

ANIMAL MEMORY AND ANIMAL WELFARE

M Mendl[†], O Burman, K Laughlin and E Paul

Centre for Behavioural Biology, Department of Clinical Veterinary Science, University of Bristol,
Langford House, Langford BS40 5DU, UK

[†] Contact for correspondence and requests for reprints

Abstract

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Retrieved memories of emotionally laden events are likely to influence the ongoing emotional state and behaviour of animals. If animals consciously experience memories and/or associated emotions, then recall of aversive or pleasurable events will affect their welfare. Even if they do not, retrieval of these (non-conscious/implicit) memories may result in behaviour, such as attempts to escape, that could lead to injury and damage. There is growing evidence that emotionally laden events are more readily stored in memory than neutral ones, and that the neurophysiological basis of this, involving acute elevations of the classic stress hormones and the action of the amygdala, is similar in humans and other vertebrate species. Thus, in humans and animals, emotional memories are likely to be stored as priority information and may readily be retrieved in the presence of relevant cues. If so, an important practical goal is to minimize the chances of negative emotional memories being cued inappropriately, especially for animals in captivity. Disruption of memory formation and retrieval is also important in an animal welfare context. Chronic or very high elevations of stress hormones appear to have both short- and long-term effects on brain structure and function that can interfere with efficient storage of information. Environmental disturbances, including common husbandry procedures, can also disrupt memory formation through retroactive interference effects. Elevated stress levels may both increase the chances of retrieval of negative information while hampering the retrieval of positive or neutral information. These effects may lead to poor learning abilities, selective or disrupted memory retrieval, and consequent inappropriate behaviour with adverse welfare consequences. If we understand them, we may be able to recommend housing or husbandry procedures that minimize the likelihood of their occurrence.

Keywords: *animal welfare, emotion, memory, stress*

Introduction

Memories are our most enduring characteristic. In old age we can remember our childhood 80 or more years ago; a chance remark can conjure up a face, a name, a vision of sea or mountains once seen and apparently long forgotten. Memory defines who we are and shapes the way we act more closely than any other single aspect of our personhood.

Steven Rose (1992) eloquently describes the fundamental importance of memory to the human condition. Memories are a major part of our conscious existence. Not only do they offer continuity to our subjective experience, they also influence how we act and feel in any situation. Sights, sounds and smells can trigger memories of previous experiences and associated emotions. Happiness, anxiety, fear, embarrassment and many other emotions may

be elicited and influence our ongoing mood. For people who have experienced very traumatic events, the intrusive recall of these can become a clinical problem that may severely disrupt their lives (Turnbull 1998). Memories can thus have a profound influence on our sense of well-being.

Although it is possible that animal memory affects animal welfare in a similar way, most scientists agree that we do not know whether non-human animals (hereafter animals) are able to consciously experience memories and emotions, or other sensations and cognitions (eg Baars [2001]; Bermond [2001]; Dawkins [2001] but see Wemelsfelder [1997] for a different view). Therefore, animals may store and retrieve information, and associated emotions, with or without conscious experience (memories that are consciously or non-consciously retrieved are sometimes referred to as, respectively, explicit and implicit memories). These possibilities are represented in Figure 1 in the context of memory retrieval. A cue triggers retrieval of a neural representation of a previous event (a memory) which may be associated with, or lead to, changes in neurophysiological activity indicative of a particular emotional state. Both the memory and the emotion, or only one, or neither of these may be consciously experienced. They may also be associated with, or cause, a behavioural response. For example, the odour of latex gloves used to handle a laboratory rat during a procedure such as injection may trigger explicit or implicit memories of that event, and associated emotional states such as anxiety or fear. Irrespective of whether these are consciously experienced or not, they may be linked with a behavioural response such as escape or avoidance.

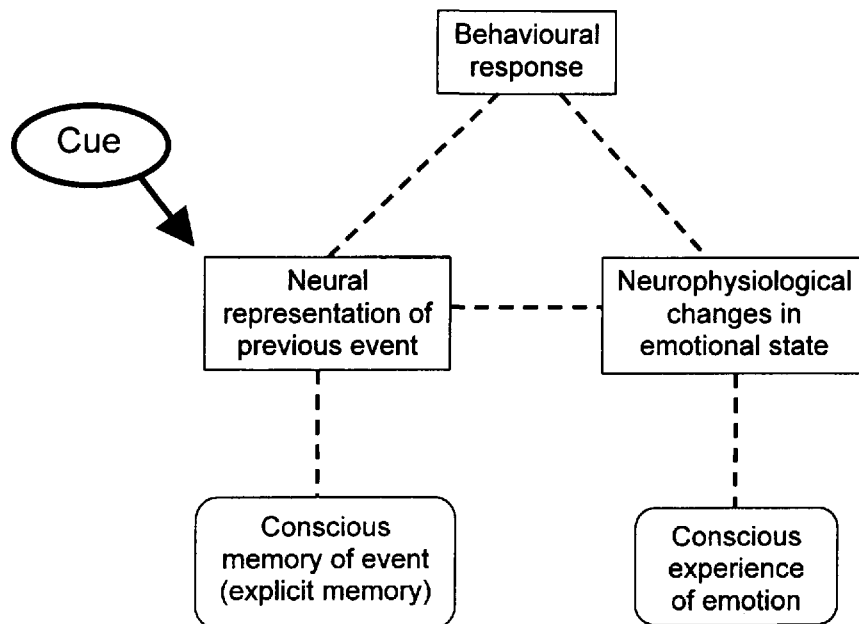


Figure 1 Diagram showing hypothetical relationships between neurophysiological events, behavioural events and conscious experience that may occur when a memory is retrieved. A cue triggers retrieval of a neural representation of a previous event. This may be associated with or lead to neurophysiological changes in emotional state. Both may or may not be consciously experienced, and may be linked with, or cause, a behavioural response.

