ZEVENDE ANIMALES-VOORDRACHT

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Stichting
ANIMALES

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ZEVENDE ANIMALES-VOORDRACHT

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INTRODUCTION

To recognise, understand, and ultimately assess pain, we need to define it. Arguably, the most complete definition of pain is that of the International Study of Pain (IASP), who currently define pain as "*Pain is an unpleasant sensory & emotional experience associated with, or resembling that associated with, actual or potential tissue damage*" (Raja et al., 2020). Although initially conceived as a definition of human pain, in 2020, the definition was expanded to encompass non-human animals (Raja et al., 2020). Based on this definition, pain can be considered to have two components that occur in response to noxious stimuli (i.e., actual or potential damage): a sensory component and an emotional component that leads to some form of output or response, e.g., behaviour. The 'sensory' or 'sensory-discriminative' component refers to the detection of noxious stimuli (i.e., the where, when, and intensity of the stimulus) and the unconscious response related to self-protection, e.g., reflex withdrawal. This component is often referred to as 'nociception', the non-conscious processing of noxious stimuli by the peripheral and central nervous systems (Tracey, 2017). The emotional component can be subdivided into the 'affective-motivational' and 'evaluative-cognitive' components (Melzack & Casey, 1968; Auvray et al., 2010). The affective-motivational component refers to how pain affects us, i.e., it hurts. The higher evaluative-cognitive component refers to the meaning of the pain to the individual, i.e., the potential consequences of the pain, and this can then make the perceived pain better or worse. For example, a painful eye could lead a person to think they are going to lose their sight, and therefore, the intensity of the pain they experience may increase. Alternatively, if they break their arm and they know their broken bones have recovered well previously, the intensity of the pain they experience may decrease.

Whether we can apply the IASP definition in its entirety to animals remains a key question. It seems universally accepted that even the simplest animal species (e.g., nematode worms) demonstrate the 'sensory-discriminative' component of pain. However, it is the ability of animal species to experience the emotional component of pain that is critical, as this component impacts our own and, therefore, their welfare. There is substantial evidence that mammalian and avian species experience at least the ‘affective-motivational’ aspect of pain in some form. However, the presence of this component in non-mammalian and non-avian species remains controversial, both in terms of their capacity to experience this aspect of pain and the quality of the supporting evidence. Whether any non-human species can experience the evaluative-cognitive component has not been considered or testable until recently, with the advent of cognitive bias testing. Ultimately, for a species to be considered as experiencing the emotional component of pain, it needs only to experience the affective-motivational aspect, as this represents the simplest level of emotional response. For the sake of brevity, the emotional component of pain (i.e., affective-motivational and evaluative-cognitive) will be referred to as’ pain experience’ in the rest of this review.

There are several detailed discussions of the evidence, or lack thereof, of pain experience in a range of species from mammals to insects (e.g., Bateson, 1991; Elwood et al. 2011, 2012; Sneddon et al., 2014; Rose et al., 2014; Sneddon, 2015; Derbyshire, 2016; Birch, 2017; Key & Drown, 2018; de Waal & Andrews, 2022; Hart, 2023; Mason & Lavery, 2022; Diggles et al., 2024). Here, we will focus on discussing a framework for assessing whether animals may experience pain, and if they do, how we can practically evaluate its presence and severity. This framework is not new, but rather a distillation of ideas put forward by others that seem appropriate and logical, encompassing the philosophy of mind, ethics, cognitive ethology, biology, and inferential reasoning to propose a combination of methods that seem most relevant and logical.

THE PROBLEM WITH PAIN & OTHER EMOTIONAL STATES

Pain, like other emotions, is a subjective state that is personal to the individual affected and is influenced by biological, psychological, and social factors (Raja et al., 2020). To quote Henry Knowles Beecher, *"Pain is what the patient says it is…"* (Beecher, 1956). Due to the subjectivity of pain, directly assessing its presence and severity in another individual is difficult, making its assessment in non-verbal humans (i.e., pre-lingual children and dementia patients) and animals particularly challenging, as they cannot communicate their pain meaningfully. 'Self-report' in the verbal is considered by many to be the 'gold standard' means of assessing the presence and severity of pain. Determining effective alternatives to self-reporting in the non-verbal (i.e., humans and animals) remains a fundamental challenge, particularly in animal welfare (e.g., Descovich et al., 2017; Lecorps & Weary, 2024). The prevention or alleviation of pain remains a primary focus in animal welfare, as illustrated by the emphasis on pain in definitions of welfare and animal protection legislation. Before moving on to how we might assess the presence and severity of pain experience in animals (and non-verbal humans), it is worth noting that the inability to communicate does not negate the possibility that humans or animals experience pain (Raja et al., 2020). This critical point is illustrated by the debate over pain experience in human infants, where the medical community did not reach a consensus on the topic until the 1980s (McGrath, 2011; Andrews, 2024), a development that now seems inconceivable.

So, how do we assess the presence and severity of pain experienced by non-verbal humans, and can these approaches be used as a framework for determining the presence and severity of pain in non-human animals (Grunau & Craig, 1987)? Almost all the techniques we use to assess whether animal species' experience pain' and if they do, the severity of that experience are based on the principle of inferential reasoning, which has led us to be reliant on proxy indicators of pain and other emotional states (Descovich et al., 2017). Over the last three decades, significant advances have been made in the development and validation of such measures (e.g., Bateson, 1991; Rutherford, 2002; Weary et al., 2006; Sneddon et al., 2014) in mammalian and avian species.

