that the honeybee is one such species (Avarguès-Weber et al., 2011, Giurfa et al., 1996, Wright et al., 2008, Zhang et al., 2004). It is perhaps therefore not so surprising that my findings show the occurrence of a misattribution error in a pollinating insect.

Overall, my result that the bumblebee *Bombus terrestris*, when required to utilise its long-term memory for multiple visual targets that had previously been rewarding, commits an error in which information from multiple memory traces 'merge' is akin to the memory conjunction error seen in humans (Reinitz et al., 1992, Reinitz and Demb,

1994, Rubin et al., 1999), and is the first example of memory 'merging' in a non-human animal.

Chapter 4: Postevent cues: Are bees susceptible to the 'misinformation effect'?

4.1 Introduction

The 'misinformation effect' is a commonly used methodology and term for the production of false memories in humans. Misleading information given between memory encoding and recall biases memory in the direction of the misinformation (Loftus, 2005). In the first example of this, Loftus et al. (1978) showed participants a slide show depicting a minor road accident. Upon subsequent completion of a questionnaire containing misleading information about details such as the colours of the cars involved and the type of road signs present at the scene, participants answers were frequently biased in the direction of the misleading information. Thus, incorrect misinformation caused memory errors leading to a lower score than if no misinformation was given, whilst information given that was consistent with the original information led to a higher score. It is known that misinformation biases memory, rather than fully interfering with it, as the original memory remains intact (McCloskey and Zaragoza, 1985). More recently, studies have shown that the use of misinformation can also lead to the creation of 'rich' false memories that are often episodic and/or autobiographical in nature (Bernstein et al., 2005).

In this chapter I explore whether non-human animals, in this case the bumblebee *Bombus terrestris* and the honeybee *Apis mellifera* are also potentially susceptible to memory inaccuracies, like those shown by humans. More specifically, I investigate the potential for memory to be biased by postevent cues, in this case colour, in a similar manner to the way in which misinformation biases human memory.

There is little information in the literature regarding the effects of misinformation in non-human animals, when compared to the plethora of work undertaken on this subject in human subjects. This is because most of the human studies rely on verbal communication, which obviously cannot be replicated in non-human animals. However, the effect of misinformation has been studied in some non-human animals using non-verbal post event cues, inserted into the delayed matching-to-sample (DMTS) paradigm. The DMTS paradigm (Blough, 1959) is a commonly used methodology for investigating learning and memory in non-human animals. In the paradigm, the subject learns to match a sample with one of two or more comparisons, presented after a delay. As such, the sample is no longer present at the decision point. Subjects are thought to utilise both working memory and long-term memory to successfully learn the paradigm (Blough, 1959). As such, the DMTS paradigm has begun to be utilised in the study of the effect of misinformation in non-human animals. The delay, given after the sample to be remembered, but before the choice test, allows 'misinformation' to be inserted, as is frequently done in human studies.

Honeybees are known to successfully learn visual DMTS tasks, using both solid colours and horizontal and vertical striped visual patterns (Giurfa et al., 2001). They have also been shown to be capable of transferring these learnt concepts of 'sameness' and 'difference' between the sensory modalities olfaction and vision (Giurfa et al., 2001). Studies with bumblebees however have shown mixed results. Dale et al. (2005) found that the bumblebee *Bombus terrestris* can use cues to prime later colour choice, but only if spatial cues can also be used to distinguish the rewarded colour.

'Misinformation' has been shown to negatively affect event memory in a gorilla *Gorilla gorilla gorilla* (Schwartz et al., 2004), and the rat *Rattus norvegicus* has also been shown to be susceptible to misleading information (Garry and Harper, 2009). Additionally, Harper and Garry (2000) biased recognition in a visual, three-colour DMTS task with the pigeon *Columba livia* using postevent cues. Memory was biased in the direction of the misinformation, such that if it was consistent with the sample and was thus consistent with the correct choice in the matching test, performance was improved, but when it was inconsistent with the sample and was thus consistent with the incorrect choice in the matching test, performance decreased. Conversely, honeybees do not appear to be affected by postevent cues in a visual DMTS task. Zhang et al (2005) found that bees trained to a DMTS task involving black and white visual patterns are not mislead by the insertion of the incorrect pattern during the delay, and continue to correctly choose the test choice that matches the sample. However, there are distinct methodological differences between the two DMTS studies. Harper and Garry (2000) found that the timing of the postevent cue presentation was critical, with memory only being biased when it was presented at the very end of the delay period. In the Zhang et al (2005) study, the postevent cue was not presented at the end of the delay period. Additionally, Harper and Garry (2000) tested three different types of postevent cue: 'consistent', 'inconsistent' and 'neutral', indicating their relationship to the sample and correct and incorrect comparisons, to fully explore the potential for memory biases, whereas Zhang et al (2005) only presented the incorrect comparison as a postevent cue. Thus the results of the two studies are not directly comparable.

Clearly, there is limited information about the extent to which misinformation may affect non-human animals. Here I investigate whether postevent cues bias memory in both the bumblebee *Bombus terrestris* and the honeybee *Apis mellifera*. I hypothesise that information given subsequent to information to be remembered biases memory, more specifically in the direction of that information, leading to memory accuracy either above, below or the same as baseline memory accuracy, depending on the direction of the secondary information. For this purpose I trained bees to a three-colour DMTS task and then inserted postevent cues at the end of the delay to potentially bias memory. My findings indicate that neither honeybees, nor bumblebees are biased by postevent cues, unlike how humans are biased by misinformation. However I note methodological difficulties in examining this type of memory error in insect models.

4.2 Materials and Methods

The general methods were based on Zhang et al. (2005), with protocol details for delayed matching-to-sample (DMTS) training and postevent cue testing adapted from Harper and Garry (2000).

4.21 Experiment A: Do postevent cues bias memory in the honeybee?

Subjects

Honeybees *Apis mellifera* were from one naturally foraging colony housed on the rooftop of the second floor of the G.E Fogg Building, Queen Mary University of London, UK (colony/N/time: KPEH1/N=3/12 days). Bees were individually marked on the thorax with coloured paint to allow identification.

Set-up

Experiments were undertaken in a wooden y-maze with a transparent UV-transmitting Plexiglas™ lid (Fig. 4.1). The y-maze consisted of several interconnected sections: the main tunnel (69cmx27cmx25cm), which was divided into the entrance/sample chamber (26cmx27cmx25cm) and the delay/postevent cue chamber (43cmx27cmx25cm) by the sample, and the decision chamber/arms (29cmx20cmx25cm) into which access was gained by flying through a hole located centrally within the postevent cue. During experimentation all samples, postevent cues and comparison artificial flowers were presented vertically, so that their appearance was to some extent independent of the bees' approach direction.

Samples, postevent cues and comparison artificial flowers

All samples were circular (Ø=14cm) with a black rimmed central hole (Ø=2.5cm), which enabled bees to fly through (Fig. 4.2a). Postevent cues were identical in size and shape to samples (Fig. 4.2a). All comparison artificial flowers were circular (Ø=7cm) with transparent Perspex™ landing platforms (1.5cmx1.5cmx1cm) in the centre. Each platform had a central well (Ø=0.6cm, depth=0.2cm) into which the experimenter could place droplets of sucrose solution, quinine hemisulfate solution or water (Fig. 4.1b).

Pre-training

Bees were trained to fly through the y-maze and forage upon the comparison artificial flowers presented at the far ends of the two arms. To achieve this, bees were transferred manually from a feeder located away from the hive (3m), to a balcony positioned at the entrance of the y-maze, using a piece of cardboard (3cmx1cmx0.2cm) doused with 50% sucrose solution (v/v). The balcony (with feeding bee) was then manually moved through the y-maze. The bee was allowed to return to the hive once satiated and independently fly back to the point in the y-maze it had departed from, until successful independent foraging at the end of the y-maze was achieved. The sample, postevent cue and comparison artificial flowers were 'blanks', such that they were white in colour (Table 4.1) (Fig. 4.3a), which matched the interior colour of the y-maze. This pre-training allowed bees to become used to the y-maze foraging scenario, familiarise themselves with foraging on the comparison artificial flowers and enable the experimenter to determine the individuals that would successfully independently forage for a minimum of three consecutive foraging bouts, and which were therefore suitable for further testing.
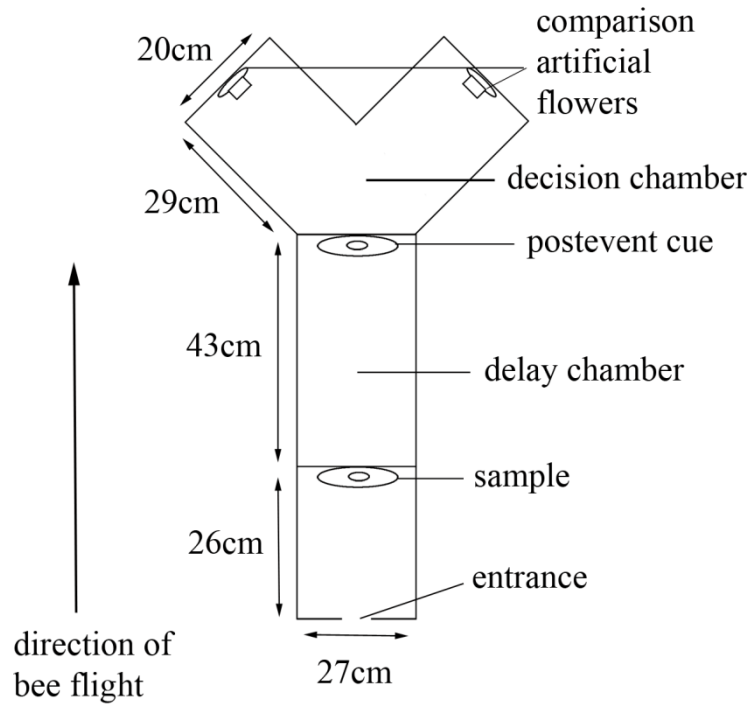
Figure 4.1 Y-maze set-up showing the interconnected chambers and the presentation positions of the sample, postevent cue and comparison artificial flowers. Each trial consisted of a bee flying from the entrance, through the hole located within the sample (to be remembered) to the delay chamber, then through the hole located within the postevent cue into the decision chamber, and into one of the two arms to forage upon one of the two comparison artificial flowers.
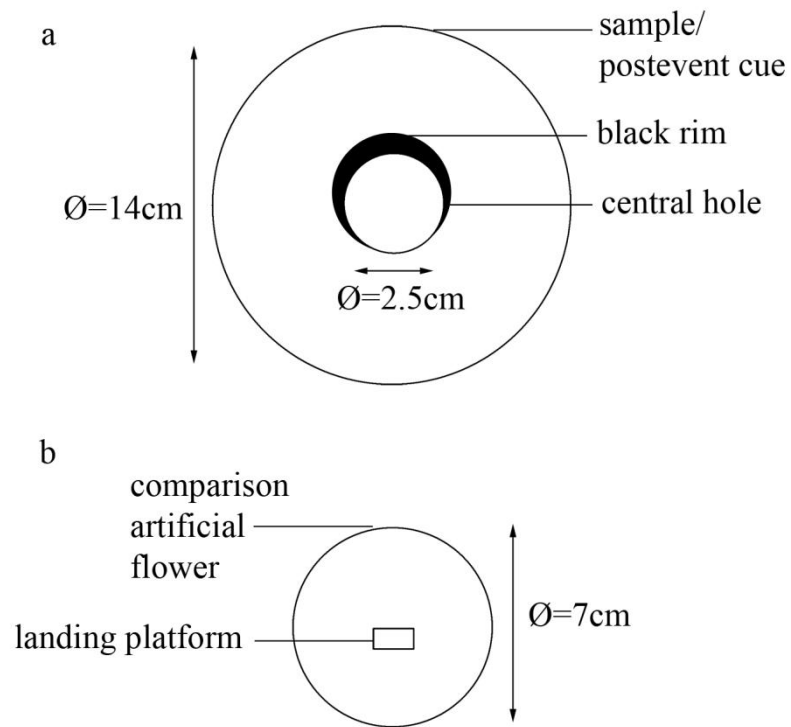
Figure 4.2 Geometry of samples, postevent cues and artificial flowers. a) sample/postevent cue (Ø=14cm), showing black rimmed central hole (Ø=2.5cm) to enable through flight and b) comparison artificial flower with attached Perspex™ landing platform (1.5cmx1.5cmx1cm). The landing platform had a central well (Ø=0.6cm, depth=0.2cm), in which droplets of 50% sucrose solution (v/v) (reward) or saturated quinine hemisulfate solution (penalty for incorrect choices) could be presented.