The dramatic effects of memory on human well-being described above are most likely to occur in animals if they do consciously experience memories and/or associated emotions. However, even if they do not, such memories may be linked to behaviour, for example attempts to escape, which could lead to injury or damage. In both cases, memories that are emotionally neutral are likely to have considerably less effect on an animal's behaviour and/or welfare than emotionally laden memories which may induce negative or positive affective states and potentially damaging behavioural responses. Therefore, one question we consider in this paper is whether emotional memories are more readily stored and retrieved than emotionally neutral memories, and whether any relationships between emotions and memory that exist in humans also occur in non-human animals.

Captive animals may have less need for certain forms of memory than their wild relatives, but they still rely on memory in a variety of situations. Recognition and memory of other individuals is likely to be important for pigs who may be housed with a much larger number of conspecifics than their ancestors evolved to live with (Mauget 1981; Mendl 1995). Mother-offspring recognition and memory remain crucially important in farmed species such as sheep (see Kendrick *et al* [1997]). Chickens housed in large indoor barns may use spatial memory abilities to locate important resources such as food, water, familiar sub-groups and nesting areas. Animal management and welfare are likely to be enhanced if animals can effectively learn and remember how to use unfamiliar equipment such as robotic milkers or electronic sow feeders, and that routine procedures such as weighing are essentially harmless.

Effective acquisition, consolidation and retrieval of memories is essential for an animal to function efficiently in all these situations. Disruption of these processes may result in failure to remember, for example, group members or the location of feeding sites, and cause inappropriate behaviour with detrimental welfare consequences, such as aggression towards familiar animals. An understanding of the processes whereby memories are formed and retrieved, and of how these can be influenced by environmental factors and the animal's own internal state, is thus of relevance to animal welfare research.

In this paper, we introduce findings from research on memory acquisition, consolidation and retrieval. In particular, we consider the role of the animal's emotional or stress state in modulating these processes. We also examine how they can be affected by environmental factors, including common husbandry procedures. We focus primarily on studies of animal memory, although we use examples from research on humans to indicate similarities or differences in memory processes. Most of the animal work we mention is based on studies of mammals, principally rodents, and some bird species. We use the word 'animal' for convenience, but the extent to which the findings presented generalize beyond the species studied is not known. Studies of human and animal memory form a vast research literature, and our overview will necessarily be selective. Our aim is to provide an introduction to this area and its relevance to animal welfare. To this end, we also review some of our recent and ongoing work on animal memory in an animal welfare context.

Throughout the paper, we follow the schema illustrated in Figure 1. Therefore, when we use the terms memory or emotional state we are not implying that these are consciously experienced by animals. They may or may not be, and we discuss this explicitly at some points in the paper. Nevertheless, the possibility exists that some, many or all animal species do indeed have the capacity for conscious experience. Given this, it is important to investigate phenomena that may influence the nature of this conscious experience and hence the welfare of the animals (see Bradshaw [1998]).

Types of memory

Memory processes or systems can be subdivided into various types. Different researchers use different terminology and sometimes different criteria to distinguish systems (see Tulving [1972]; Baddeley [1996]; Pearce [1997]; Kandel & Pittenger [1999]). A common distinction is between short-term (working) and long-term (reference) memory. The former usually holds (limited) information for a few seconds or minutes, while the latter stores information for longer periods and appears to have a vast capacity.

Long-term memory can be further subdivided into semantic (memory for factual information), and episodic (memory for specific events). Another type of distinction is between so-called implicit (or procedural/non-declarative) and explicit (or declarative) long-term memory. The term implicit memory is often used to refer to memory underlying simple learning phenomena such as habituation, simple classical conditioning, certain forms of non-associative learning, and motor and skill learning. Explicit memory, on the other hand, refers to memory for events and facts. A different distinction mentioned earlier, and one which is often made in studies of humans and sometimes generalized to animals, is that implicit memories can be accessed without awareness or consciousness, while retrieval of explicit memories requires conscious involvement (see Seger [1994]; Shanks & St John [1994]). This latter distinction is most relevant in the context of this paper, and we will return to it later.

Emotion, stress and the enhancement of memory

In what follows, we use the word 'emotional' in the sense that an 'emotional event' is one that induces a particular brain state (eg by altering activity in certain brain areas such as the amygdala), and associated neurophysiological changes such as arousal or an acute physiological stress response. In humans, these responses are likely to have a conscious correlate which can be reported, and which we commonly refer to as an 'emotion' (eg the feeling of fear, anxiety, happiness, etc). In animals, we cannot be sure about conscious experience, but we can measure neurophysiological and behavioural indicators of 'emotion'. The possibility that neurophysiological changes in emotional state are not consciously experienced is openly acknowledged by some researchers (see Rolls [2000] and commentaries therein).

Most of us would probably agree that events which had an emotional impact seem easier to remember than those which were emotionally neutral. Experimental studies of human memory support this intuition (eg Christianson *et al* [1991]; Cahill *et al* [1994]; Reisberg & Heuer [1995]). In some way, situations which induce states of positive or negative emotional arousal (as indicated by, for example, elevated activity of the sympathetic nervous system) are more readily stored in and/or retrieved from memory. A similar process in animals would indicate that negative experiences under captive conditions are readily committed to memory, with the potential to influence an animal's emotional state when recalled.