INFERENTIAL REASONING

Inferential reasoning refers to inferring the presence of pain experience (and other emotions) in animals from behavioural, anatomical, and physiological similarities to humans. Inferential reasoning has not only been used to provide evidence for pain experience in animal species but also offers a potential means for assessing pain (e.g., behaviour, facial expressions). The underlying principle is that if pain experience in humans is associated with a behavioural, anatomical, and physiological changes, and these changes can be reduced or prevented by any means reported to relieve pain (e.g., analgesia, post procedural care, etc.), and that same relationship is observed in an animal, then we assume this can be used as evidence of pain experience in that species and can provide a means of assessing it. It is important to note that inferential reasoning does not imply that the species needs to experience pain in the same way as humans, as this may or may not be the case.

WHERE DO WE START?

When discussing the experience of pain or other emotions, we most often refer to the evidence of 'consciousness' (also referred to as sentience) in that species. There are numerous definitions of consciousness; at its simplest, it refers to 'subjective experiences (either positive or negative), such as pain, suffering, pleasure, frustration, anxiety, fear, happiness and joy (Birch, 2018). Consciousness can be broadly classified into two levels of complexity. Primary or "phenomenal" consciousness refers to the ability to generate a mental scene in which diverse information is integrated to direct behaviour (Edelman, 1989), i.e., the ability to feel or be aware (Mason & Lavery, 2022).

‘Access’ consciousness (Mason & Lavery, 2022) refers to the ability to utilise mental representations for reasoning, controlling actions, and reporting (Block, 1995), i.e., consciousness that can be influenced by actions (Mason & Lavery, 2022). Within access consciousness, there are several subtypes, including episodic memory (i.e., memory of autobiographical events), the ability to plan for the future, and self-awareness (i.e., being aware of your own existence), theory of mind (i.e., the ability to attribute mental states to oneself and others), and metacognition (i.e., thinking about your own thoughts) (see Figure 1). These higher-order forms of consciousness are generally considered to be reliant on or underpinned by phenomenal consciousness (Mason & Lavery, 2022). Consequently, if consciousness, like all biological functioning, has evolved from simple to complex on a continuum, then it seems logical to propose that if animals show evidence of higher-order consciousness, then they must be capable of some aspects of phenomenal consciousness, i.e., taking a top-down approach. For example, suppose there is evidence of a species demonstrating the more complex evaluative-cognitive aspect of pain. In that case, they must be capable of the simpler affective-motivational aspect of pain.

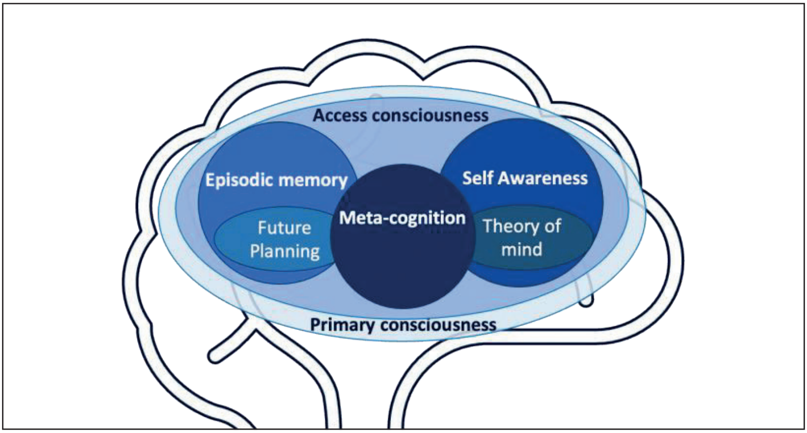


Figure 1: Diagram illustrating the broad levels of consciousness and their hierarchical structure. This diagram is adapted from that presented by Mason & Lavery (2022).

Although most evidence for consciousness or higher-order capacities in various species does not directly relate to pain, this evidence is relevant when considering pain experience, as it suggests that they may possess a form of phenomenal consciousness and could therefore have the capability to experience pain. Although further discussion about consciousness is beyond the scope of this work, there have been several detailed reviews of the evidence for consciousness across the animal kingdom (e.g., de Waal, 2008; Birch, 2017; Key, 2015; Key & Brown, 2018, Lagisz et al., 2020; Mason & Lavery, 2022; de Waal & Andrews, 2022; Andrews, 2024; Callaway, 2024; Diggles et al., 2024; Andrews, 2024).

EVIDENCE

Using this framework and an appropriate definition of pain (e.g., IASP definition), we can assess the emotional component of pain in two ways: firstly, by examining the anatomical and physiological correlates of pain experience (based on humans), and secondly, by evaluating the outputs or responses to stimuli that we find painful. The following sections discuss how we can utilise this evidence to determine the most effective and practical methods for identifying the presence and then assessing the severity of pain experienced by a species. Most of the evidence discussed comes from research with mammals and birds; however, where research is available in other vertebrate and invertebrate species, it will be reported.

Evidence from anatomy

Evidence for a species being capable of the emotional component of pain has often focused on the presence or absence of anatomical and physiological correlates present in humans and what that means for their capacity to experience such pain (e.g., Key, 2015, 2016; Sneddon et al., 2014; Sneddon, 2015; Key & Brown, 2018; Diggles et al., 2024). One of the key pieces of evidence used to ascribe pain experience in animal species is electrical activity in the somatosensory areas (e.g., cortex, insula, medial thalamus, etc.) in response to stimuli that would induce the same activity in the same regions in humans and be described as pain. Such evidence has been observed in many mammalian species (for a review, see Murrel & Johnson, 2006). One of the functions proposed for emotions, including pain, is to induce empathy in conspecifics (De Waal & Andrews, 2022), thereby recruiting altruistic assistance (Langford et al., 2006; de Waal, 2008), which increases the chances of survival. In humans, the anterior cingulate cortex (ACC) is considered one of the brain areas activated when experiencing pain and witnessing others in pain (Lamm et al., 2011). Similar activations have been observed in some mammal species. For example, Carrillo et al. (2019) demonstrated that the anterior cingulate cortex in rats is activated when a rat experiences pain and witnesses another rat in pain (induced by foot shock), and this response is reduced by deactivation of the cingulate (via neuronal inhibition).