Table 4.1 Sample, postevent cue and comparison artificial flower colour information: Spectrophotometer measurements (hue, brightness, saturation and UV reflectivity) for all colours used.

Colour	Hue	Brightness	Saturation	UV Reflectivity
White	Blue-Green	1.679	0.232	0.417
Black	Uncoloured	0.156	0.013	0.048
Yellow	Green	0.668	0.261	0.146
Green	Green	0.680	0.202	0.184
Purple	Blue	1.090	0.112	0.338

Training

Bees were trained to a three colour delayed matching-to-sample (DMTS) paradigm. A random training regime was used, such that the sample colour, correct side and incorrect comparison artificial flower colour were only the same for a maximum of two consecutive trials. Forty-two trials were given in total. The three colours used for the sample and comparison artificial flowers were yellow, green and purple (Table 4.1) (Fig 4.3b). The postevent cue was again a 'blank' (Fig 4.3a). Each trial consisted of the bee flying from the entrance/sample chamber, through a hole in the sample (to be remembered) to the delay/postevent cue chamber, then through a hole in the postevent cue into the decision chamber, and into one of the two arms to forage upon one of the two comparison artificial flowers. The correct comparison artificial flower was rewarded with a droplet of 50% sucrose solution (v/v), whilst the incorrect comparison artificial flower contained a droplet of saturated quinine hemisulfate solution. Quinine hemisulfate solution is distasteful to bees and was used as a punishment as it has been shown that bees quickly learn to avoid it and its use leads to stronger discrimination than using unrewarded flowers (Chittka et al., 2003). However for the first two trials, the incorrect comparison artificial flower was empty to prevent bees from being dissuaded from returning. The definition for a 'choice' was the landing of the bee upon the landing platform of a comparison artificial flower. After a correct choice bees were allowed to consume the reward and fly back to the hive. After an incorrect choice bees were allowed to discover the correct comparison artificial flower and obtain the reward before returning to the hive. Between trials the sample and comparison artificial flowers were changed in accordance with the pseudorandom training regime. Additionally all landing platforms were cleaned with 70% ethanol to remove any scent marks left by the bees. All bees were trained individually.
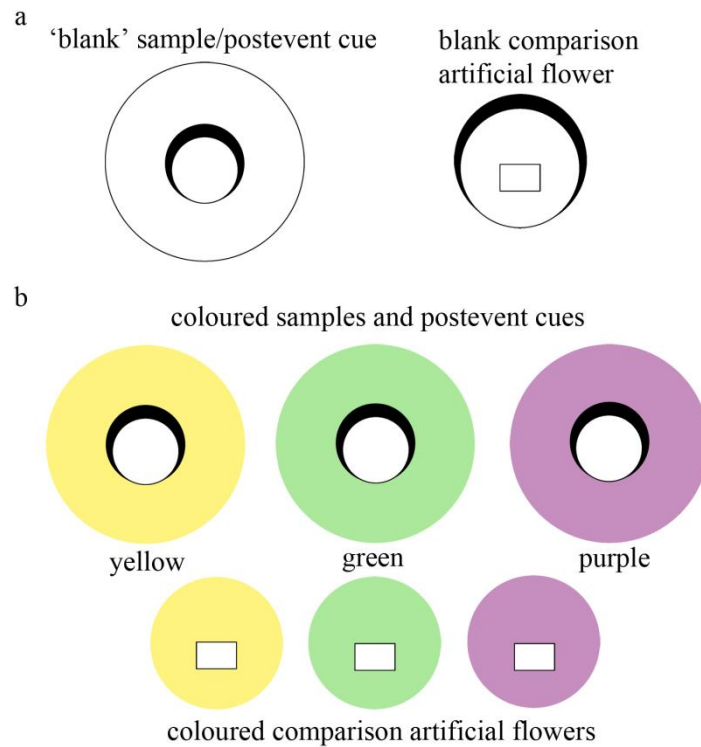
Figure 4.3 Samples, postevent cues and comparison artificial flowers. a) 'blank' postevent cue (white, with a black-rimmed central hole) used in pre-training, training and testing: baseline data, and 'blank' comparison artificial flower (white, black-rimmed, with centrally placed landing platform) used in pre-training. b) coloured samples (yellow, green and purple, with black-rimmed central holes) used in training and testing: postevent cues, coloured postevent cues used in testing: postevent cues, and comparison artificial flowers (yellow, green and purple, with centrally placed landing platforms) used in training and testing: postevent cues.

Testing

Four tests were performed. Each consisted of one 1-minute trial, during which both comparison artificial flowers were unrewarded, but filled with water to visually encourage foraging. In each test the number of times the bee made a choice for each of the two comparison artificial flowers was recorded. Additionally the delay time (the time taken for the bee to fly through the delay chamber between the sample and the postevent cue) was recorded. The first test was to determine the baseline level for DMTS learning. As such this test was the same as a training trial in terms of using a coloured sample and comparison artificial flowers, but a 'blank' postevent cue (Fig. 4.3). The colours for the sample and comparison artificial flowers were randomly chosen so that they were different for each bee. The other three tests were to determine the effect (if any) of postevent cues on memory. Three types of postevent cue were used, one for each test. The postevent cue was either 'consistent' (the same colour as the sample and as such the correct comparison artificial flower), 'inconsistent' (the same colour as the incorrect comparison artificial flower), or 'neutral' (the colour not represented by the sample and correct comparison artificial flower, nor the colour represented by the incorrect artificial flower). Again the colours were randomly chosen so they were different for each bee. Furthermore, the order of the three postevent cue tests was randomised between bees. Between each of the four tests a six trial training 'refresher' was given to re-establish the aim of the task. Again between trials/tests all landing platforms were cleaned with 70% ethanol. All bees were tested individually. The full training and testing protocol required one full day per bee.

4.22 Experiment B: Do postevent cues bias memory in the bumblebee?

Subjects

Bees were from three commercially obtained colonies of *Bombus terrestris* (Syngenta Bioline Bees, Weert, The Netherlands), and were housed in bipartite wooden nest boxes (28x16x11cm). Bees were individually marked on the thorax with coloured, numbered markers (Opalith tags, Christian Graze KG, Germany) to allow identification. A differing number of bees were used from each colony and each colony was utilised for a different length of time (colony/N/time: KPE5/N=8/8 days, KPE6/N=7/12 days, KPE8/N=5/15 days). Prior to experimentation bees were kept naive with no exposure to colour given in association with food. Colonies were provided ad libitum with defrosted pollen (Koppert BV, Berkel en Rodenrijs, The Netherlands) directly into the nest and any extra feeding required in addition to the products of the experimental foraging was with 30% sucrose solution (v/v) provided directly into colonies' honey pots.

The set-up was as described in section 4.21 (Fig. 4.1), with the modification that access to the entrance of the y-maze was by means of a transparent Plexiglas™ tube. Shutters along the length of the tube enabled the traffic of bees into and out of the arena to be controlled. Samples, postevent cues and comparison artificial flowers were identical to those described in section 4.21 (Fig. 4.2). Pre-training was also as depicted in section 4.21, with the exception that the balcony was moved through the y-maze when the bee was not present on it. Thus it was moved in between foraging bouts, upon bees' return to the nest.

Training

Bees were trained on a three colour delayed matching-to-sample (DMTS) paradigm, with the colours and 'blank' used the same as those described in section 4.21 (Table 4.1) (Fig. 4.3). Training was of a block design*, in which each colour (sample) was learnt individually, for fifteen trials, with the correct side being alternated every three trials and the incorrect comparison artificial flower colour being assigned randomly, with a maximum of two consecutively. Thus, a total of forty-five training trials were given. The correct comparison artificial flower was rewarded with a droplet of 50% sucrose solution (v/v), whilst the incorrect comparison artificial flower contained a droplet of water**. The definition for a 'choice' was identical to that in section 4.21. A correct choice was followed by manual removal of the bee from the y-maze, who was then returned to the nest box to empty their crop. After an incorrect choice bees were allowed to discover the correct comparison artificial flower and obtain the reward before being returned to the nest***. Between trials the sample and comparison artificial flowers were again changed in accordance with the training regime and all landing platforms were cleaned with 70% ethanol. All bees were trained individually.

*Preliminary work showed that bees would fail to return to complete training if the training protocol was completely random.

**Preliminary work showed that bees would fail to return to complete training if punishment was given for an incorrect choice.

***Preliminary work showed that bees would fail to return to complete training if they repeatedly obtained no reward.

Bees completing the forty-five training trials were then given an additional ten trials, which were random, with a maximum of two consecutively, with respect to the sample colour, the correct side and the colour of the incorrect comparison artificial flower. Choice determination, reward obtainment, inter-trial handling and cleaning were as described above. Those bees scoring 70% or more correct within those ten trials were then carried forward to testing.

Testing

Baseline data

Bees were given ten trials, identical to those just described. From this a baseline score for DMTS learning was obtained.

Postevent cues

Bees were then given thirty trials, during which a coloured postevent cue was added. The three postevent cue types used were identical to those depicted in section 4.21. The protocol design was such that each of the three postevent cue types was used an equal number of times (10) and that they were randomly displayed, with a maximum of two of the same type used consecutively. Additionally, each of the three colours was used as a postevent cue approximately the same number of times (yellow=11, green=10, purple=9), which again were randomly displayed, with a maximum of two consecutively. The sample colour and incorrect comparison artificial flower colour were also random with a maximum of two consecutively, and the correct side was random with a maximum of three consecutively. From this, scores for the effect of postevent cues were obtained. Again choice determination, reward obtainment, inter-trial handling

and cleaning were as described above. All bees were tested individually. Again, the full training and testing protocol required one full day per bee.

Data Analysis

The effect of postevent cues on memory was examined by calculating the pure probability of the bees making the number of correct choices observed, for the baseline test and all three postevent cue test types. However, due to a low sample sizes (N=3 and N=1) and therefore a lack of statistical power, no direct comparison between treatments was undertaken. Additionally, the number of choices for each arm of the y-maze was examined for all bees to look for any side biases. These numbers were analysed using a chi-squared test to look for any significance. Furthermore, learning was calculated for some bees using the percentage of correct choices over the course of training, with training divided into bins of five trials. All data were also converted to give percentages to display graphically. All analyses were carried out using R statistical software (v.2.14.1).

4.3 Results

4.31 Experiment A: Do postevent cues bias memory in the honeybee?

The pure probability of all bees (N=3) making the number of correct choices observed was both low and significant for all treatments (baseline: p=0.001, consistent: p=0.004, inconsistent: p=0.003, neutral: p=0.013). Therefore postevent cues had no effect on memory accuracy for the three-colour delayed matching-to-sample (DMTS) task, regardless of the postevent cue type used. However, due to a low sample size (N=3) and therefore a lack of statistical power, I could not directly compare between treatments. Average memory accuracy was 83% for the baseline test, 77% for the 'consistent' postevent cue treatment, 79% for the 'inconsistent' postevent cue treatments and 69% for the 'neutral' postevent cue treatment (Fig 4.4a).

Additionally the average delay time for all four treatments was within the known five second working memory time limit of honeybees (Zhang et al., 2005): 'baseline'= 3 seconds, 'consistent' = 2 seconds, 'inconsistent'= 3 seconds, 'neutral'= 2 seconds (Fig. 4.4b).