Recent research has indicated that the stress or arousal state of an animal at the time of an event does indeed modulate, and can enhance, the storage of the event in long-term memory. Furthermore, the underlying neurophysiological mechanisms involved appear to be strikingly similar to those seen in humans. The majority of animal studies involve one-trial learning tasks, often active or passive avoidance, where retention in memory is inferred from behaviour (eg is avoidance shown?) in a test several hours after the training experience. Although aversive tasks have been most common, appetitive tasks have also been used and have shown similar results (Sternberg *et al* 1985; Packard & White 1990).

A major finding of these studies is that administration of the classic 'stress' hormones, the catecholamines (eg adrenaline) and glucocorticoids (eg cortisol), at the time of the to-be-learned event can enhance memory for that event (eg Gold [1992]; Sandi & Rose [1994]). This enhancement could occur by alteration of attentional processes during the event itself (reviewed by Lupien & McEwen [1997]; Mendl [1999]). However, studies of humans have indicated that changes in attention cannot fully account for enhanced memory of emotionally arousing events (eg Christianson *et al* [1991]). Furthermore, in animal studies, memory-enhancing effects are also observed if stress hormones are administered during the hour or so following an event, ruling out an effect of attention (eg Sandi *et al* [1997]). A growing body of evidence from the animal studies indicates that one action of these hormones is to enhance consolidation of the event in memory; ie to ensure that, during the period following the event, information is more effectively stored in long-term memory (Cahill & McGaugh 1996, 1998).

In humans, too, there is evidence that the actions of catecholamines, in particular, can enhance memory for events (Cahill *et al* 1994; Nielson & Jensen 1994; Nielson *et al* 1996; van Stegeren *et al* 1998). For example, Cahill *et al* (1994) showed that subjects recalled and recognized emotionally arousing parts of a story better than a similar but less arousing story when tested 1 week later. However, if given a β -adrenergic receptor blocker an hour before viewing the stories, the enhanced memory for the emotional parts of the story was eliminated (Figure 2). The implication is that elevations in catecholamine levels induced by witnessing an emotionally charged event can act to enhance storage of that event in memory. In this and other studies it is difficult to determine whether the effects are the result of action on memory consolidation or attentional processes or both, because the β -blocker is provided before, rather than after, presentation of the story. In what follows, we will concentrate mainly on memory modulation rather than attentional effects (for the latter, see Lupien & McEwen [1997]; Mendl [1999]).

Although peripheral administration of stress hormones can lead to memory modulation, it is clear that central action is also important (see Cahill & McGaugh [1996]; Roozendaal [2000]). Glucocorticoids readily cross the blood-brain barrier and may exert their effects by binding to high affinity mineralocorticoid (MR; type I) and low-affinity glucocorticoid (GR; type II) receptors in the hippocampus, a brain structure known to play an important role in memory (Eichenbaum *et al* 1994). At moderate levels of glucocorticoids, most binding is to MR, with some binding to GR, and this appears to stimulate a phenomenon known as long-term potentiation in hippocampal cells (Lupien & McEwen 1997; de Kloet *et al* 1999). This might be linked with the development of new synaptic connections which may underlie memory enhancement effects (Gallistel 1995; Holscher 1999).

Catecholamines do not readily cross the blood-brain barrier, but one possible route of action is through their effects on peripheral glucose metabolism and increased cerebral perfusion rate resulting in increased glucose delivery to the brain. Elevated levels of brain glucose are thought to aid memory processes (Gold 1995). It also appears that central catecholamine action is important in memory formation in both animals and humans (Introini-Collison *et al* 1992; van Stegeren *et al* 1998).

Various lines of evidence indicate that, in both humans and animals, the amygdala, a structure long known to be involved in the processing of emotion-related information (Gallagher & Chiba 1996; Adolphs 1999), is important in mediating the memory-modulating effects of stress hormones. In particular, the basolateral amygdaloid nucleus appears to be involved in enhancing the storage of memories at other sites in the brain, such as the hippocampus. In animals, both catecholamines and glucocorticoids can exert memory-

modulating effects through receptors at this site (eg Ferry *et al* [1999]; Roozendaal *et al* [1999]), and antagonists or damage to this nucleus block these effects (Quirarte *et al* 1997). In humans, there is also some evidence that damage to the amygdala prevents emotionally induced enhancement of memory (Cahill *et al* 1995; Adolphs *et al* 1997). Furthermore, amygdala activity, as measured by positron emission tomography scanning at the time of viewing either emotionally arousing or relatively neutral images, has been shown to correlate with the amount of information recognized or recalled about the emotional but not the neutral material (Cahill *et al* 1996). In one study, this finding generalized to both pleasant and aversive emotional stimuli (Hamann *et al* 1999).