Although similarities to humans in anatomy and physiology are essential criteria for judging whether a species can experience pain, Bateson (1991) posed a critical question: Should such similarities be the sole means or the gold standard on which we base our judgments? Focusing on structures, processes, and functions is likely a good starting point for species with which we are closely related, such as mammals. However, the greater the evolutionary distance between us and another species, the less valid this stance potentially becomes, as biology, through evolution, has engineered many different means to solve the same problem, e.g., flight in bats, birds, and insects because of the differing evolutionary pressures these species experience (Bateson, 1991). The principle of convergent evolution means that entirely different anatomical structures, physiological processes, or behavioural responses could have evolved to have the same function. For example, fish lack the mammalian six-layered cortex, which is considered essential for primary consciousness and, therefore, the ability to experience pain (Mason & Lavery, 2022). These differences in brain anatomy have led many authors to argue that fish cannot experience pain (e.g., Rose, 2002, 2007; Rose et al., 2014; Key, 2015, 2016; Derbyshire, 2016). However, applying this principle means that other species that lack a complex cortex, such as birds, reptiles, cephalopods, etc., are also incapable of experiencing pain (or having primary consciousness) despite their apparent behavioural or neurological complexity (Mason & Lavery, 2022). In these species, pain experience may be supported by other neurological structures that have evolved to perform functions like those of the mammalian cortex.

The outputs that are likely to be key

A more convenient and practical means of assessing the emotional component of pain, which is less influenced by the requirement for mammalian neurobiology, would be to examine the outputs of this individualistic, private, and entirely internal process. The starting point is to use the outputs or responses that we associate with the human experience of pain.

Evidence from behaviour

The most obvious and easily observable output is behaviour, which can range from simple, spontaneous behaviour to complex responses that likely require more complex cognitive input. Although behavioural responses that seem consistent with pain experience in humans offer potential evidence, the strength of this evidence depends on those responses being dependent on consciousness, i.e., cannot be explained through non-conscious processes (Mason & Lavery, 2022; Key & Brown, 2018; Birch, 2020).

Spontaneous behaviour

Spontaneous behavioural responses to noxious stimuli that we associate with pain are one of the most apparent means of assessing pain (e.g., abnormal gaits and postures, limb guarding, etc.). So, it is not surprising that behaviour-based pain scoring systems have been developed for a relatively wide range of species, including rodents (e.g., Roughan & Flecknell, 2003), rabbits (e.g., Leach et al., 2009), cattle (e.g., Gleerup et al., 2015), sheep (e.g., Molony & Kent, 2002), pigs (Ison et al., 2016), dogs (e.g., Firth & Haldane, 1999), and cats (Morela & Mill, 2016). These are considered a practical and effective means of assessing pain at the cage or pen side. Behavioural responses appear more explicitly linked to the potential pain state of the animal than more traditional methods (e.g., heart rate, body weight change, etc.). There is a growing body of evidence linking specific spontaneous behaviours and pain in terms of the change in the magnitude of a behavioural response mirroring the likely change in underlying pain state (i.e., due to the administration of analgesia) and the successful differentiation of animals that are likely to be painful compared to those that are not painful (e.g., post-surgical compared to control animals; e.g., Miller et al., 2022). Finally, behaviour provides a more immediate assessment of pain state, i.e., it is not a retrospective assessment. For example, if we assume a 10% loss in bodyweight indicates the presence of pain, then by the time we have observed such a loss, the animal is likely to have been in pain for around 12-24 hours, and their pain may be naturally resolving (Leach et al., 2009).

Despite the practical advantages that assessing spontaneous behaviour offers when evaluating pain, the evidence for whether it indicates that a species can experience pain and, therefore, whether it can be used to assess pain experience, is less clear. Spontaneous behavioural reactions could represent outputs of the 'sensory-discriminative' component of pain and therefore do not require consciousness to perform (e.g., Diggles et al., 2024; Mason & Lavery, 2022); thus, the animal does not experience any form of emotional reaction to the painful stimulus. Mason and Lavery (2022), in their review of the evidence for fish experiencing pain, argue that reactions to noxious stimuli that are present in SPUD organisms (see Table 1) cannot be used as evidence of consciousness, along with other reactions such as simple approach or withdrawal responses, changes in reactivity to analgesia, etc.

(S)	Spines disconnected from brains
(P)	Animals lacking nervous systems (e.g. plants and protozoa)
(U)	Humans in unaware states
(D)	Decerebrate mammals and birds

Table 1: SPUD organisms taken from Mason and Lavery (2022)

The issue with these outputs (in isolation, at least) is that they cannot be used to definitively demonstrate an underlying experience of pain (Key & Brown, 2018), as they do not add evidence for or against the presence of the emotional component of pain, i.e., are "theory neutral" (Mason & Lavery, 2022). Therefore, responses to painful stimuli in humans, which are observed in animals but not in SPUD organisms, offer more valuable evidence for the emotional component of pain and its assessment in animals.