Furthermore, no bee showed a significant side bias during the forty-two trial training paradigm, selecting neither the left or right arm more often than predicted by chance ('yellow': χ^2=0.857, df=1, p=0.355, 'white': χ^2=0, df=1, p=1, 'gold': χ^2=0.381, df=1, p=0.537) (Fig. 4.5). Thus, postevent cues do not appear to bias memory in the honeybee.

Fig 4.4 a) Effect of postevent cues given as mean percentage of correct choices ± SE for treatments: 'baseline, 'consistent', 'inconsistent' and 'neutral'. N=3, solid line indicates chance level, b) mean delay time (seconds) ± SE for treatments: 'baseline, 'consistent', 'inconsistent' and 'neutral'. N=3. No effect of postevent cues, memory accuracy remained high for all four treatments (pure probabilities for correct choices achieved: baseline: p=0.001, consistent: p=0.004, inconsistent: p=0.003, neutral: p=0.013). All delay times within known time limit for working memory (5 seconds).

Figure 4.5 Choice percentages for each y-maze arm: left or right, compared against the potential choice percentages for each side if perfect learning occurred. N=3, solid line indicates chance level. No side biases exhibited ('yellow': χ^2=0.857, df=1, p=0.355, 'white': χ^2=0, df=1, p=1, 'gold': χ^2=0.381, df=1, p=0.537).

4.32 Experiment B: Do postevent cues bias memory in the bumblebee?

Only one bee (Orange9B) successfully completed the full training and testing regime. The pure probability of the bee making the number of correct choices observed was low and significant for all treatments (baseline: p=0.011, consistent: p=0.011, inconsistent: p=0.001, neutral: p=0.011). Therefore, postevent cues had no effect on memory accuracy for the three-colour delayed matching-to-sample (DMTS) task, regardless of the postevent cue type used. However, due to a low sample size (N=1) and therefore a lack of statistical power, I could not directly compare between treatments. Memory accuracy was 90% for the baseline test, 90% for the 'consistent' postevent cue treatment, 100% for the 'inconsistent' postevent cue treatment and 90% for the 'neutral' postevent cue treatment (Fig. 4.6a).

Additionally, the bee showed a significant side bias, selecting the right arm more often than predicted by chance during the forty-five trial training regime (χ^2=8.022, df=1, p=0.005) (Fig. 4.6b). However this was predicted from the training regime (in which perfect learning would mean 60% choices for the right arm and 40% choice for the left arm), with further analysis showing a bias towards making correct choices to the right, as expected (χ^2=32.207, df=3, p<0.01). Thus, as shown above in the honeybee postevent cues do also not appear to bias memory in the bumblebee.
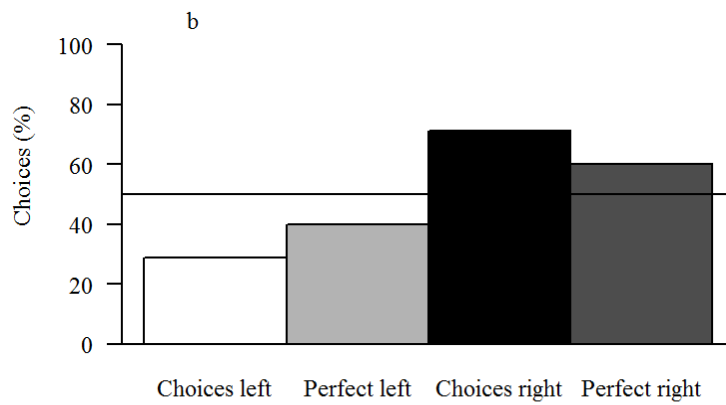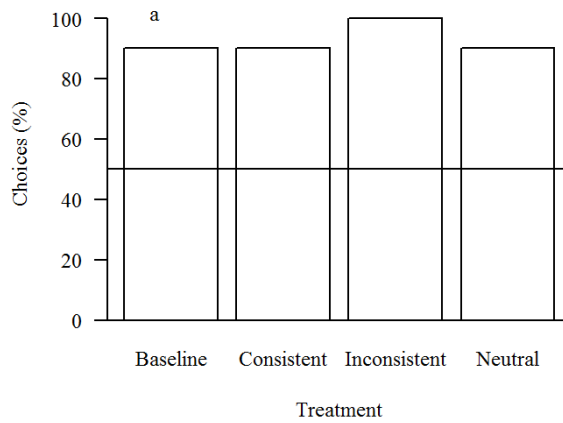
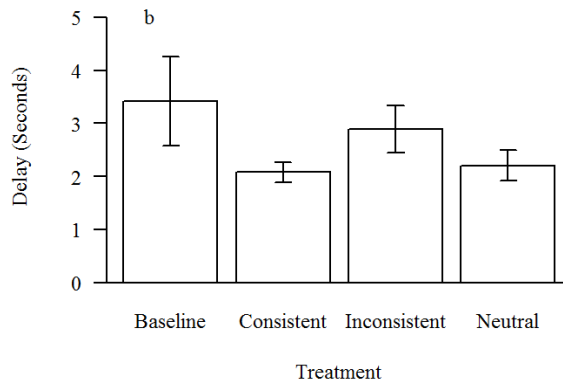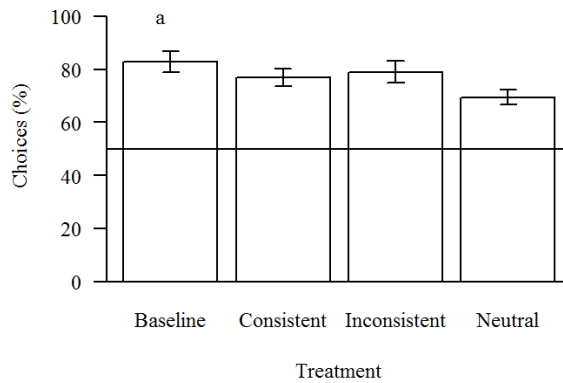**Figure 4.6** a) Effect of postevent cues given as mean percentage of correct choices for treatments: 'baseline, 'consistent', 'inconsistent' and 'neutral'. N=1, solid line indicates chance level. b) choice percentages for each y-maze arm: left or right, compared against the potential choice percentages for each side if perfect learning occurred. N=1, solid line indicates chance level. No effect of postevent cues is observed; memory accuracy remained high for all four treatments (pure probabilities for correct choices achieved: baseline: p=0.011, consistent: p=0.011, inconsistent: p=0.001, neutral: p=0.011). Right side bias observed, as expected from successful learning (χ^2=32.207, df=3, p<0.01).

An additional twenty bumblebees failed to successfully complete the training regime (achieve 70% or more correct choices in the ten trials administered after the forty-five trial training phase), and as such were not carried forward to testing. Ten of the bees failed to continue to return from the nest box within the first ten training trials. No analysis was performed on these data. Four bees continued to return from the nest box after the tenth training trial, but then either failed to continue to return from the nest box before the forty-fifth training trial or the training regime was halted as it was clear learning was not taking place. Finally, six of the bees completed the forty-five training trials, but either failed to achieve 70% or more on the ten additional, or failed to return to complete the ten additional trials.

All these ten bees showed a significant side bias, selecting either the left arm or the right arm of the y-maze more often than predicted by chance (Orange14: χ^2=9.8, df=1, p=0.002, OrangeB: χ^2=33.8, df=1, p<0.001, Green11 χ^2=10.667, df=1, p= 0.001, Orange43: χ^2=11.267, df=1, p<0.001, Orange89: χ^2=5, df=1, p=0.025, Yellow26: χ^2=5.765, df=1, p=0.016, Orange20: χ^2=18.689, df=1, p<0.001, Orange82: χ^2=16.2, df=1, p<0.001, Yellow66: χ^2=30.422, df=1, p<0.001, Orange65: χ^2=16.2, df=1, p<0.001). For six of the bees, the side bias was to the left, opposite to that predicted from the training regime (in which perfect learning would mean more choices for the right arm than for the left arm) (Fig. 4.7a), whilst for four of the bees the side bias was an exaggeration of that predicted from the training regime (4.7b). Therefore successful learning of the three-colour DMTS task by bumblebees was hampered by side biases, which appear to be pre-existing rather than being a result of my training procedure.
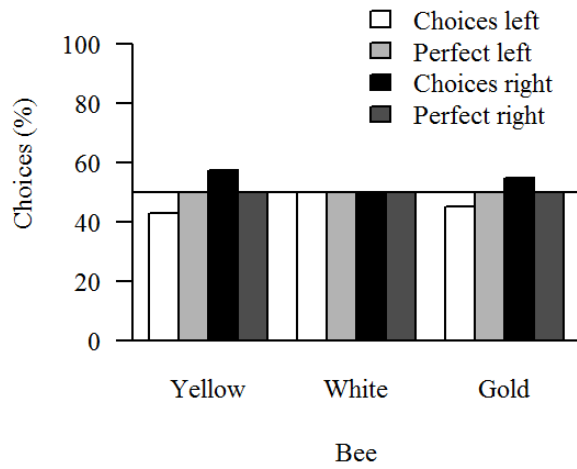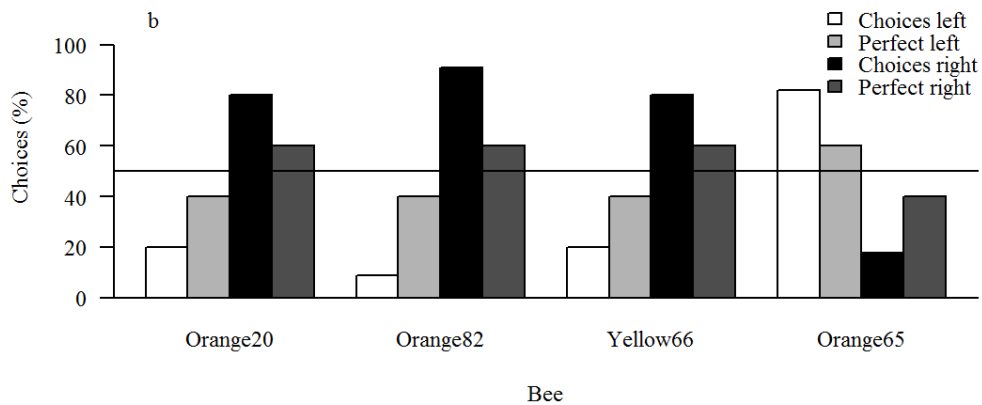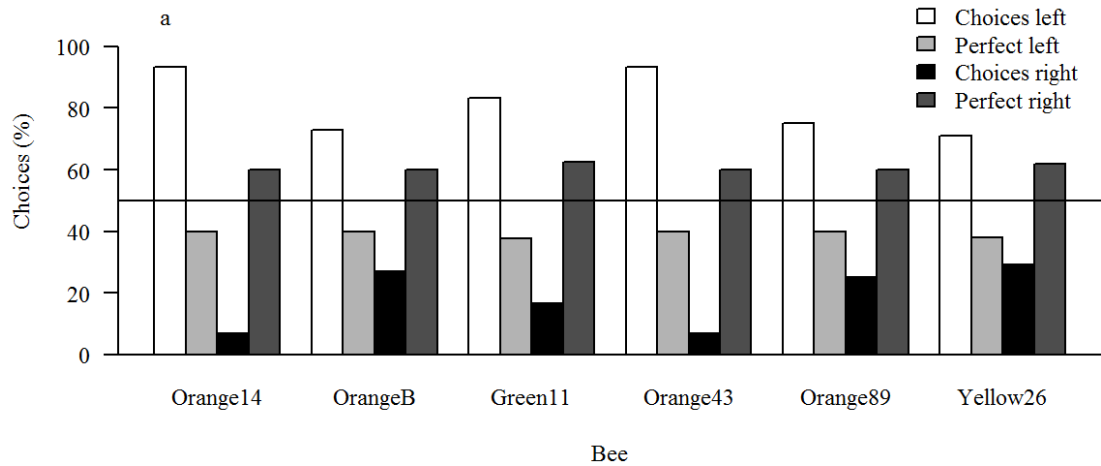
Figure 4.7 Choice percentages for each y-maze arm: left or right, compared against the potential choice percentages for each side if perfect learning occurred. a) bees showing side biases opposite to those predicted from training. N=3, solid line indicates chance level. b) bees showing side biases exaggerated from those predicted from training. N=3, solid line indicates chance level. All biases were significant (χ^2: all P<0.01).