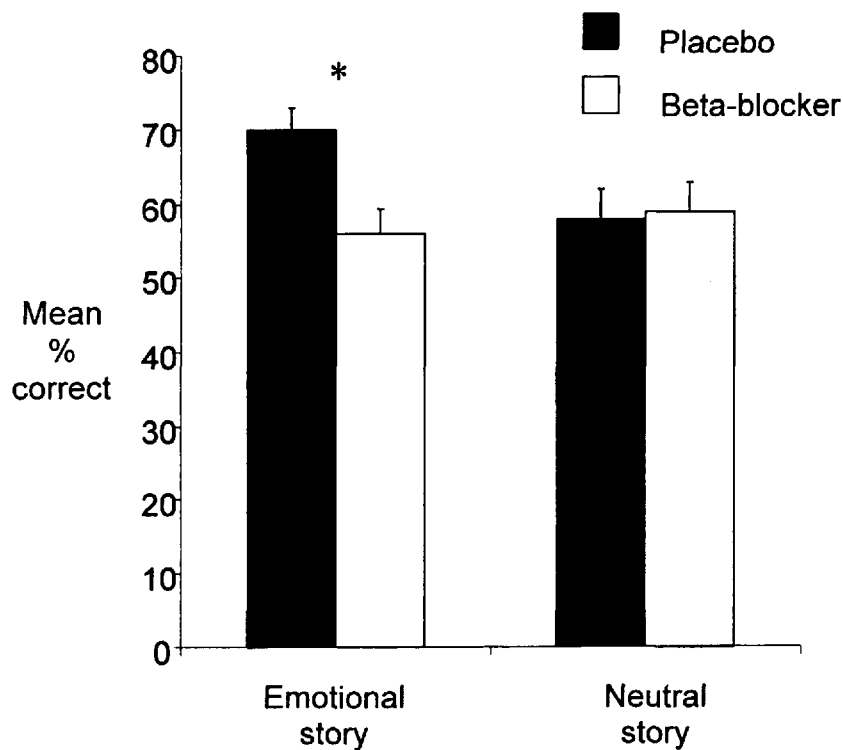


Figure 2 Mean percentage of recognition memory questions (\pm SEM) answered correctly 1 week after human subjects had viewed either an emotional or a neutral story. Subjects received either a placebo or β -blocker 1h before viewing the story. The asterisk indicates a significant difference ($P < 0.02$) between the placebo and β -blocker group for the emotional story. Modified by permission from *Nature* (Cahill *et al* 1994), ©1994, Macmillan Magazines Ltd.

The picture emerging is that, in both humans and animals, situations which induce acute stress or emotional arousal activate stress hormone systems which interact with the amygdaloid complex to enhance memory storage in other parts of the brain. It is important to note that neutral events are stored in memory without this system being activated, but that emotional events appear to be given preferential access to memory through this train of events. A common interpretation is that the stress hormones not only play a role in organizing the animal's immediate response to an emotionally loaded or threatening situation

(Cannon 1935; Selye 1976) but, together with the amygdala, also facilitate storage of the event in memory such that future responses are aided. Both actions are viewed as having adaptive value (Cahill & McGaugh 1998). It is likely that emotional stimuli, whether pleasant (eg sexual) or aversive (eg predation threat), are more likely to contribute to survival and reproductive success than neutral stimuli (Hamann *et al* 1999).

From an animal welfare perspective, the implications of this research are that emotionally loaded events, including stressful and negative events, are likely to be stored as priority information in memory. Under captive conditions, it is possible that these prominent memories are frequently triggered by unavoidable cues (eg the odour of an aggressive conspecific, the sight of a restraining device), leading to re-experience of the events and associated emotions. Captive conditions may prevent appropriate or adaptive behavioural responses to the cues (eg avoidance or escape), and this may result in injury as repeated attempts are thwarted, and lead to the induction of states such as chronic anxiety.

At least two important questions remain unanswered. The first, raised at the start of this paper, is whether memories and associated emotions are consciously experienced. As mentioned earlier, one distinction between implicit and explicit memory is that the former allows information in memory to be accessed without apparent conscious awareness. This idea is controversial, with some claiming that 'unconscious learning', and hence memory without awareness, has not been adequately demonstrated in humans (Shanks & St John 1994). Nevertheless, it does raise the possibility that only humans are consciously aware of emotional memories, and that animal memory is mainly of the implicit (*sensu non-conscious*) type.

Although we cannot address this issue directly, the striking similarity of the behavioural and neurophysiological substrates of emotional memory in humans and animals indicates that these systems are deeply rooted in evolutionary history. If human conscious experience of emotional memory has some adaptive value, then we might expect that it has also evolved in other animal species sharing similar brain structures and functions. It is also conceivable that emotional memory systems evolved primarily to provide an emotion-based alert about the dangers or positive aspects of a situation, rather than to relay detailed information of exactly what happened previously. In other words, emotions may have been consciously experienced, but not their associated event memories (the schema in Figure 1 allows for this possibility). The ability to explicitly recall the events associated with the emotions may have evolved later, and perhaps only in humans.

A second important question is how emotional memories are stored and retrieved and in what ways this differs from the storage and retrieval of neutral memories. Emotional memories can be thought of as 'important' memories. To forget them is likely to be more costly to survival and reproductive success than to forget a 'neutral' memory. If this is so, then we might expect that they are stored in such a way that they are relatively long lasting, resistant to interference, and easily retrievable. Dukas (1999) suggests that one way in which to store such memories is to build in a certain amount of redundancy such that each piece of information is represented in several ways, or by a network of related pieces of information. For example, the memory for a stockperson who handles animals roughly could include linked information on facial characteristics and colouring, hair colour, size, gait, odour, sound of voice and so on, while the memory of a less interactive, gentle or 'neutral' stockperson might be restricted to gait, odour and voice cues (Figure 3).