Complex behaviour

As the complexity of a behavioural response increases, the more likely it is that this response will require higher cerebral processing and primary consciousness (Mason & Lavery, 2022), and the likelihood that it represents an underlying emotional state also increases. Such behavioural responses go beyond what would be likely to be possible with a simple 'stimulus-reflex' response. Again, we can look to ourselves to identify candidate behavioural patterns, as we know that in humans, pain affects complex behavioural patterns, such as the daily activities of getting dressed, washing, and keeping the house clean (Verbunt et al., 2009). Many mammal species exhibit potentially comparable complex behaviour patterns that are influenced by pain. Mice construct highly complex nests to create a preferred microclimate within their cage (Gaskill et al., 2012); their willingness and ability to build these complex nests are influenced by pain (Arras et al., 2007). In this study, mice that underwent abdominal surgery constructed nests of poorer quality than before they underwent surgery, when compared to mice that did not undergo surgery (i.e., anaesthesia controls) and those that underwent surgery with an effective dose of analgesia. Burrowing behaviour in rodents is an ancient and well-conserved behaviour, considered an indicator of ‘global well-being’ (Deacon, 2006). The willingness of rodents to burrow is affected by pain (Jirkof et al., 2010). In this study, mice that underwent abdominal surgery were less willing to burrow than before surgery, compared to mice that did not undergo surgery (i.e., anaesthesia and analgesia controls) and those that underwent surgery with an effective dose of analgesia. Nest building and burrowing represent highly motivated behavioural needs that animals will work to exhibit, so changes in these behaviours are likely to be effective indicators of welfare, including pain. There has been little research into identifying equivalent complex and highly motivated behaviours in other vertebrate and invertebrate species, though this would provide evidence for the presence of pain experience.

Although the increased complexity of these responses would suggest the need for higher cerebral processing and primary consciousness, there remains a risk that these behaviours do not require conscious control, as there are examples of potentially complex behaviours being observed in SPUD organisms and so may again be “theory neutral” (Mason & Lavery, 2022). Thus, the evidence of pain experience from some complex behaviours could face the same issue as spontaneous behaviour, in that it may or may not be dependent on the underlying experience of pain (Key & Brown, 2018).

Operant paradigms

The use of operant paradigms has been proposed as a viable means of assessing the pain experience in animals (e.g., de Waal & Andrews, 2022; Mason & Lavery, 2022). An operant paradigm refers to where a specific behaviour (the operant) is modified by its consequences, such as reinforcement or punishment. Such paradigms offer a potential means of assessing pain experience in both humans and animals, as the behavioural responses observed in these paradigms require animals to have access to their internal state (i.e., be aware of their pain), to use these valenced experiences to guide their behaviour in complex ways, that in turn require aspects of access consciousness such as working memory, and declarative learning *(i.e., the process of acquiring explicit knowledge that can be consciously recalled, e.g., episodic memory)*, which are considered akin to self-report (Emmet-Oglesby et al. 1983; Wood & Lal, 1987; Mason & Lavery, 2022). Several different paradigms can be used to probe the emotional experience of pain in animals, including self-selection/administration of analgesics, conditional discriminations, and assessment of cognitive bias.

Self-administration of analgesia

Both humans and some animal species (e.g., mammals and birds) have been shown to self-administer analgesia when in pain. For example, human patients were observed to self-administer analgesia in the hours following abdominal and orthopaedic surgery, with patients undergoing abdominal surgery administering higher doses than those undergoing orthopaedic surgery (Lehman & Tenbuhs, 1986). Humans who are not in pain do not self-administer analgesia due to the unpleasant side effects associated with these drugs. Similarly, rats experiencing adjuvant-induced arthritis have been shown to self-administer higher doses of analgesia compared to control (non-arthritic) animals (Colpaert et al., 1980). Importantly, increased self-administration of analgesia by rats with arthritis (over the controls) only begins at the point at which the arthritis occurs and returns to control levels when the arthritis naturally resolves. Broiler chickens that are lame (due to their rapid growth rate) consume more food containing analgesia and less normal food (not containing analgesia) than sound birds, with those individuals with the most severe lameness selecting more food containing analgesia (Danbury et al., 2000). An alternative to self-administration is the use of conditional discriminations, where animals use their ‘feeling’ of pain, and its change in intensity, to make a choice. Three of the most widely used conditional discriminations are ‘conditioned place aversion’, ‘conditioned place preference’ and reward-conflict paradigms.

Conditioned place aversion

For conditioned place aversion, animals choose to spend less time in a location previously associated with a negative experience, thus inducing a place aversion. Place aversion studies typically involve confining an animal in one location (e.g., a chamber or room) where it is exposed to a noxious stimulus (e.g., pain) and then confining it in a different location where it is not exposed to the noxious stimulus. The locations are demarked in some way (e.g., colour, pattern, scent, sound, etc.) to aid discrimination. Animals are then ‘tested’ by giving them a free choice of the two chambers. We expect the animal to avoid the chamber associated with the noxious stimulus. Johansen et al. (2001) used a conditioned place aversion paradigm to demonstrate that rats with a lesion of the anterior cingulate cortex (a brain area associated with pain experience in humans) showed no change in location aversion from before to after administration of formalin into the footpad (i.e., inducing localised pain). By comparison, rats without a lesion exhibited a distinct aversion to the location where formalin was administered. Notably, there was no difference in foot licking (spontaneous behaviour associated with nociception) between rats with and without a lesion, suggesting the lesion blocked the pain experience but not the nociceptive response.

Conditioned place preference

For conditioned place preference, animals tend to spend more time in a location previously associated with a rewarding experience, thereby developing a place preference. Place preference studies typically involve confining an animal in one location (e.g., a chamber or room) where it is exposed to a reward (e.g., pain relief) and then confining it in another location where it is not exposed to the reward (e.g., no pain relief). Again, the locations are demarked in some way (e.g., colour, pattern, scent, sound, etc.) to aid discrimination. Animals are then ‘tested’ by giving them a free choice of the two chambers. We expect an animal in pain to choose the chamber (i.e., develop a place preference) associated with pain relief, as it will be rewarding. Sufka (1992) used a conditioned place preference paradigm, demonstrating that rats with an inflamed paw, induced by the administration of complete Freund's adjuvant (causing localised pain), exhibited a preference for a location previously associated with analgesic administration (morphine). Rats without an inflamed paw failed to show a preference for either the morphine or control-associated locations. The preference of zebrafish that had undergone a potentially painful treatment (e.g. acid administration) was shifted from an enriched environment to a barren and brightly lit environment (i.e., likely to be mildly aversive) when analgesia was administered in the barren and brightly lit environment (Sneddon, 2012).