In an attempt to avoid the effects of the spatial bias found in bumblebees trained in a y-maze (i.e. consistent preferences by individuals for one arm or the other), an additional experiment was undertaken using a modified flight arena. Full methodological details and results for this can be found in section 4.5: Appendix 1.

4.4 Discussion

My findings show that in the honeybee and the bumblebee *Bombus terrestris*, memory may not be biased by postevent cues. Bees that have successfully learnt a three-colour delayed matching-to-sample (DMTS) task continue to show high memory accuracy for the sample even when different postevent cues are inserted at the end of the delay period. However, due to methodological issues, the sample sizes obtained were very low (N=3 and N=1), and as such caution should be taken when drawing any conclusions. Additionally, bumblebees show significant side biases when attempting to learn in a maze-based paradigm. These side biases appear to be pre-existing, rather than a result of any training regime.

Bee memory does not therefore seem to be as susceptible to the biasing influence of postevent cues in the way in which human memory is biased by misinformation (Loftus and Palmer, 1974, McCloskey and Zaragoza, 1985). My results also differ from the findings from studies with other non-human animal species, which show that the gorilla (Schwartz et al., 2004), rat (Garry and Harper, 2009) and pigeon (Harper and Garry, 2000) are all biased by misinformation/postevent cues in a similar way to humans.

However for the honeybee, my results are consistent with findings of Zhang et al. (2005), who showed that memory accuracy for bees that had successfully learnt a visual DMTS task remained high even when the incorrect comparison was inserted as a potential distracter during the delay period. Their explanation for their finding is that the distance of the sample presentation within the tunnel was fixed throughout training, and as such the bees, rather than learning specifically to remember what was presented,

were more simply learning to attend to and remember whatever was at this specific distance. This explanation was confirmed with their further finding that when the distance was altered during testing, memory accuracy fell to chance level (Zhang et al., 2005). This explanation is also potentially applicable to both my honeybee and bumblebee findings, as the sample was always presented at the same fixed distance from the entrance to the y-maze. Thus, if true, in order to truly test for any effect of postevent cues, bees would need to first be trained to a DMTS task in which the sample distance was varied in order to prevent this learning of a distance and promote a more general learning of the overall concept/rule: to remember the sample seen before the delay period.

My finding of a strong side bias in attempting to train bumblebees to spatially separated artificial flowers is striking. It appears that this may be pre-existing, rather than learnt, as it was often opposite to that expected from the training regime and virtually impossible to overwrite through training. At present there is a lack of information about this specific potential side bias in the published literature, however there is some recent evidence to suggest that bumblebees exhibit a behaviour akin to 'handedness' (also termed lateralisation). 'Handedness' is a behaviour shown by humans in which a side bias for motor output, perception and/or information processing occurs (Goulson et al., 2013). Kells and Goulson (2001) found that three species of bumblebee (*Bombus lapidarius*, *Bombus lucorum* and *Bombus pascuorum*) showed a tendency for rotation in the same direction around inflorescences on successive trials. Interestingly however, they did not find such 'handedness' in *Bombus terrestris* (Kells and Goulson, 2001). Additionally, Anfora et al. (2011) found that this lateralisation occurs in olfactory learning in the bumblebee *Bombus terrestris*. Bees trained using the classic proboscis

extension reflex (PER) paradigm, in which the left and right antennae were used independently, showed a right-sided bias in the short-term memory recall of an odour (Anfora et al., 2011). This right-sided bias has also previously been shown to occur in the both olfactory and visual learning in the honeybee *Apis mellifera* (Letzkus et al., 2006, Letzkus et al., 2008). Furthermore, upon consultation with colleagues I have learnt that this side-bias is a potentially well-known, yet under-published problem. This highlights the importance of information sharing, to try to avoid known problems with experimental design.

My finding that bumblebees in this paradigm were reluctant to return from trial to trial to complete training is also interesting. Perhaps if a task is deemed too hard to learn, or no reward reinforcement is obtained within a certain timeframe, a bee will choose to simply give up. This therefore also has implications for protocol design.

Overall, my results show that memory in the honeybee and the bumblebee *Bombus terrestris* may not be biased by postevent cues, like human, gorilla, rat and pigeon memory, are influenced by 'misinformation'. This conclusion is however drawn with caution due to the low sample sizes obtained. My finding of significant side biases in the bumblebee highlights the importance of experimental design, and a possible problem that may arise from potentially innate spatial biases when administering maze learning paradigms.

4.5 Appendix 1: Experiment C: Do postevent cues bias memory in the bumblebee (using a modified arena)?

To try to circumvent the effects of the spatial bias found in bumblebees trained in a y-maze (i.e. consistent preferences by individuals for one arm or the other), an additional experiment was undertaken using a modified flight arena, such that instead of the comparison artificial flowers being presented in spatially separate 'arms', they were presented twice on a single wall: once as a pair on the left hand side, and once as a pair on the right hand side (Fig. 4.8).

4.51 Materials and methods

The flight arena design and general method for the delayed matching-to-sample (DMTS) training was adapted from Schumacher (2010) and Spaethe, J. (personal communication 4th January 2012). Subjects were obtained, labelled, housed and fed as described in section 4.22 (colony/N/time: KPE9/N=5/7 days, KPE10/N=5/25 days).

Set-up

Experiments were undertaken in a wooden flight arena with a transparent UV-transmitting Plexiglas™ lid (Fig. 4.8). The arena consisted of several interconnected sections: the main tunnel (50x27x25cm), which was divided into the entrance/sample chamber (25cmx27cmx25cm) and the delay/postevent cue chamber (25x27x25cm) by the sample, and the decision chamber (40x60x30cm) into which access was gained by flying through a hole located centrally within the postevent cue. Access to the entrance of the main tunnel was by means of a transparent Plexiglas™ tube. Shutters along the

length of the tube enabled the traffic of bees into and out of the arena to be controlled. During experimentation all samples, postevent cues and comparison artificial flowers were presented vertically, so that their appearance was independent of the bees' approach direction.

All samples, postevent cues and comparison artificial flowers were as depicted in section 4.22 (Table 4.1, Fig 4.2, 4.3). Additionally, the procedures for pre-training, training and testing were as described in section 4.22, with the exception of the following modification: a saturated quinine hemisulfate solution, not water, was offered on the landing platforms of the incorrect comparison artificial flowers.

Moreover, to prevent bees from forming a positional bias that may result from the use of the block training regimen, a separate set of bees were trained using a pseudorandom training regime, such that the sample colour, correct side (within each pair presented) and incorrect comparison artificial flower colour (for both pairs) was only the same for a maximum of two consecutive trials. Furthermore, this training lasted for sixty trials, with the last ten trials counting as the baseline DMTS performance if 70% or more correct choices were achieved.
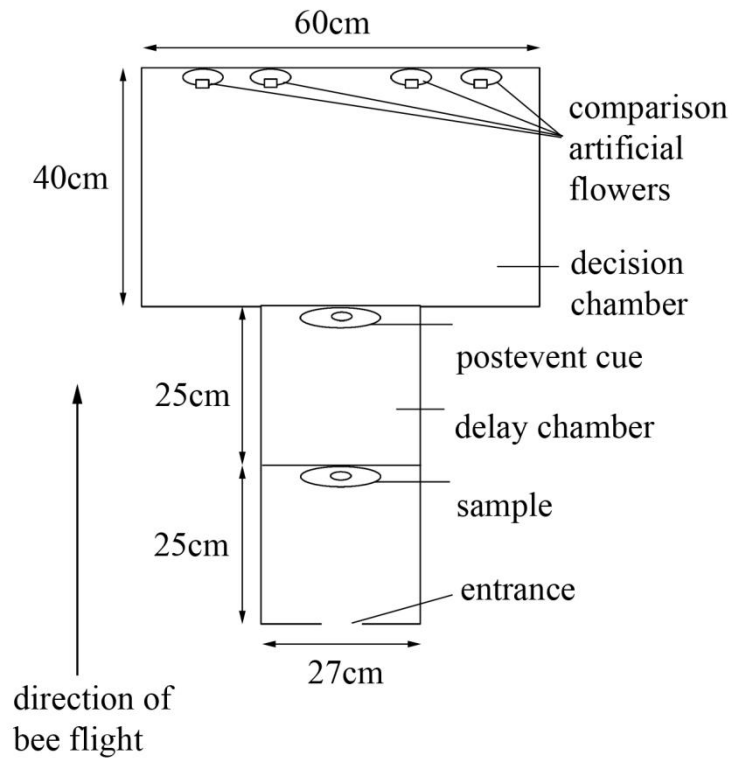
Fig 4.8 Modified flight arena set-up showing the interconnected chambers and presentation positions of the sample, postevent cue and comparison artificial flower pairs. Each trial consisted of a bee flying from the entrance, through the hole located within the sample (to be remembered) to the delay chamber, then through the hole located within the postevent cue into the decision chamber, to forage upon one of the comparison artificial flowers.

4.52 Results

Block training

All five bees failed to successfully complete the training regime (achieve 70% or more correct choices in the ten trials administered after the forty-five trial training phase), and therefore were not carried forward to testing. Three of the bees failed to continue to return from the nest box within the first ten training trials. No analysis was undertaken on these data. One of the bees (Orange37) completed the forty-five training trials, but failed to achieve 70% or more on the ten additional trials, scoring only 50% correct choices. Finally, one bee (Orange30) continued to return from the nest box after the tenth training trial, but the training regime was halted as it was clear learning was not taking place. This bee only chose artificial comparison flowers within the left hand side pair, showing a significant bias for the left comparison artificial flower within that pair (χ^2=17.286, df=1, p<0.001) (Fig. 4.9a).

Pseudorandom training

All five bees failed to successfully complete the training regime (achieve 70% or more correct choices in the last ten trials of the sixty training trials), and as such were not carried forward to testing. Three of the bees failed to continue to return from the nest box within the first twenty training trials. No analysis was undertaken on this data. One of the bees (Brown37) completed the sixty training trials, but failed to achieve 70% or more during the last ten trials, scoring only 60% correct choices. Finally, one bee (White87) continued to return from the nest box after the twentieth training trial, but failed to return from the next box after forty-five trials. This bee initially showed a preference for the comparison artificial flower in location 'left left' (the left flower

within the pair on the left of the presentation wall), but switched to choosing the comparison artificial flower in the location 'right right' (the right flower within the pair on the right of the presentation wall) over the course of training (Fig. 4.9b). Thus, it appears bumblebees suffer from side biases, which do not appear to be caused by training.
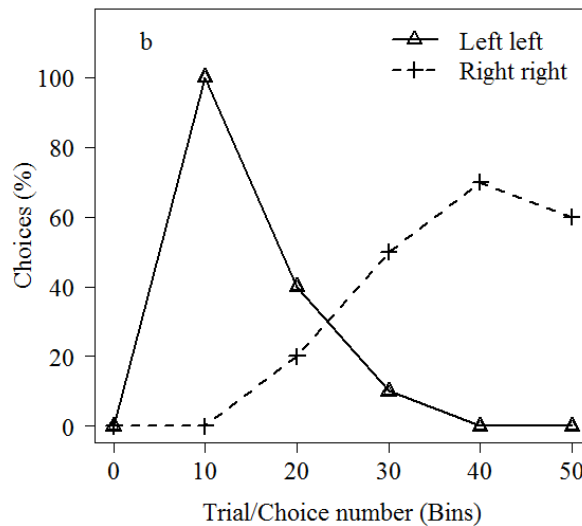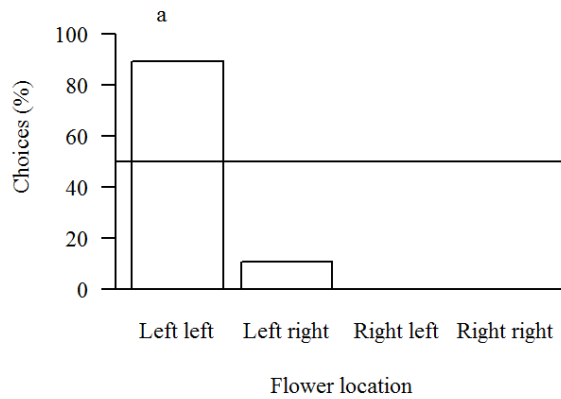
Figure 4.9 Choice percentages for each side (left or right), within each pair (left or right) of comparison artificial flowers. a) a bee (Orange 30) reaching twenty-eight trials of the block protocol. N=1, solid line indicates chance level within a pair. A significant side bias for the left flower within the left hand pair was observed (χ^2=17.286, df=1, p<0.001). b) a bee (White87) trained to the pseudorandom protocol. Training data divided into bins of five trials. A changing side bias from flower 'left left' to flower 'right right' was exhibited.