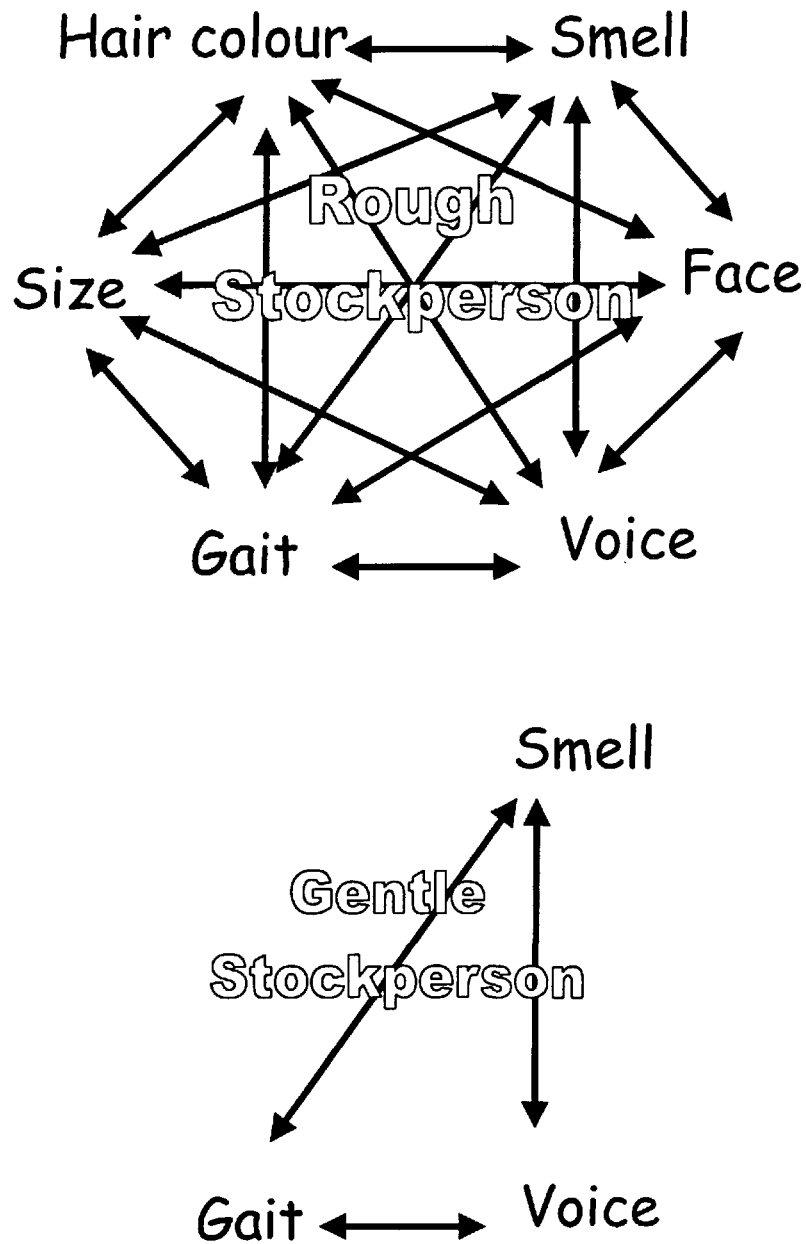


Figure 3 Schematic representation of hypothetical memory networks linking various cues. A representation of the rough stockperson might be triggered by a greater number of cues and a greater variety of cue combinations than a representation of the gentle stockperson.

Such a system might allow the important memory to be accessed or retrieved by several routes (eg hearing a voice, seeing hair of a particular colour, etc), including a variety of combinations of potent multicomponent cues (Rowe 1999), while the less important memory would only be retrieved in the presence of a more limited number of cues. A consequence of this might be more 'false retrievals' of the important memory, for example when a stockperson with similar hair colour arrives. But frequent retrievals of this nature could, in fact, function to rehearse and reorganize the memory and maintain it intact for longer (see Pearce [1997]; Przybyslawski & Sara [1997]; Przybyslawski *et al* [1999]). Multiple or network representations may also be inherently more resistant to interference and decay across time because, even if one piece of information is lost, the memory remains retrievable by other routes.

In recent work, we (Laughlin & Mendl 2000a) have shown that pigs appear to more rapidly learn and store in memory the requirements of a food-searching task if errors are penalized by a small time cost than if they are not. The costly task also seems to be more resistant to retroactive interference (see below) thus supporting the idea that 'important' memories are stored in a more robust way.

The possibilities outlined above remain to be investigated in detail. They are important because if we understand the nature and diversity of cues required to trigger emotional memories, this helps to address the important welfare question of how easily memories of aversive events can be triggered in other contexts. We could then make practical recommendations on housing and husbandry in order to minimize or perhaps maximize (in the case of positive events) the chances of such memories being cued in the home pen environment. Such recommendations would be useful if memory retrieval resulted in potentially damaging or injurious behaviour (eg aggression, escape), and even more important if the memory and associated emotions were also consciously experienced.

Disruption of memory

So far we have emphasized the enhancing role that arousal and stress can have on memory processes. These are typically observed when a situation or event induces acute stress or arousal (Cahill & McGaugh 1998). However, it is also the case that very pronounced and prolonged stress responses can disrupt memory processes. This is important from a welfare perspective because temporary or permanent failure to remember information about, for example, conspecific identity or the location of resources may lead to inappropriate behaviour and welfare problems (see Mendl [1999]).