Reward-conflict paradigm

Reward-conflict paradigm (or selective attention) studies typically require an animal to titrate exposure to a noxious stimulus against their willingness to access a reward (Neubert et al., 2006). In this type of paradigm, animals must decide (or titrate), based on their perception of the noxious stimulus, whether to complete the task to obtain a reward. Nolan et al. (2012) demonstrated that rats could be trained to accept the application of painful thermal stimulus to the face to gain access to a palatable reward (e.g., a sweet solution). Their willingness to accept the thermal stimulus decreases as the temperature of the stimulus increases, but is restored when increasing doses of analgesia are administered (e.g. morphine). Interestingly, the analgesic effect persisted when analgesia was replaced by a placebo, suggesting that the expectation of receiving an analgesic reduced their pain experience. Ede et al. (2018) showed that calves will accept an intramuscular injection (i.e., a painful experience) if they expect to receive substantial reward (1L milk), but their willingness to do so decreases if the reward decreases (i.e., less milk provided). The same calves could also be trained to accept a subcutaneous injection (i.e., less painful experience) when a smaller reward was expected than with an intramuscular injection. Appel and Elwood (2009) demonstrated that hermit crabs will accept higher voltage shocks (i.e., more painful) before evacuating higher-quality shells than lower-quality shells, as the former provide greater protection for their abdomens. The reward-conflict paradigm demonstrates that animals will make trade-offs based on their expectations of the pain they will experience and the reward they will receive. (Lecorps & Weary, 2024).

Cognitive bias

In humans, emotional valence (i.e., positive vs. negative emotions) is associated with adaptive biases in information processing (Parsons et al., 2021), meaning that our emotional state influences the decisions we make. For example, when we are in a negative emotional state, we tend to be risk-averse and have a greater expectation of poor/adverse outcomes. These biases in information processing can be evaluated using cognitive bias tests (Parsons et al., 2021), a method that is increasingly popular for exploring the emotional states of animals and is increasingly recognised as a valuable tool for exploring various aspects of animal welfare (see Mendl et al., 2009; Crump et al., 2018), including pain. For a more detailed review, see Lagisz et al. (2020) and Neville et al. (2020). In humans, it is known that pain influences information processing and induces cognitive biases (e.g., Paul et al., 2005; Mendl et al., 2010). For example, patients with a negative pre-operative emotional state (i.e., more anxious, depressed or painful) report more severe post-procedural pain and require more analgesia than patients in a positive pre-operative emotional state (e.g., Kastelik et al., 2019). Cockburn et al. (2018) showed that Cavalier King Charles Spaniel dogs (CKCS) with syringomyelia (a condition associated with severe pain) exhibit a pessimistic bias compared to CKCS without this condition. In this study, the dogs were trained to associate one coloured bowl with a positive outcome (e.g., blue meant food) and a different coloured bowl with a negative outcome (e.g., red meant no food). When exposed to bowls of ambiguous colours in test sessions, individuals with syringomyelia exhibited a higher latency to approach the ambiguous food bowls compared to unaffected animals, indicating they were potentially more risk-averse. Neave et al. (2013) showed that calves that had undergone hot-iron disbudding (a painful procedure) exhibited pessimistic bias, indicating that post-procedural pain induced a negative emotional state. In this study, calves were trained using a go/no-go task to approach the 'positive screen' (either a white or red screen) and avoid a different 'negative screen' (the opposite colour to the positive screen). When they were exposed to screens of ambiguous colours in test sessions, the animals approached the ambiguous screens less after disbudding compared to before, suggesting they had become more risk-averse.

The application of operant paradigms to study the potential of non-mammalian and non-avian species to experience pain would be highly persuasive for those who doubt that these species experience pain (Mason & Lavery, 2022). However, to date, there have been very few studies using such techniques (Appel & Elwood, 2009). Although these operant paradigms offer a potential means of determining if a species can experience pain, they cannot be considered as practical cage or pen-side assessments of pain experience. They do, however, offer useful means of validating other, more practical cage-side methods of assessing the emotional component of pain, such as spontaneous behaviours.

FACIAL EXPRESSIONS

Returning to the concept proposed by Grunau and Craig (1987), where we use the same techniques for assessing pain experience in animals as we do with nonverbal humans (i.e., pre-lingual children and dementia patients), facial expressions offer the most routinely used proxy assessment of pain (Williams, 2002). Facial expressions have long been linked to and used to assess underlying emotions in humans (e.g., Darwin, 1872; Ekman, 1993; Hole and Bourne, 2010; Descovich et al., 2017). They are considered temporally relevant, measurable and sensitive indicators of emotional valence (Dimberg and Thunberg, 1998) expressed through prototypical facial configurations or expressions. Thus, as pain has a significant impact on our welfare, which we can effectively evaluate using facial expressions, the same is likely to be true for some animal species (Williams, 2002).

Facial expressions are considered the 'gold standard' means of assessing pain in non-verbal patient populations. Facial expression-based pain scales require a relatively limited number of indicators that are easy to recognise and provide excellent accuracy, providing an effective and rapid means of assessment. Facial expressions also provide a more general response to pain that is not limited to the source (e.g., somatic, visceral, or mixed) or location (e.g., body area) of the pain (Williams, 2022). There is also increasing evidence from human studies suggesting facial expressions are subject to "emotional leakage" when we attempt to suppress them and so offer more reliable indicators of emotional state than body movements, i.e., spontaneous behaviour (e.g., Craig et al., 1991; Williams, 2002; Ekman & Rosenberg, 2005; ten Brinke et al., 2012; Porter et al., 2012). A similar phenomenon has been observed in primates, which seem to have less voluntary control over facial expressions than motor behaviour (Jürgens, 2009; Hopkins et al., 2011). This lack of voluntary control suggests that facial expressions in animals may offer "honest" signals of welfare state (Descovich et al., 2017). Facial expressions in humans are typically assessed using the Facial Action Coding System (FACS), which comprises the individual components of facial expressions, known as Facial Action Units (FAUs) (Ekman, 1993). In humans, pain is associated with a specific subset of action units, which are routinely used to assess pain (see Figure 2).