Chapter 5: False memory susceptibility is correlated with categorisation ability in humans

5.1 Introduction

When remembering the past, we typically feel that our memory allows retrieval of events as they really occurred. Yet a large body of work shows that memory is often surprisingly inaccurate, with errors ranging from misremembering minor details of events to generating illusory memories of entire episodes (Loftus, 1997). False memory, the phenomenon of remembering something that actually never occurred, has become a widely studied topic since its origins in Binet's (1900) *La Suggestibilité* and Bartlett's (1932) *Remembering*. The pervasiveness of such false memories generates an evolutionary puzzle; in the face of selection pressure for accuracy of memory (Dukas, 1999, Mery, 2013, Raine and Chittka, 2008), how could such systematic failures have persisted over evolutionary time? As with perceptual illusions, false memories might be inevitable by-products of otherwise adaptive cognitive processes. In this chapter I explore whether individuals with a higher propensity to form false memories are better at other cognitive tasks, thus generating a trade-off by which certain cognitive capacities (in this case forming links between distinct memories, as in categorisation) cannot be achieved without the cost of memory inaccuracies.

A plethora of experimental paradigms exist for eliciting differing types of false memories in declarative memory, i.e. people's conscious memory for facts (Brainerd and Reyna, 2005). Episodic (and as such autobiographical) false memories are commonly elicited using the misinformation paradigm, in which information provided or questions asked after an event can bias memory (Loftus, 2005). Conversely, semantic

false memories can be elicited using the presentation of lists of semantically related words (Deese, 1959, Roediger and McDermott, 1995). The so called Deese-Roediger-McDermott (DRM) paradigm has become widely used for exploring the malleability of memory. In this paradigm, participants begin by studying lists of words; for example a list may comprise the words *mad, fear, hate, rage, temper, fury, ire, wrath, happy, fight, hatred, mean, calm, emotion, enrage*. Each list is composed of the 15 strongest associates of one critically non-presented word, for example *anger* for the above list. Upon free recall of the lists or during a recognition test, the non-presented words are remembered at high rates and with high levels of confidence. This high proportion of false memories is attributed to the strength of the associations between the words presented in the lists and the words falsely remembered (Deese, 1959).

While such tests might be viewed as rather remote from real-life situations in which the accuracy of memory matters, including episodic memories (DePrince et al., 2004, Freyd and Gleaves, 1996), it has recently been proposed that different types of false memories may share the same underlying mechanisms (Otgaar et al., 2012). These authors showed that children who generate a rich false memory when subjected to a typical false memory implantation paradigm, such as being led to believe they once took a ride in a hot air balloon (which in fact never occurred), are also more susceptible to false memories in a DRM test than children who do not develop a rich implanted false memory. Thus the DRM paradigm, artificial though it may seem, is a useful laboratory paradigm to test individual false memory susceptibility more generally.

Clearly false memories cannot in themselves be useful, but like other memory inaccuracies (such as forgetting) they might be by-products of the otherwise adaptive nature of memory processes (Schacter, 1999, Schacter and Dodson, 2001, Schacter et al., 2011). But what cognitive processes might facilitate the generation of false memories as a by-product? It is possible that our abilities for rule learning, association and categorisation might come at a cost when it comes to memorising isolated facts, events, or indeed words. Specifically with respect to the semantic false memories tested in the DRM paradigm, errors might be produced by the ability of individuals to group words together, placing them in categories based on rules for membership. It therefore seems plausible that the creation of these semantic false memories may be a by-product of our ability to group words into categories.

Categorising items is known to generate adaptive benefits such as the ability to learn information more quickly and to show greater efficiency during decision-making (Merritt et al., 2010), but McClelland (1995) argues that whilst such categorisation "is central to our ability to act intelligently" it however "gives rise to distortion as an inherent by-product" (p. 84). It is therefore possible that memory errors are an inevitable fluke of a powerful, adaptive cognitive phenomenon, in the case of semantic false memories our ability to learn rules and concepts, and to classify novel objects by category memberships (Carey, 2011, Chittka and Jensen, 2011). Indeed, categorisation is a strategy to economise on memory, since it allows recognising objects by a limited set of features that define the category, rather than memorising every single possible member of the category (Chittka and Niven, 2009).

One possibility to explore the potential trade-off between categorisation ability and false memory susceptibility is to exploit variation between individuals, and to test whether superior performance on the one comes with increased error rates on the other. Inter-individual variation is the raw material for evolution, and offers the possibility to quantify the fitness benefits of cognitive traits in natural settings (Raine and Chittka, 2008) and to test potential trade-offs between one cognitive capacity and another (Raine and Chittka, 2012). Here I investigate a potential correlation between an individual's proneness to semantic type false memories and their categorisation ability. For this purpose I subjected participants to a DRM paradigm to assess their semantic false memory susceptibility and a test consisting of verbal reasoning questions to assess their ability to form categories. My findings indicate that false memories, to some extent, might be a by-product of our ability to learn rules, categories and concepts.

5.2 Materials and methods

The general method for eliciting false memories was based on Roediger and McDermott (1995) and Stadler et al. (1999). The protocol for the visual presentation of the wordlists was adapted from Peters et al. (2008). The categorisation test was constructed from educational aids published by Coordination Group Publications Ltd (Parsons, 2002b, a), Chukra Ltd (2007) and Eleven Plus Exam Group (2010).

Participants

Thirty-nine 2nd year undergraduate students from the School of Biological & Chemical Sciences, Queen Mary University of London participated in the study. The participants were one full class undertaking a 'statistics' module and as such the experiment formed part of their learning, with a report writing task set from the results. Participant demographics were as follows: seven male, thirty-two female, aged nineteen to thirty years and of varying ethnicities. Full ethics approval was obtained from Queen Mary University of London Research Ethics Committee (Ref #0355) and all participants gave written consent of their acceptance to participate in the study.

Materials

To elicit the false memories, eighteen wordlists were used. Each wordlist consisted of the fifteen most commonly associated words of a critical non-presented word. For example the list *mad, fear, hate, rage, temper, fury, ire, wrath, happy, fight, hatred, mean, calm, emotion, enrage* is composed of the fifteen strongest associates of the word

anger and whilst the fifteen words in the list were shown to participants, the critical word *anger* was not.

The wordlists were constructed using the first fifteen words listed in the Russell and Jenkins (1954) norms for the critical non-presented words (see Roediger and McDermott, 1995, Stadler et al., 1999 for full details of list construction). The eighteen wordlists were chosen for their known ability to elicit a high proportion of false memories during recall (Stadler et al., 1999). The eighteen critical non-presented words used (and their corresponding fifteen wordlists) were: *Window, Sleep, Smell, Doctor, Sweet, Chair, Smoke, Rough, Needle, Anger, Trash, Soft, City, Cup, Cold, Mountain, Slow, River* (Stadler et al., 1999).

The wordlists were put into an automated computerised visual presentation in which each word was displayed in bold, black 'Calibri Headings' typeface, font size eighteen. Each word was displayed in the centre of a white screen at a rate of one second per word, with an inter-word interval of approximately five hundred milliseconds. To mark the start and end of a wordlist a white screen containing a black cross was displayed for one second. Following the end of each wordlist a blank white screen was displayed for two minutes. This coincided with the two minute free recall period (see below). The list order was randomised and the words within each list were presented in order of their associative strength to the critical non-presented word, strongest to weakest.

The recognition test was comprised of one hundred and eight words randomly ordered in four columns of twenty-seven on a sheet of paper. The one hundred and eight words were those from serial positions one, eight, and ten of each of the eighteen studied lists, the eighteen critical lures, and thirty-six unrelated words not found in any of the eighteen lists. The thirty-six unrelated words were selected from the other eighteen word lists published in Stadler et al. (1999) and from the Oxford English Dictionary.

The categorisation test consisted of forty-five printed questions. Each question consisted of five words, three of which were associated with one another and two of which were not. Participants were required to circle the two words that were not associated. An example of a question is as follows: *1. curve, arc, crouch, bend, medicine*, where *curve*, *arc* and *bend* are the three words associated with one another and *crouch* and *medicine* are the words to be correctly circled. Source materials for the categorisation test were example verbal reasoning questions for UK 11+ exams (secondary school entry exams). Questions were reproduced with copyright permission from Coordination Group Publications Ltd (Parsons, 2002a, b), Chukra Ltd (2007) and Eleven Plus Exam Group (2010).

Protocol

All participants were tested in one sitting. Participants were advised that they would be tested on their memory for lists of words and that they would be required to solve some word puzzles.

Participants viewed the visual presentation containing the eighteen wordlists on a large screen. At the end of each list a two minute recall period was given. During these free recall periods, participants were instructed to write down as many of the words from the list they had just seen as they could remember. Participants were instructed not to guess, but to only write down words that they were reasonably sure they had seen. Participants were provided with a booklet in which to write down their responses.

Participants then undertook the recognition test. They were instructed to carefully read the words on the sheet provided and to circle any words that they remembered being presented in the eighteen wordlists. Again participants were instructed not to guess but to only circle words they were reasonably sure they had seen.

After the final recall period a ten minute break was given, but participants were instructed not to talk to each other about the study. Participants were then given seven minutes to work through the categorisation test. Again they were instructed not to guess, but to only answer those questions to whose answer they were reasonably sure of. Upon completion participants were fully de-briefed as to the purpose of the study.

Data Analysis

The number of critical non-presented words recalled (false memories), the number of critical non-presented words recognised (false memories), and the number of errors made on the categorisation test were calculated for each individual. These were also converted to give percentage errors (out of those possible to produce) to display graphically. Two Spearman's rank correlations (Shapiro-Wilk normality test: $p<0.001$, skewness= 1.830, kurtosis=5.094 (leptokurtic distribution)) were used to look for a potential link between categorisation ability (categorisation test errors) and false memory susceptibility (recall and recognition errors). Additional correlations were used on subsets of the data to check for any biasing effects of priming, outliers and age. Finally, the numbers of recall, recognition and categorisation errors were compared between males and females using Wilcoxon rank sum tests to look for an effect of gender. All analyses were carried out using R statistical software (v.2.14.1).

5.3 Results

There were substantial inter-individual differences in both participants' verbal categorisation abilities and their scores on a standardised false memory test. Categorisation errors ranged from 7% to 78% in different individuals, showing that even though the test we had chosen was originally designed for pre-teens, the task was sufficiently challenging for the tested population to capture a large range of inter-individual variation (Fig. 5.1a). It was important to establish this since if all participants had had near-perfect scores (or indeed if all had had equally poor scores), the test would not have been suitable to correlate individual variation with other assessments of cognitive performance.