The memory modulating effects of catecholamines and glucocorticoids appear to follow an inverted-U shaped curve. At intermediate levels typical of short-term stress or arousal, the enhancing effects discussed above occur, while at low levels (eg during 'neutral' events) these are absent. However, at high levels, and in individuals experiencing chronic elevations of, in particular, glucocorticoids, memory formation may be disrupted in both animals and humans (Newcomer *et al* 1994, 1999; Bodnoff *et al* 1995; McEwen & Sapolsky 1995; McLay *et al* 1998; de Kloet *et al* 1999). One explanation is that chronic elevations of glucocorticoids can actually induce both reversible and irreversible changes and damage to hippocampal neurones and thus have a general detrimental effect on the memory functions of this brain area (Luine *et al* 1994; Bodnoff *et al* 1995; Conrad *et al* 1996). Such effects may underlie the impaired cognitive function that is often observed in depressed humans (Reus 1984; Rubinow *et al* 1984; Lupien *et al* 1999). It is thus possible that housing conditions or husbandry procedures which lead to prolonged activation of the hypothalamic-pituitary-

adrenal axis may induce impaired memory abilities in captive animals. This issue is currently being investigated in the context of segregated early weaning in pigs (see Yuan *et al* [1999]).

An explanation for shorter-term detrimental effects of elevated glucocorticoids on memory is that, at high concentrations, glucocorticoids readily occupy low-affinity glucocorticoid (GR, type II) receptor sites in the hippocampus. The action of GR may be to decrease long-term potentiation and perhaps, through this effect, decrease consolidation of information into memory (McEwen & Sapolsky 1995; Conrad *et al* 1999; de Kloet *et al* 1999). These shorter-term effects mean that very high levels of stress or arousal at or soon after an event may actually impede its storage in memory. Such effects may contribute to the phenomenon of retroactive interference in which stimuli encountered following the to-be-remembered event appear to interfere with storage, and/or subsequent retrieval, of that event from memory (eg Maki *et al* [1979]; Roberts [1981]). Part of this interfering effect may be due to stress responses induced by the novel stimuli (de Kloet *et al* 1999). However, non-stress related effects are likely to be equally, and perhaps more, important. For example, the novel stimulus may divert attention from the previous event and thus interfere with rehearsal and consolidation processes. If the novel stimulus contains similar information to the to-be-remembered event, there may be direct interference with information storage in memory.

Retroactive interference could be of relevance in various situations encountered by captive animals. For example, in group-housed cattle, agonistic encounters with other group members following a first experience of a new piece of automated equipment (eg a robotic milker), might interfere with the formation of a memory for how to use the apparatus. This effect is likely to be even more pronounced when animals are forming memories of new group members, because of the similarity between the to-be-remembered and the interfering stimuli (both involve interactions with conspecifics). Likewise, pigs might fail to learn that being weighed in a weigh crate is essentially a benign procedure if, following weighing, they are exposed to novel stimuli such as unfamiliar rooms or individuals which interfere with memory for the preceding event.

So, does retroactive interference occur in farm and laboratory animals exposed to common husbandry procedures? We have extended studies of retroactive interference to a farm animal species, the pig, and have started by using easily controlled spatial memory tests as our model memory system. We have also initiated studies of rat social recognition memory, for which tests have already been developed (Thor & Holloway 1982; Engelmann *et al* 1995), because an understanding of properties of social memory such as decay rate and susceptibility to interference could have important management and welfare implications. In both species, we are investigating how procedures similar to those encountered under normal husbandry conditions may interfere with memory.

Our spatial memory tasks require pigs to search a radial arm maze, or similar foraging arena, for randomly distributed food and, once they have found and eaten it, to accurately relocate (win-stay) or avoid (win-shift) the food sites in a recall trial 10min later (Laughlin & Mendl 2000b). We have found that performance during recall trials is significantly worse (ie more errors are made) when interference stimuli are presented during the retention interval than when they are not. These effects are more clearly observed in a task requiring memory of four food locations, rather than just one (Mendl *et al* 1997; Laughlin *et al* 1999). The performance deficits involve one or two extra error visits to locations not containing food which are usually situated close to the actual food location. The effect of interference may thus be to reduce the accuracy of memory storage or retrieval without completely eradicating it (Mendl *et al* 1997), although apparent eradication may be observed in some situations (see below). Further research, using 2h retention intervals, has shown that some stimuli can cause

interference effects when presented both at the start (soon after the to-be-remembered event) and at the end (close to the recall test) of the interval (Laughlin 2000). This indicates that these stimuli interfere with both memory consolidation and memory retrieval processes.

The interfering stimuli we have used include isolation, exposure to another pig, confinement in a weighing crate, exposure to a novel environment, and exposure to the foraging arena itself. The only stimulus which has affected performance so strongly that the searching pig is no better than a random searcher at relocating the food sites is exposure to the foraging arena (ie placing the animal in the arena but not allowing it to search). This indicates that stimuli which are similar to features of the to-be-remembered task have a more potent effect on performance than those which are dissimilar but induce a more general stress or arousal state in the animal (eg exposure to a weighing crate). The former may act by inducing an attentional shift (see Mendl [1999]) which perhaps interferes with some form of 'rehearsal' of the task (Laughlin *et al* 1999). It is possible that this sort of effect occurs through glucocorticoid-mediated alterations in memory consolidation (de Kloet *et al* 1999). However, further studies have so far failed to confirm that similar interference stimuli which induce different amounts of attention shifting lead to differing levels of performance deficit (Laughlin 2000).