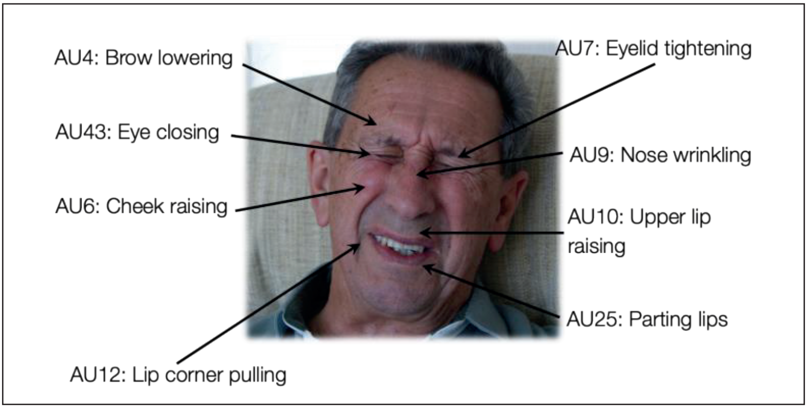


Figure 2: Individual components of facial expressions observed in response to pain in humans and routinely used to assess it in non-verbal patients (Adapted from Prkachin, 2009).

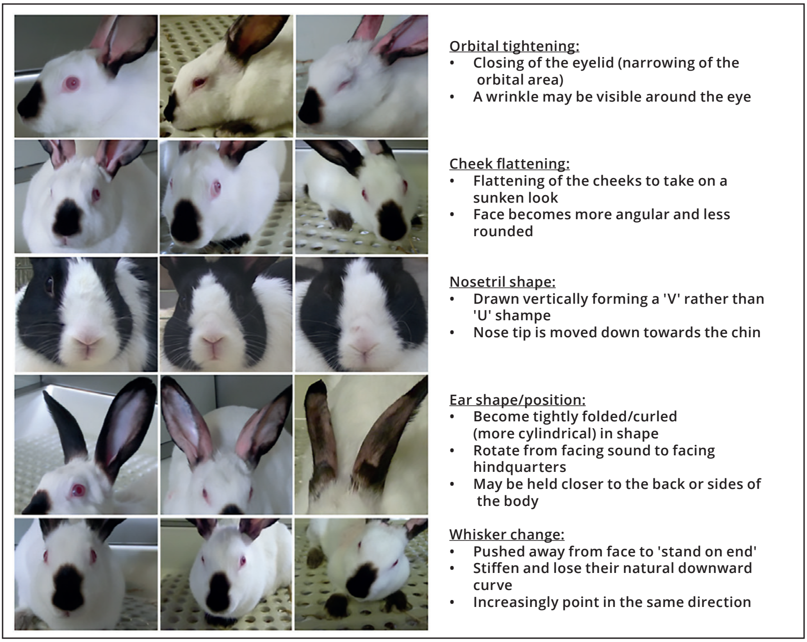
For many mammalian species, including humans, the same action units are observed in response to similar painful stimuli, with many facial movements (i.e., action units) being evolutionarily conserved across species (Darwin, 1872; Diogo, 2009; Waller & Micheletta, 2013). For example, units associated with pain are located in the eyes, cheeks, ears, whiskers, mouth, and jaw in humans, mice and horses (Chambers & Mogil, 2015). Consequently, these units have the potential to reliably indicate emotional experiences in animals (Descovich et al., 2017). For non-human mammal species, these action units are often combined to create specific facial expression-based pain scales (often referred to as ‘Grimace Scales’). These scales offer a simplified version of the FACS approach, where muscle movements are defined by changes in the appearance of key facial features that occur during pain states, which are often scored on a 3-point scale based on their presence or intensity. If the action unit is not present, it is scored as a ‘0’; if it is moderately present, then it is scored as a ‘1’; and if it is obviously present, then it is scored as a ‘2’. Grimace scales have been developed for a wide range of species (see Table 2 for examples).

Grimace Scale	Source
Mouse (MGS)	Langford et al. (2010)
Rat (RGS)	Sotocina et al. (2011)
Rabbit (RbtGS)	Keating et al. (2012)
Horse (HGS)	Dalla Costa et al. (2013)
Cat (FGS)	Evangelista et al. (2019)
Sheep (SGS)	Häger et al. (2017)
Ferret (FGS)	Reijgwart et al. (2017)
Piglet (PgGS)	Viscardi et al. (2017)

Table 2: Examples of grimace scales in different mammalian species.

For example, the Rabbit Grimace Scale (RbtGS) comprises five action units (see Figure 3: Keating et al., 2012). This scale has been shown to offer an effective means of assessing postoperative pain as grimace scores increase from pre- to post-surgery, where they were reduced by the administration of efficacious analgesia and correlated with other potential indices of pain in this species (Keating et al., 2012; Miller et al., 2022).