Variation in individual false memory scores was likewise extensive. Recall false memory scores ranged from 0% to 78% of possible false memories made (Fig. 5.1b). Two individuals did not recall a single critical non-presented word and thus had a score of zero (and 0%) for recall false memories. Conversely three individuals recalled thirteen out of the possible eighteen false memories (and thus scored 72%), and one participant even scored fourteen (78%). Recognition false memory scores ranged from 17% to 94% of possible false memories made (Fig. 5.1c). Five individuals recognised five or less of the critical non-presented words (and thus scored 28% or less), whilst eighteen individuals recognised thirteen or more out of the eighteen possible false memories (and thus scored 72% or more).
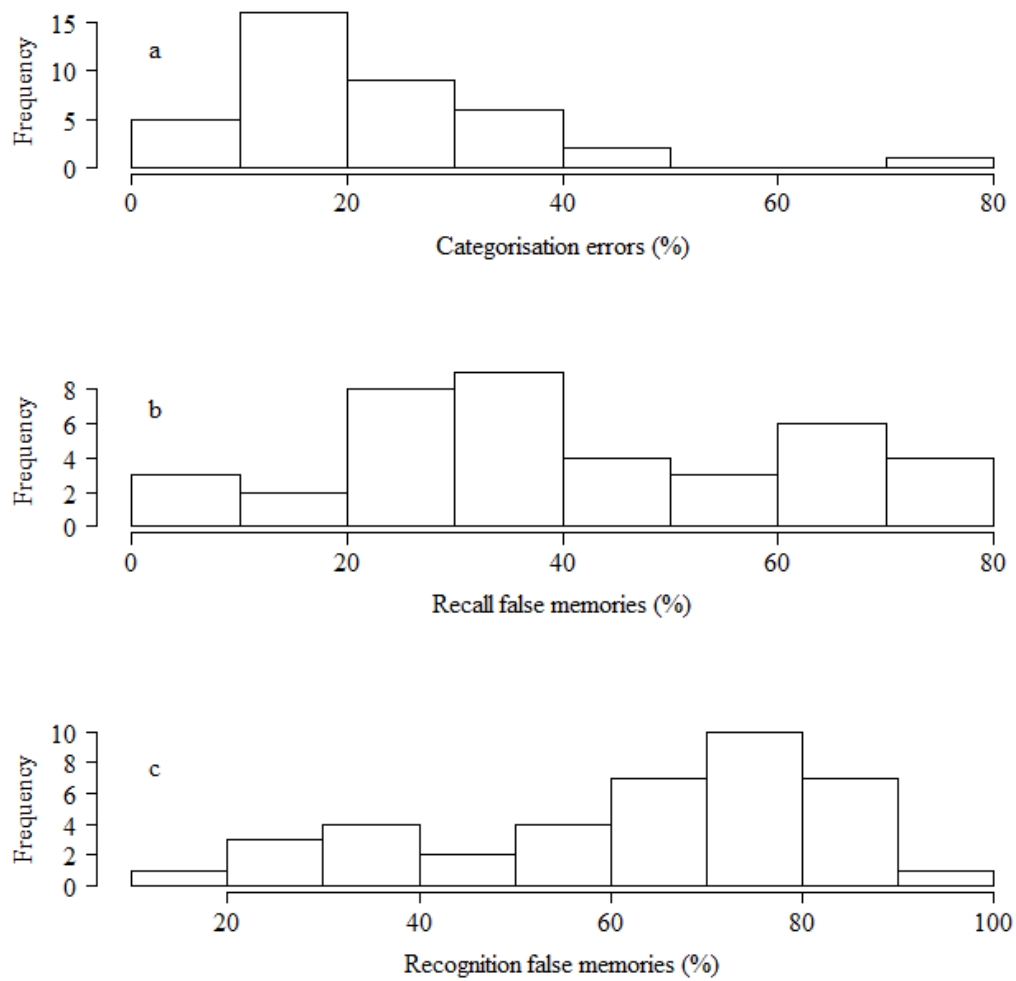
Figure 5.1 Frequency histograms for a) the percentage of errors scored by individuals on the categorisation test, b) the percentage of false memories (out of those possible to elicit) recalled by individuals during the DRM paradigm and c) the percentage of false memories (out of those possible to elicit) recognised by individuals during the DRM paradigm. N=39. All show a spread of inter-individual variation.

I found a significant negative correlation between individuals' categorisation error scores (given as the number of questions answered incorrectly on the categorisation test) and their false memory susceptibility during free recall (given as the number of critical non-presented words recalled) (r_s=-0.345, df=37, p=0.032, Fig. 5.2a), thus those individuals scoring fewer errors on the categorisation test were more susceptible to false memory intrusions during free recall. In other words, participants that performed worse on the one test performed better on the other, and vice versa – indicating an inter-individual trade-off between categorisation ability on the one hand and false memory susceptibility during free recall on the other.

Likewise, I found a negative correlation between individuals' categorisation error scores (given as the number of questions answered incorrectly on the categorisation test) and their false memory susceptibility during recognition (given as the number of critical non-presented words recognised), however this trend was not significant (r_s=-0.202, df=37, p=0.219, Fig. 5.2b). Thus, again, the trend shows that those individuals scoring fewer errors on the categorisation test were more susceptible to false memory intrusions during recognition.
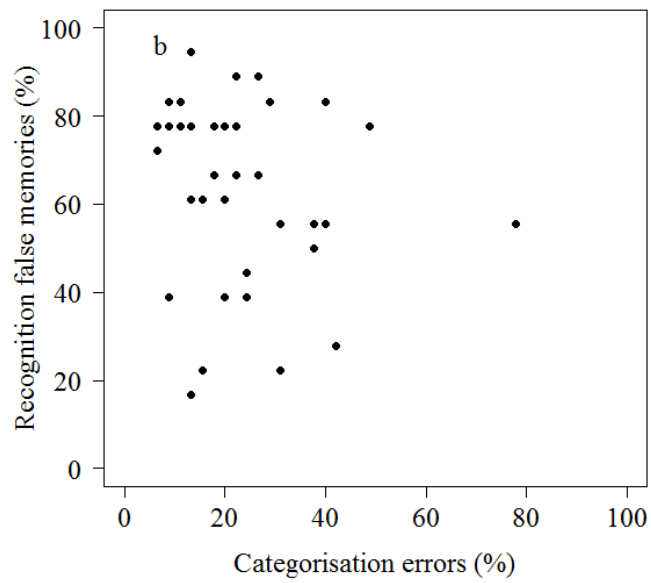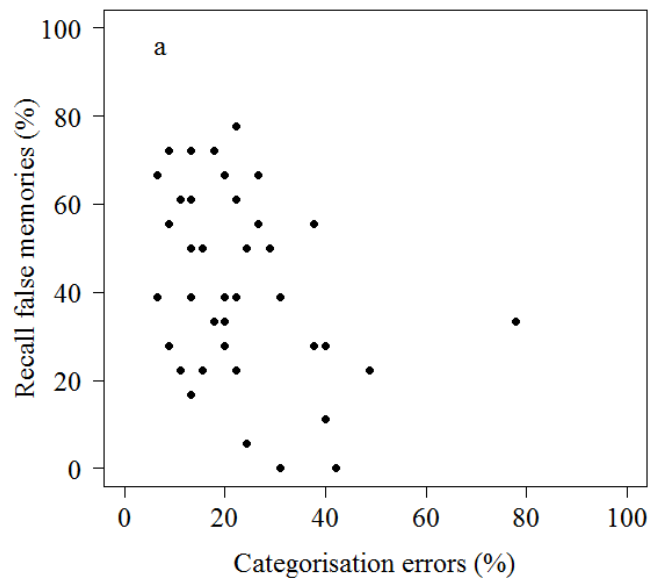
Figure 5.2 Individuals' categorisation abilities (given as the percentage of questions answered incorrectly on the categorisation test) plotted against their susceptibilities to false memories (given as the percentage of critical non-presented words a) recalled and b) recognised, out of those possible). Those individuals scoring fewer errors on the categorisation test were more susceptible to false memory intrusions and correspondingly had a higher false memory score.

To exclude the possibility that any correlation could be caused by priming, the data were also analysed excluding those categorisation test questions that contained words previously presented in the wordlists, and non-presented as one of the critical non-presented words. In our experiment for example, priming may have meant that the word *eye* presented as part of a question in the categorisation test: *41. Eye   neck   nose mouth   shoulder*, may have been preferentially selected as an answer due to its previous presentation in the word list associated with the critical non-presented word *needle − thread, pin, **eye**, sewing, sharp, point, prick, thimble, haystack, thorn, hurt, injection, syringe, cloth, knitting*. As such the scores for twelve questions were removed. A significant negative correlation was still found for free recall and a negative correlation still found for recognition; thus priming cannot account for the result (recall: r_s=-0.362, df=37, p=0.024, recognition: r_s=-0.206, df=37, p=0.208).

Additionally, the removal of an outlier (a residuals vs. leverage plot showed a Cook's distance greater than 0.5 for data point 24) did not change the statistical significance of the original result, thus it was not skewing the data unnecessarily in one direction and was therefore not the cause of the significant negative correlation found (recall: r_s=-0.341, df=36, p=0.036, recognition: r_s=-0.175, df=36, p=0.293).

The ages of the participants were not greatly varied, with thirty-six out of thirty-nine participants aged nineteen to twenty-one, one participant aged twenty-three, one participant aged thirty and one participant not stating their age. The removal of the data for the participant aged thirty did not change the statistical significance of the original result, thus the greater age of this participant in comparison to the others was also not the cause of the significant negative correlation found (recall: r_s=-0.387, df=36,

p=0.016, recognition: r_s=-0.251, df=36, p=0.129). Furthermore, the imbalance in the number of male and female participants (seven male, thirty-two female) is unlikely to have caused any bias in the data as there was no significant difference found between the two genders in the mean values for the recall errors (Wilcoxon rank sum test: W=114, p=0.956), recognition errors (Wilcoxon rank sum test: W=97.5, p=0.605) nor the categorisation test scores (Wilcoxon rank sum test: =102, p=0.727). Finally, the ethnicities of the participants were not taken into account when analysing the data due to inconsistencies in the responses received. Several participants failed to provide any information pertaining to their ethnicity, and many more provided details comprising of three different ethnic components. As such it was impossible to either elucidate which was the main ethnicity of these participants and/or to partition them into meaningful and comparable groups.

5.4 Discussion

My findings show a trade-off between word categorisation ability and semantic false memory susceptibility, so that individuals that make more errors on the false memory test make fewer errors on the categorisation test, and vice versa. Thus my results cannot simply be explained by differences in level of education, literacy, vocabulary or intelligence. If such an underlying factor would have explained performance on *both* tasks, then superior performance on one task would have been a predictor of superior performance on the other task. For example, short term memorisation of word lists recruits working memory, which is often regarded as a general predictor of intelligence (Oberauer et al., 2005, Oberauer et al., 2008) and likewise the categorisation tests used here are typical components of standardised intelligence tests (Wechsler, 2004, 2008). Thus one might have predicted a *positive* correlation of error scores in both tasks if an underlying single factor such as intelligence would explain the data. However, the correlation of error scores in the two measured tasks was *negative*. Thus even though this study is clearly correlative in nature, and therefore does not allow me to conclude with certainty that the two performances are based on the same underlying mechanisms, it is intriguing that having a lower tendency to generate false memories comes at a cost, i.e. lower categorisation scores.