Our studies on rats have also demonstrated that stimuli likely to be encountered under normal husbandry conditions can induce apparent disruption and failure of memory. In rats, investigation of the same conspecific (or an odour cue such as urine) decreases (habituates) over repeated presentations. This is taken to indicate recognition of that individual, because a dishabituation of the investigation response is observed if a novel conspecific (or odour) is presented. Tests of social memory have been developed which investigate the extent of habituation to a conspecific shown in the second of two exposures; the rationale being that a drop in investigation across the two exposures indicates recognition (Thor & Holloway 1982). Whether this test demonstrates recognition of an individual as a distinct entity with a particular combination of characteristics is debatable (see Barnard & Burk [1979]; Johnston & Jernigan [1994]), but it does indicate whether the subject is able to discriminate one conspecific from another and to recognize that they are different. We have shown that presentation of stimuli, such as handling and temporary exposure to a novel environment or conspecific, between the two exposures appears to disrupt social recognition memory (Burman & Mendl 2000). At present, it remains unclear whether this effect is on consolidation or retrieval processes or both. It is also possible that any apparent effects on retrieval may be due to non-specific arousal or motivational changes in behaviour in the test situation.

These studies indicate that events and procedures that could be encountered under normal husbandry conditions can exert retroactive interference effects on performance in pig spatial and rat social memory tasks. In fact, the effects of the relatively mild stimuli used are quite pronounced in comparison to previous studies of rat spatial memory (eg Maki *et al* [1979]; Beatty & Shavalia [1980]; Cook & Brown [1985]). Further work is required to elucidate in more detail whether the effects are on storage and/or retrieval, whether they are temporary or long-lived, and what links they have to attentional processes and physiological changes, especially those involving glucocorticoid and catecholamine hormones. This may vary between stimuli, and a related goal will be to establish which specific husbandry procedures, and what general properties of these, are most effective at inducing interference effects. It will also be important to examine whether such effects are observed for information stored in longer-term memory (see Mateo & Johnston [2000]). For example, if individuals have been

housed together for several days or weeks, how vulnerable are their memories of each other to interference?

Information of this sort may be particularly useful in the context of social recognition memory. In group-housed species such as pigs or rats, where individuals may be temporarily removed from their home pen for husbandry or research reasons, the events occurring between removal and return to the group may influence retention and/or retrieval of memories for group members. Minimizing interference and disruption effects in order to preserve social recognition memory should enhance the chances of rapid reintegration, with minimal aggression, when groups are re-formed.

Factors affecting memory retrieval

Both internal and external cues play an important role in memory retrieval. In humans, there is some evidence that, if there is a match between mood, emotion or other aspects of internal state at the time of information acquisition and that experienced at the time of recall, then memory retrieval is enhanced (Schare *et al* 1984; see Ucros [1989]). This is termed mood-state-dependent recall. Another phenomenon known as mood-congruence refers to the observation that information may be learnt or retrieved more effectively when its affective value and the mood of the subject correspond. This is most clearly seen for emotionally loaded, as opposed to emotionally neutral, information (Bower 1981; Bower *et al* 1981). It may play a role in the tendency of depressed people to selectively recall unpleasant incidents from the past, thus further lowering self-esteem and deepening depression (Beck 1967; Baddeley 1996; Gotlib & Krasnoperova 1998). Animals under stress appear to be more attentive to threatening stimuli (see Mendl [1999]) and we are currently investigating whether, as in humans, they show more negative expectations about future events (Harding *et al* 2001). However, to our knowledge, it is not known whether they selectively retrieve more negative memories. If so, this would clearly have important implications for their welfare.

A more general effect of internal state is suggested by recent research on rats in which individuals experiencing a state of physiological stress, caused by environmentally or pharmacologically induced elevations of glucocorticoid hormones, show changes in their ability to retrieve long-term memory of spatial information (de Quervain *et al* 1998). The exact mechanism underlying this effect is not clear. It is possible that the spatial information is really more difficult to retrieve, but it is also possible that changes in attention and behavioural patterning (eg alterations in search behaviour) underlie the apparent failure of memory. The latter effects could be mediated by differential stimulation of GR and MR receptors in the hippocampus resulting in altered search patterns in which the relevant spatial locations are located as quickly as in control groups, but there is a decreased persistence to search in these locations (de Kloet *et al* 1999; Yau *et al* 1999).

Related work in humans indicates that elevations in glucocorticoid levels interfere with subjects' ability in free-recall tests to remember and write down words that they were presented with 24h previously. However, no effect is seen on performance in recognition tests where subjects are asked to identify these words from a list (de Quervain *et al* 2000). The authors interpret this as indicating a specific effect of glucocorticoids on memory recall. Non-memory effects on, for example, attention would be expected to interfere with both recall and recognition. However, another interpretation is that interference effects are more pronounced for tasks where a marked conscious effort is required to search for and retrieve

information. Effects on both retrieval processes and attentional mechanisms could thus be occurring.

These studies have examined memories for 'neutral' or 'positive' information (eg nouns, location of a safe area). They indicate that, for whatever reason, animals and humans under stress may be less able to retrieve these sorts of long-term memories. This may not be the case for memories of 'negative' information, as discussed above, in relation to mood-congruency effects on memory retrieval. Nevertheless, it is possible that, under stressful conditions of social mixing or transport, detrimental effects of stress on memory retrieval could underlie apparent failures of individual recognition and fighting between familiar individuals (eg pigs, Mount & Seabrook [1993]; Giersing & Andersson [1998]). Techniques that minimize stress may facilitate effective memory retrieval and the consequent expression of appropriate behaviour in a variety of management situations.

In humans and animals, external cues also play an important role in memory retrieval. Cues that were present at the time of an event can subsequently prompt or facilitate recall of that event (Tulving & Thomson 1973; Baddeley 1996). From an animal welfare perspective, knowledge about the sorts of external cue that most reliably trigger memory retrieval, how these interact, and how this varies according to memory type (eg spatial, social, appetitive, aversive) is useful. As mentioned earlier, it can indicate how readily a negative memory may be triggered outside the original context of the event. It can also be used to suggest how to employ cues to aid husbandry procedures and enhance animal welfare. For example, if laboratory or farmed animals are moved from their pens, either to undergo aversive husbandry or experimental procedures, or for more benign reasons, it is important to know which contextual cues are the most effective signals of the 'safety' or otherwise of particular areas, and whether there are particular treatments which may overcome these contextual cues (see Rushen *et al* [1999]).