In humans, pain asymbolia (the disassociation of the emotional experience from the nociceptive response to pain) is associated with lesions of the rostral anterior insula, one of the brain areas linked to the emotional component of pain (e.g., Berthier et al., 1987). In developing the Mouse Grimace Scale (MGS), Langford et al. (2010) demonstrated that lesioning the rostral an-



Orbital tightening:
- Closing of the eyelid (narrowing of the orbital area)
- A wrinkle may be visible around the eye

Cheek flattening:
- Flattening of the cheeks to take on a sunken look
- Face becomes more angular and less rounded

Nosetril shape:
- Drawn vertically forming a 'V' rather than 'U' shampe
- Nose tip is moved down towards the chin

Ear shape/position:
- Become tightly folded/curled (more cylindrical) in shape
- Rotate from facing sound to facing hindquarters
- May be held closer to the back or sides of the body

Whisker change:
- Pushed away from face to 'stand on end'
- Stiffen and lose their natural downward curve
- Increasingly point in the same direction

Figure 3: The Rabbit Grimace Scale - RbtGS (Keating et al., 2012)

terior insula attenuated the mouse grimace score compared to animals without a lesion. Interestingly, abdominal writhing remained intact in both groups. Writhing is a reflex response linked to the sensory rather than the emotional component of pain. Although this study involved a small number of animals (n = 6), it suggests that facial expressions in mice may represent the emotional component of pain, as they do in humans (Langford et al., 2010).

Although facial expressions appear to offer a valuable means of assessing the emotional component of pain in mammals, they seem to have limited utility outside mammalian species, as other taxa (e.g., birds, reptiles) have comparatively reduced structural capabilities to exhibit facial expressions (Cooke, 2015). Having said this, non-mammalian taxa may have evolved other means of visually expressing pain that are comparable to facial expressions in mammals, such as changes in plumage in birds, surface colour and morphological modifications in reptiles, amphibians, and cephalopods; however, this has yet to be fully explored.

WHERE DOES THIS LEAVE US?

Sneddon (2015) provides the most up-to-date summary of criteria that can be used to indicate the sensory and emotional components of pain across terrestrial vertebrates, teleost fish, molluscs, and decapod crustaceans (see Table 3).

Evidence	**Mammals & Birds**	**Reptiles & Amphibians**	**Teleost fish**	**Cephalopod**	**Decapod crustaceans**
Nociceptors	✓	✓	✓	✓	✓
Pathways to CNS	✓	✓	✓	✓	✓
Central processing in the CNS	✓	✓	✓	✓	✓
Receptors for analgesic drugs	✓	✓	✓	✓	✓
Physiological responses	✓	✓	✓	✓	✓
Movement away from noxious stimuli	✓	✓	✓	✓	✓
Abnormal behavioural changes	✓	✓	✓	✓	✓
Protective behaviour	✓	✓	✓	✓	✓
Responses reduced by analgesic drugs	✓	✓	✓	✓	✓
Self-administration of analgesia	✓		✓		
Responses with high priority over other stimuli	✓	✓	✓	✓	✓
Paying a cost to access analgesia	✓		✓		
Altered behavioural choices/preferences	✓	✓	✓	✓	✓
Rubbing, limping or guarding	✓		✓	✓	✓
Paying a cost to avoid stimulus	✓		✓	✓	✓
Trade-offs with other requirements	✓		✓		✓

Table 3: The criteria indicating sensory and emotional components of pain across vertebrate and invertebrate species (Taken from Sneddon, 2015). R indicates criteria shown, £ indicates criteria yet to be shown, and * indicates not seen in birds yet.

Based on these techniques and others (many of which are discussed here), there is a strong consensus that mammals and birds experience both the sensory and emotional components of pain. However, for other classes of vertebrates (i.e. fish, reptiles, and amphibians) and invertebrates (i.e., cephalopods, decapods, insects, etc.), there remains either a lack of consensus around whether the evidence supports the experience of pain or not (see Key, 2015; Key & Brown, 2018; Mason & Lavery, 2022; Diggles et al., 2004), or a lack of sufficient evidence currently to evaluate whether a species can experience pain. This will require further research into pain experience in these species, including the expression of complex behaviour, and the use of operant conditioning paradigms in more species. However, identifying and evaluating evidence of pain experience in non-mammalian and non-avian species remains challenging (Hart, 2023), as the validity of techniques developed to assess pain in mammals and birds could be questioned for species in other vertebrate and invertebrate classes. The greater the evolutionary distance between us and another species, the less likely techniques based on behavioural, anatomical, and physiological similarities to humans will be valid (de Waal & Andrews, 2022). The principle of convergent evolution means that entirely different anatomical structures, physiological processes, or behavioural responses can evolve to have the same function due to the variety of different evolutionary pressures that each species experiences. In addition, as capacities evolve, they can combine with other capacities (which have evolved for quite different reasons) to create new characteristics that have evolutionary life of their own (Bateson 1991). Furthermore, comparing pain indices across different species is fraught with difficulty because a test that accurately measures the abilities of one species related to its evolutionary niche may be entirely inappropriate for another adapted to a different, yet equally challenging, niche.

Therefore, a species that lacks a structure, process or behavioural response that is taken to indicate pain in humans or other mammals is not evidence of the absence of emotions, including pain, in that species. Ultimately, specifying design criteria does not specify the solution (Bateson 1991). Additionally, inferential reasoning is often taken to imply that animals must experience pain in the same way and/or using the same pathways as in humans or other mammals, for it to be considered representative of the emotional component of pain. The same argument as described above applies here: why would species that evolved under different pressures experience pain (or other emotions) in the same way as humans? If they do not, does this mean that their experience of pain is any less important or valid to their welfare? This line of thought runs the risk of speciesism, i.e., "*the assigning different values or 'experiences' to beings based on their biological species and/or our relationship with them, rather than according to the characteristics they possess*" (Adapted from Richard Ryder in Singer, 1990, page 6).