To date the majority of scholars interested in false memories have focused on factors which may exacerbate or reduce the occurrence of such memory errors (Dodson et al., 2000). The adaptive nature of the human memory system as a potential reason for the occurrence false memories has been suggested (Schacter, 1999, Schacter, 2001), yet the ultimate reasons for their existence has been infrequently explored empirically. More recently, however, evidence has grown for links between individuals' differing

susceptibilities to false memories and their variations in a range of cognitive features. False recall and/or recognition rates in a DRM paradigm have been shown to vary with individuals' variations in levels of vivid mental imagery (Winograd et al., 1998), specific area expertise (Baird, 2003, Castel et al., 2007), working memory capacity (Watson et al., 2005) and need for cognition (Graham, 2007).

Additionally it has been shown that when survival-related (i.e. evolutionarily relevant) information is used in a list-learning paradigm, increased susceptibility to false memories occurs. Howe and Derbish (2010) found that when participants are asked to process words for their survival value and when the words presented were themselves survival relevant (i.e., *'death: burial, casket, cemetery, funeral, grave, life, murder, suicide, tragedy, widow*), veridical and false recognition were significantly higher (leading to an overall decrease in net accuracy) than when the words viewed were neutral or negative and were processed for pleasantness. They concluded that whilst it does not at first seem adaptive for survival-related memories to be less accurate and in fact be more prone to false intrusions than other types of memory, it does make sense if considered as a by-product of the adaptive processing of information related to survival. They argue that during the processing of information related to survival, any related information in memory is then primed, which may or may not be *false*, but that this information is then used to guide attention to other survival-related items, which may be crucial in the current situation (Howe and Derbish, 2010).

It has even been postulated that this greater inaccuracy may actually have adaptive significance, being more helpful in real-world scenarios. For example, in responses to predation threat, false alarms, such as generalising to a large set of cues that might indicate predator presence are clearly less detrimental errors than missing predator presence based on interpreting predators' cues too narrowly (Howe and Derbish, 2010). Thus my finding of a significant positive correlation between susceptibility to semantic false memories in a free recall DRM paradigm and word-based categorisation ability, with the creation of these errors a by-product of our ability to group words, is in keeping with recent findings.

The population from which the subjects for this study were drawn is ethnically and culturally diverse. As a result some may argue that a small number of the words presented in the study, which was constructed from American and British materials may have had different meanings to some of the participants. One example is the non-presented critical word *needle* and one of its corresponding associates *haystack*. Whilst participants with a western cultural background would have been expected to connect the two words due to the use of the famous saying *needle in a haystack*, participants with Chinese heritage may not have as it is known that the saying is largely unknown in China (Lee et al., 2008). I would argue however that as all participants were studying for an undergraduate university degree taught only in English, any non-native participants, potentially with a different primary language would have had to have met a minimum requirement for English language comprehension dictated by one of three internationally renowned assessors (IELTS, IBTOEFL or PTE Academic) to be granted a place at the university. This would at least have partially negated any potential non-comprehension of the words used. Additionally no other previous DRM-based studies

have looked at the potential effects of ethnicity on semantic false memory production. I was unable to include this variable in the analysis due to the inconsistencies in the responses given by the participants. In order for this variable to be analysed in any future studies it may be prudent to provide participants with pre-set ethnicity categories to place themselves into.

Whilst the age range of the subjects tested was narrow (nineteen to twenty-one years old in the majority) many of the key studies using the DRM paradigm have used only participants also of average undergraduate college study age (Roediger and McDermott, 1995, Stadler et al., 1999). Additionally the only significant difference in spontaneous false memory creation, caused by the DRM paradigm that is known to occur between participants of different ages, is between children and adults. Several studies have shown that children are less prone to these memory errors, with an increase in their propensity occurring during both childhood and early adolescence (Brainerd et al., 2002, Brainerd et al., 2004, Forrest, 2002) . As such, inferences made from my findings are not just applicable to young adults but should also be to the 'average' adult population as a whole.

My result of a significant negative correlation between individuals' errors on a categorisation test and their susceptibilities to semantic type false memories during free recall demonstrates that false memories, to some extent, might be a by-product of our ability to learn rules, categories and concepts. For example, once we have learnt the concept/category of *mammals*, we can identify new animals as members of this category even if we have never seen them before. In this case, labelling the new animal as mammal is not based on false classification, but a correct one based on category

membership: the simple flipside of the DRM paradigm, where inferences based on concepts and categories are classed as errors. Thus, my findings add to the increasing body of literature that proposes that false memories might be an inevitable by-product of adaptive cognitive processes as is the case with other memory aberrations (Abbott and Sherratt, 2011, Beck and Forstmeier, 2007).

Chapter 6: General Discussion

6.1 Summary of Chapters

It has long been known that human memory is surprisingly fallible, with errors ranging from the incorrect recall or recognition of simple words (Deese, 1959, Roediger and McDermott, 1995) to the insertion of current beliefs and stereotypes into a 'remembered' scenario (Bartlett, 1932), to the false 'remembering' of entire autobiographical events (Loftus, 1975, Loftus, 1993). Recently, the known transgressions of human memory have been re-classified into seven types, with a comparison made to the seven sins of the bible (Schacter, 1999, 2001). Further to the re-classification it has been proposed that whilst these 'memories' are obviously erroneous, they may not be the evolutionary paradox they that they appear. Schacter (1999, 2001) insinuates that these errors are in fact the inevitable by-products of our adaptive memory processes. However, to date the majority of research has focused primarily on the formation and incidence of these errors in human memory, with only a few studies looking into the potential occurrence of such errors in non-human animal species (Harper and Garry, 2000, Schwartz et al., 2004).

The overall aim of this thesis has been to investigate whether two species of social insects are also susceptible to the types of false memory errors known in humans. Additionally I have discussed the potential scope for the use of animal models in the study of false memories. Using the bumblebee *Bombus terrestris* and the honeybee *Apis mellifera,* the preceding chapters have explored how the memory of pollinating insects may be effected by an innate preference (similar to known biases/stereotypes), multiple memory traces and postevent cues (akin to misinformation). I have also examined the

potential relationship between an adaptive cognitive process (categorisation), utilised for memory efficiency and the formation of semantic type false memories as elicited by the Deese-Roediger-McDermott (DRM) paradigm. My investigations have explored, on both bees and human subjects, the adaptive perspective on false memories proposed by Schacter (1999, 2001). The data presented in my dissertation imply that a pollinating insect may be susceptible to at least one type of memory error that humans are: the memory conjunction error, but that the methodological changes required and the potential differing learning and memory processes utilised, may make animal models, or in this specific case pollinating insect species unsuitable for the study of some specific memory errors, such as those created by pre-existing beliefs/biases about the world, and to some extent the influence of misinformation. Additionally, a relationship does exist between an adaptive cognitive process and a known human memory error, more specifically our ability to categorise and the semantic errors created by the (DRM) paradigm. This lends weight to the adaptive perspective argument.

6.11 Memory fallibility in bees

Despite the lack of literature on the susceptibility of non-human animals to known human memory errors, the small amount of work undertaken has revealed perhaps surprisingly analogous results, with the pigeon *Columba livia* (Harper and Garry, 2000), the rat *Rattus norvegicus* (Garry and Harper, 2009) and a gorilla *Gorilla gorilla gorilla* (Schwartz et al., 2004) all being shown to be biased by postevent cues, akin to misinformation. The potential occurrence of false memories in pollinating insect species are the focus of Chapters 2, 3 and 4.

In Chapter 2 I found that the innate preference for bilateral symmetry in the bumblebee *Bombus terrestris*, akin to a bias/stereotype in humans (Banaji and Bhaskar, 2000, Bartlett, 1932), does not influence memory degradation in the way in which pre-existing thoughts about the world directionally alter human memory. Memory simply weakened over time, such that three days post training all possible artificial flowers were chosen with roughly equal frequencies, rather than the flower containing the innate preference (bilateral symmetry) being chosen at a higher frequency.

In Chapter 3 I found that the bumblebee *Bombus terrestris*, when utilising long-term memory commits a 'merging' error akin to the memory conjunction error known to occur in humans (Reinitz et al., 1992). Twenty-four hours after learning first a black and white pattern, then a colour, bees erroneously chose a hybrid flower that comprised a combination of the two learnt visual features: colour and pattern. This is, to my knowledge the first example of memory 'merging' in a non-human animal.

In Chapter 4 I explored the potential for the effect of 'misinformation' in two further non-human animal species: the bumblebee *Bombus terrestris* and the honeybee. My findings indicate that neither species is susceptible to the 'misinformation effect' in the way that humans (Loftus and Palmer, 1974, McCloskey and Zaragoza, 1985), pigeons (Harper and Garry, 2000), rats (Garry and Harper, 2009) and a gorilla are (Schwartz et al., 2004), with memory retention for original colour information remaining high regardless of the type of postevent cue used. However, my findings also highlight important methodological issues with using these pollinating insect species to study this type of memory error.

6.12 Human false memories: semantic errors and categorisation ability

Chapter 5 investigated the potential adaptive perspective argument of false memories, as postulated by Schacter (Schacter, 1999, 2001). I found a trade-off between word categorisation ability and semantic false memory susceptibility, such that individuals who made fewer errors on a categorisation test, made more errors on a false memory test, and vice versa. Whilst only correlative in nature, my results lend weight to the argument that misattribution errors of which the semantic errors elicited using the DRM paradigm are, are inevitable by-products of our adaptive cognitive ability to generalise, and form categories and concepts (Schacter, 1999, 2001).

6.2 Bees as a model for memory errors?

Bees have been extensively used as model systems to study learning and memory (Giurfa, 2003, Menzel, 1968, 1969, Menzel and Giurfa, 2001, Von Frisch, 1967), with much in the literature regarding the capabilities of both honeybees and bumblebees. Many bee species are known to utilise similar cognitive abilities to those proposed to cause a variety of memory errors in humans (Avarguès-Weber et al., 2012, Dukas, 1995, Rodriguez et al., 2004, Zhang et al., 2004). As a result this thesis used the bumblebee *Bombus terrestris* and the honeybee *Apis mellifera* to explore the potential use of bees as animal models for the study of known memory errors.

In humans preferences, biases and stereotypes are known to cause 'bias' errors in declarative memory, such that memories are subconsciously 'altered' to fit in with the subjects' pre-existing beliefs about the world (Bartlett, 1932). It is thought that this type of error could be caused by our ability to generalise, e.g. our ability to group people and or objects based on past experiences (Schacter, 1999), to economise memory so that items or events may be remembered based on just a few rules rather than a large number of specific details (Chittka and Niven, 2009). The bumblebee *Bombus terrestris* is known to have an innate preference for bilateral symmetry (Rodriguez et al., 2004), with naive individuals preferentially choosing bilaterally symmetric black and white patterned artificial flowers when given the choice between those and asymmetric ones (Rodriguez et al., 2004). Additionally honeybees can detect and generalise symmetry and asymmetry (Giurfa et al., 1996), with bees trained to discriminate bilaterally symmetric from asymmetric patterns both successfully learning the task, and also transferring the learnt cues to novel artificial flowers (Giurfa et al., 1996, Giurfa and Menzel, 1997). Thus, as bees are capable of generalisation they and show an innate

preference, which may be considered akin to a bias or preference shown by humans, they were considered potentially suitable for use as non-human models for the study of such a memory error.

However the bumblebee *Bombus terrestris* showed no such memory error, with no effect of the innate preference for symmetry seen on memory degradation. Both those bees trained to a bilaterally symmetrical artificial flower and those trained to an asymmetrical flower showed a general decrease in memory retention over time, with all artificial flower types being chosen at around chance levels three days after training. Whilst there is some evidence that methodologies adapted from human false memory studies for use with non-human animals produce results that are comparable (Garry and Harper, 2009), the method used in my study differed vastly from that used for humans (Bartlett, 1932). Many of the classic human false memory studies (Loftus and Palmer, 1974, Roediger and McDermott, 1995), such as the one this experiment was based on (Bartlett, 1932) rely on verbal communication which is potentially why so few have been successfully adapted for work in non-human animals. Additionally, it could be argued that the innate preference for bilateral symmetry is not truly akin to a bias, preference or stereotype in humans, as it is innate and not learnt. As such bumblebees may not be suitable for studying this type of memory error.