In recent studies, we have examined the role of contextual cues in the retrieval of social recognition memory in rats. We are interested in whether individuals are able to recognize others independently of the context in which the individual has previously been encountered (eg Falls & Brooks [1975]; Waas & Colgan [1994]). If contextual cues are important in aiding individual recognition, this would mean that moving individuals or mixing them in an unfamiliar pen might result in failure of recognition memory. Using social recognition tests, similar to those described above, we have shown that, in rats, recognition of previously encountered conspecifics seems to be possible even when this is tested in a different context to that in which the individual was previously encountered (Burman & Mendl 1999). This is clearly the case when the context is familiar to the subject animal, but further studies indicate that a completely novel context might interfere with retrieval of recognition memory (Burman unpublished data). The latter finding remains to be confirmed. It may be the result of differences in external cues hampering retrieval of the memory and/or more general effects of the stress of an unfamiliar context interfering with memory retrieval as discussed earlier. Whatever the precise mechanism, such a finding would indicate that moving or mixing rats in an environment with which they are familiar is likely to maximize the chances that individuals recognize their group mates.

Conclusions, limitations and animal welfare implications

In this paper, we have attempted to show how an understanding of various aspects of animal memory can be of relevance in an animal welfare context. We argue that memory has the potential to exert a profound effect on the ongoing emotional state of animals, and hence on

their welfare. It is clear that, in both animals and humans, emotional events are more readily stored in memory than neutral events. Even though we are unable to directly access the conscious experiences of animals, the similarities between the behavioural and neurophysiological substrates of emotional memory in animals and humans highlight the possibility that at least some animal species may be able to consciously recall and re-experience both positive and negative emotional feelings. Even if memories and associated emotional states are not consciously experienced by animals, the behaviour that occurs as a result of memory retrieval may in some cases be damaging or injurious. Therefore, an important practical issue is how to minimize the chances of negative emotional memories being cued inappropriately under captive conditions, and to increase the recall of positive memories. To do this, we need to understand better how memories of different 'emotional value' or 'importance' are stored and retrieved.

Disruption of memory storage and retrieval is also important in an animal welfare context. Chronic or very high elevations of stress hormones appear to have both short- and long-term effects on brain structure and function that can interfere with efficient storage of information. Elevated stress levels at the time of retrieval may both increase the chances of retrieval of negative information while hampering the retrieval of positive or neutral information. Retroactive interference of memory may also be caused by novel or unexpected stimuli occurring after the to-be-remembered event. Such effects may lead to poor learning abilities, selective or disrupted memory retrieval, and consequent inappropriate behaviour with adverse welfare consequences.

Further information is required about all these effects. For example, we may be able to recommend designs of housing and husbandry procedures which enhance welfare if we understand which types of stimuli or contexts are most effective at inducing retroactive interference, or disrupting memory retrieval. We also need to know whether the effects that these have on shorter-term memory extend to long-term memory, and whether rearing animals under stressful captive conditions can have long-term disruptive effects on their memory abilities later in life. For practical purposes, it may appear unnecessary to understand whether any disruptive effects seen reflect true interference with memory processes, or more general and perhaps short-lived arousal or motivation-related changes in behaviour. However, it is important to get a better understanding of the mechanisms involved, both from a fundamental perspective and also practically, so that accurate predictions about the extent and longevity of disruptive effects can be made.

As we stated at the start of this paper, our overview has been necessarily selective of the large amount of scientific information available on human and animal memory. There are, doubtless, relevant issues that we have not covered, and limitations to the ideas and interpretations that we have put forward. We briefly discuss two here. First, throughout this paper we have emphasized how acute arousal and elevations of stress hormones may act to prioritize the storage and consolidation of important information in memory. At the same time, we have shown that chronic and/or very high elevations of stress hormones, especially the glucocorticoids, can have disruptive effects on memory processes. An inverted-U shaped relationship between stress and memory performance is often used to describe these opposite actions (Mendl 1999; see also Baumler [1994]; Tiegen [1994]). It is thus possible that if an event induces a very strong stress response, this could act to suppress rather than enhance storage of information about it.

In popular human psychology, the Freudian idea that memories of very unpleasant events can be repressed is often encountered. However, it has proved difficult to demonstrate repression of these memories in controlled laboratory situations (see Christianson [1992];

Baddeley [1996]), and it is clearly the case that, at least in some people, the intrusive recall of such memories is a frequent and very distressing occurrence (Turnbull 1998; Tarrier & Humphreys 2000). Nevertheless, the possibility remains that very high levels of stress hormones induced by particularly traumatic events could disrupt memory for these events in animals. This should be borne in mind in future research in this area.

Secondly, it is important to remember that many of the animal studies on the effects of stress on memory consolidation have focused on one-trial learning tasks and how these are affected by manipulations of single hormones. Studies of 'real-life' stressor effects are relatively uncommon (but see Diamond & Rose [1994]; Johnston & Rose [1998]), as are studies of different forms of learning and longer-term memory. The extent to which conclusions from this work generalize to other situations and memory systems is thus unclear, but should be the subject for further investigation, including that by applied ethologists (see Mendl [1999]).

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