Given that previous studies of known human memory errors in non-human animal species have focused on postevent cues (akin to misinformation, in which secondary information biases an existing memory) inserted into delayed matching-to-sample (DMTS) tasks (Garry and Harper, 2009, Harper and Garry, 2000, Schwartz et al., 2004), this thesis investigated whether bees would make ideal candidates for the study of the

effect of postevent cues ('misinformation') in an animal model. Bees have shown the pre-requisite cognitive requirements to be utilised in such a study, more specifically the ability to utilise non-elemental learning, in which knowledge as to the relationship between objects, rather than the specific physical features of the objects is needed to solve a task (Dale et al., 2005, Giurfa et al., 2001). Honeybees can successfully learn both DMTS tasks and delayed non-matching-to-sample (DNMTS) tasks using both solid colours and horizontal or vertical striped patterns, with the ability to transfer these concepts between the sensory modalities of olfaction and vision (Giurfa et al., 2001). Bumblebees have also shown some ability to learn a colour-based DMTS task, but only if spatial cues were also available to find the rewarded colour (Dale et al., 2005). It has been inferred that 'misinformation' causes declarative memory errors due to our inability to correctly attribute memories to their original source (Schacter and Dodson, 2001). In turn this error type could therefore be considered as an unwanted by-product of our ability to group things together, for example by generalising or categorising, which allows a large amount of information to be stored and retrieved, using only a small number of presented exemplars (Chittka and Niven, 2009, Schacter, 1999). Honeybees can categorise objects based on general features, such as 'landscapes', 'plant stems' and 'flower types' (Zhang et al., 2004) and can utilise olfactory (Wright et al., 2008) and number-based visual generalisations (Gross et al., 2009). Additionally the bumblebee *Bombus terrestris* is known to generalise to colours after learning, such that those test colours most similar in colour to the learnt colour are chosen with the greatest frequency (Gumbert, 2000).

However, again, bees showed no memory error, which is inconsistent with both the literature on the 'misinformation effect' in humans (Loftus and Palmer, 1974, Loftus, 1975) and the effect of postevent cues on other non-human animal species (Garry and Harper, 2009, Harper and Garry, 2000, Schwartz et al., 2004). In both the honeybee and the bumblebee *Bombus terrestris* memory retention was not affected by postevent cues, such that bees that successfully learnt the three-colour DMTS task continued to show high levels of memory accuracy for the sample regardless of the type of postevent that was inserted at the end of the delay. Additionally, due to methodological issues, the sample sizes obtained were low. Furthermore bumblebees showed significant side biases, which appeared to be innate, rather than learnt and as such may be akin to 'handedness' in humans (Goulson et al., 2013, Kells and Goulson, 2001). Three species of bumblebee (*Bombus lapidarius*, *Bombus lucorum* and *Bombus pascuorum*) have previously been shown to exhibit such behaviour (Kells and Goulson, 2001). Thus bumblebees may not be a suitable model system for the study of 'misinformation' which if adapting protocols from other non-human animal studies involves the use of a spatially separated maze-based paradigm. Additionally honeybees may not have actually been successfully learning the DMTS task in its truest sense. In a traditional bee DMTS paradigm the sample is always presented at a fixed distance along the tunnel. As such Zhang et al. (2005) proposed that honeybees are simply learning to attend to whatever is at that fixed distance as opposed to really learning the concept of the task – to remember what the sample is, no matter what it is, as long as it is the first 'item' encountered. They found that after training to fixed distance samples, if the distance of the sample was then varied during the test, bees' memory retention was severely affected and choices for the correct comparison flowers fell to chance level. Therefore honeybees may also not be suitable for the study of the effect of

'misinformation', or at least not without significant alterations being made to the existing protocols.

The memory conjunction error, in which memories for multiple items are combined to create a hybrid 'memory', occurs for words, sentences and pictures of faces in humans (Reinitz et al., 1992, Reinitz and Demb, 1994). It is thought that this type of error may be caused by a retrieval error in which 'memories' are recalled based on a feeling of familiarity, rather than from identifying specific features (Rubin et al., 1999). In turn this may be due to our ability to gain storage and retrieval efficiency by generalising and/or categorising (McClelland, 1995). The bumblebee *Bombus occidentalis* has been shown to be capable of both simultaneously holding and alternately retrieving memories for two different colours in order to solve two separately presented colour choice tasks (Dukas, 1995). Additionally, the honeybee can simultaneously utilise two concepts, such that both an abstract involving spatial relationships: either above/below or left/right, and an abstract concept involving the perception of difference can not only be learnt, but also successfully transferred as a dual-concept to correctly locate unknown targets that are the best match of both concepts: the learnt spatial relationship and those different from one another (Avarguès-Weber et al., 2012). Furthermore, interference, in which multiple memory traces interfere with one another, has been shown to occur in several bumblebee species. Retroactive interference, in which newly learnt information impedes the recall of prior learnt information (Müller and Pilzecker, 1900), effects the sensorimotor memories of flower handling in *Bombus impatiens* (Chittka and Thomson, 1997, Gegear and Laverty, 1995) and *Bombus bimaculatus* (Woodward and Laverty, 1992), and colour memory in *Bombus occidentalis* (Dukas, 1995). As previously mentioned, several bee species are capable of generalising (*Bombus pascorum*, *Bombus*

vtteranus, *Bombus urratris*, *Bombus lapidarius*; Chittka et al., 1997, *Apis mellifera*; Giurfa et al., 1996, Wright et al., 2008), categorising (*Apis mellifera*; Dukas and Waser, 1994, *Bombus flavifrons*; Zhang et al., 2004) and even forming concepts (*Apis mellifera*; Avarguès-Weber et al., 2012), Thus, again bees were considered a potentially good model to investigate a known human memory error, in this case an error specific to the integration of multiple memories.

The bumblebee *Bombus terrestris* was indeed found to commit this type of memory error. When required to utilise long-term memory for multiple visual targets that were previously rewarded bees committed an error in which information from multiple memory traces 'merged'. Bees initially trained to a black and white concentric circle pattern and then a solid yellow colour preferentially chose an artificial flower comprised of components of both training flowers: yellow and white concentric circle pattern, twenty-four hours post training. This is, to my knowledge, the first example of this known human memory error occurring in a non-human animal species.

It therefore appears that differences in learning and memory processes utilised by bees when undertaking the classic DRM paradigm in comparison to both humans (Garry and Harper, 2009) and the non-human animal species the pigeon (Harper and Garry, 2000), rat (Garry and Harper, 2009) and gorilla (Schwartz et al., 2004), combined with the known problem of adapting verbal-based human methodologies for use in non-human animal species, may make bees unsuitable animal models for the study of known human memory errors. However, this thesis has reported, for the first time in a non-human animal, a memory 'merging' error akin to the memory conjunction error shown by humans (Reinitz et al., 1992). Thus bees may still be suitable for the study of certain

human memory errors. What is clear is that the learning and memory processes utilised by bees in cognitive tasks need to be thoroughly considered when both designing new protocols and adapting existing methodologies.

6.3 Memory errors: An adaptive perspective?

Schacter (1999, 2001) has proposed that whilst memory errors may seem maladaptive, they may in fact be the inevitable by-products of the many adaptive features of human memory. One common type of memory error is the semantic memory error, experimentally elicited using the DRM paradigm. In this paradigm, participants study lists of words each comprising of associates of one critically non-presented word. During subsequent recall or recognition of the wordlists, the critically non-presented words are remembered both with high frequency and with high levels of confidence. The high proportion of false memories produced is attributed to the strength of the associations between the words actually presented and the words falsely remembered (and thus, critically non-presented) (Deese, 1959). Under Schacter's (1999, 2001) recent re-classification or memory errors, these semantic false memories fall under the category 'Misattribution' and as such are thought to occur due to assigning information to the incorrect source. In turn it is thought that they may be caused by our ability to generalise and form categories and concepts (Schacter, 1999, 2001). Categorising is adaptive as it economises memory, allowing us to both store and recall a large amount of information based on just a few criteria (Chittka and Jensen, 2011). However, as a result we may occasionally erroneously 'remember' members of a category, as although they were not actually presented themselves they were thought of when their exemplars were presented (McClelland, 1995). Thus, my finding of a correlation between individuals' susceptibility to semantic false memories elicited by the DRM paradigm and their categorisation ability lends weight to Schacter's (1999, 2001) theory. Individuals that made more errors on the false memory task made fewer errors on the categorisation test, and vice versa. My results therefore add evidence to support the increasing that postulates that false memories may be inevitable by-products of adaptive cognitive processes.

6.4 Improvements and future work.

The mixed results reported in this thesis give rise to the potential for both improvements of the existing work and further experiments that may build upon the work set out here:

As previously stated it could be argued that the innate preference for symmetry in bumblebees is not completely akin to a human bias, preference or stereotype and as such the results reported in Chapter 2 may not be sufficient to form a firm conclusion as to whether bees memories' are affected by this types of error, as human memory is. In humans biases, preferences and stereotypes tend to be learnt rather than innate, even if they are somewhat subconsciously learnt, simply through observation and imitation, rather than actively learnt, through more direct experience (Mackie et al., 1996). Therefore there is perhaps scope to repeat the experiments in Chapter 2 using a learnt preference (i.e. bees previously trained to prefer a set colour/pattern/orientation), rather than an innate preference, as this may be more similar to human bias.

Additionally, the experiments reported in Chapter 4 did not generate sufficient data for analysis. It appears that the bumblebee *Bombus terrestris* is incapable of learning the traditional DMTS paradigm, potentially due to side biases akin to handedness in humans (Kells and Goulson, 2001). This would make it virtually impossible to repeat the experiment in order to gain more data. Upon consultation with a colleague I was informed that bumblebees have been successfully trained to a two-colour DMTS using a modified arena (Schumacher, 2010), but I was not able to replicate their results. On the other hand the honeybee data could easily be extended upon, as the protocol worked well, but was simply limited by the weather conditions. As such more data could easily

be generated when weather conditions were more optimal (i.e. hot, with little wind), to confirm the tentative results found in this thesis. However my results showed that although honeybees do not appear to be effected by postevent cues, in the way in which humans are by misinformation, this may actually be due to both the way in which honeybees learn the DMTS task and the experimental design. Bees may simply have been remembering what was presented at a fixed distance, rather than what was specifically presented (Zhang et al., 2005), thus in order to truly test for any effect of postevent cues on memory, the honeybee experiment in Chapter 4 would need to be repeated, but using a DMTS task in which the sample distance was varied, in order to prevent the learning of a distance and promote a more general learning of the overall concept/rule: to remember the sample seen before the delay period.

Again, it is apparent that the learning and memory processes utilised by bees in undertaking cognitive tasks need to be well understood when designing protocols to both improve and extend any work reported in this thesis.

Furthermore, whilst my finding in humans of a correlation between an adaptive cognitive ability: categorisation, and a known type of memory error: semantic false memories elicited by the DRM paradigm lends weight to Schacter's (1999, 2001) theory that memory errors are the inevitable by-products of our adaptive cognitive processes, it would be interesting to see widely this correlation holds true. The experiment in Chapter 5 could be extended to investigate different types of categorisation ability, i.e non-verbal (pictoral), and include alterations to the modalities of delivery of the two tests i.e visual vs. auditory, to look at whether saliency is needed for the correlation to occur.

6.5 Conclusion

The work presented and reviewed in this thesis illustrates that a pollinating insect is to some extent susceptible to the types of errors known from studies of human memory. It presents the first example of a memory merging error, akin to the memory conjunction error in non-human animal species. However, my dissertation also highlights the potential difficulties in adapting known and successful methodologies for use with different species. Furthermore false memories may not be quite the evolutionary paradox they first appear to be, but might in fact be the inevitable by-products of our adaptive cognitive abilities that on the whole enable the intricacies and efficiencies shown by human memory.

Acknowledgments

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