This issue is illustrated by the 'Octopus Conundrum', i.e., an octopus is likely the closest entity on our planet to an intelligent alien life form (Callaway, 2024), and thus as far from human understanding as we potentially can get. For example, octopi exhibit behaviours not seen in higher vertebrate classes, such as autotomy (shedding of limbs), autophagy (eating one's own body parts), auto-mutilation (e.g., Budelmann, 1998), and regrowth of lost limbs (Murayama et al., 1994; Mariappan et al., 2000). Consequently, do we have the capacity to understand what it is like to be an octopus, i.e., what they experience, that would enable us to identify whether they have emotions or not? Furthermore, why would those emotions be akin to those of a human or another mammal? After all, the evidence that human emotions (including pain) are equivalent across individuals is at best indirect, as we all experience emotions in different ways (de Waal & Andrews, 2002). Many cephalopod species demonstrate capabilities and behavioural complexity that most would consider indicative of emotions (including pain) if a mammal exhibited them. Some cephalopods will trade off the effectiveness of a specific hunting technique against the likelihood of experiencing a potentially painful stimulus, e.g., using a less effective hunting technique that has a lower risk of injury when predating on hermit crabs with a stinging anemone on their shells (Elwood, 2011). Crook et al. (2009, 2011) demonstrated that some cephalopod species change their predation defence strategy due to injury, e.g., using crypsis rather than escape when injured and initiating their defensive behaviours earlier when injured compared to healthy, indicating greater awareness. Interestingly, this change in defence strategy is reduced by analgesia administration (Crook et al., 2009). More generally, cephalopods demonstrate a high level of cognitive capacity, as illustrated by tool use (Finn et al., 2009), reversal learning (Wilson & Saunders, 2011), recognition of individuals of their own and other species (Anderson et al., 2010), and spatial learning (Crook et al., 2011), among other abilities. Although these capabilities do not directly indicate emotions per se, they are considered indicative in mammals.

Importance of pain assessment & the precautionary principle

The continued development of techniques to assess pain experience in non-human animals remains critically important. However, the focus for developing and implementing these techniques currently differs between higher vertebrates (i.e., mammals and birds) and other vertebrates and invertebrates. For mammals and birds, the focus is on developing effective (i.e., valid, reliable, and practical) methods for assessing pain experience at the cage or pen-side, enabling better evaluation and alleviation of pain that we often inadvertently cause. For other vertebrates and invertebrates, it is necessary to develop new and species-appropriate means to determine whether these species can or cannot experience pain and to what degree. Using this evidence, we can then develop effective means of assessing pain experience in those species of concern in the clinical sense.

What do we do until we have techniques to gain a more empirical understanding of the existence of pain experience in other species? Do we assume a species does not experience pain until the evidence proves otherwise, or do we assume that they may experience pain (either in the same or in a different way than humans) and protect them accordingly until the evidence proves otherwise (i.e., apply the precautionary principle)? Recently, Diggles et al. (2024) raised concerns about the widespread application of the precautionary principle to pain experience in non-mammalian and non-avian species. They advocated for the application of rigorous scepticism and self-correction, where the scientific method is applied to collect data and test hypotheses in an empirical and repeatable manner before concluding pain or other emotional states are present in non-mammalian and non-avian species. However, the precautionary principle is not at odds with rigorous scepticism and self-correction, as we should thoroughly and scientifically assess the evidence for pain (or other emotions). However, until we can do that for each species, the application of the precautionary principle seems appropriate, particularly if the question we ask is not what evidence indicates pain experience, but rather what evidence suggests they do not experience pain (Mason & Lavery, 2022; Andrews, 2024). This middle ground appears to be the best way forward, striking a balance between science, welfare, and ethics.

Triangulation and pragmatism

While we attempt to determine whether and to what extent different species experience pain (or other emotional states), we often resort to pragmatism and triangulation in the absence of definitive evidence.

Pragmatism is the approach to dealing with a problem in a sensible way that suits the existing conditions, rather than adhering to fixed theories, ideas, or rules (Dictionary, C., 2025). Generally, most people seem to take a pragmatic view and assume that most species experience pain. For example, the UK public considers the prevention of suffering to be key to supporting the use of animals in research, and suffering is often defined in terms of emotional experience. In a 2018 survey, 68% of respondents were willing to accept animal use in research if there were no unnecessary suffering and no alternative (Ipsos, M.O.R.I., 2018). The principle of ‘Replacement’, which is defined as “*The replacement of sentient animals with non-living or non-sentient alternatives*” (Russell et al., 1959), directly implies that animals are sentient and therefore can experience. Animal protection legislation globally accepts that animals experience pain (and other emotional states), for example, the European Directive 2010/63 states "*…any experimental or other scientific procedure applied to a protected animal which may have the effect of causing that animal pain, suffering, distress or lasting harm*" (European Union, 2010). The ability to experience emotions (including pain) is a fundamental part of most of the modern definitions of animal welfare. For many, the ability to experience emotions is the most critical and defining characteristic, as seen in the Five Domains Model (Mellor et al., 2020). Finally, and potentially most critically, those who use animals as models of humans and other sentient organisms seem to assume at least to a limited extent that animals experience emotions, including pain. For example, affective neuroscience research relies on animals to study which brain areas and neural circuits are activated during specific emotional reactions, such as fear, anger, disgust, and attraction (de Waal & Andrews, 2022).

Triangulation refers to the use of multiple datasets, methods, and theories to address a research question. Science disciplines have routinely used the principle of triangulation, where a definitive answer cannot be directly measured (Sneddon et al. 2014). For example, dark matter in the universe cannot be measured directly; yet, its existence is inferred from the gravitational effects of visible matter, radiation, and the large-scale structure of the universe (Trimble, 1987). Bateson (1991) summed this up in relation to pain in animals, '*No single criterion provides an all-or-none test for the existence of the subjective sense of pain. The evidence needs to be considered as a whole…*'. Many authors have advocated this position in relation to pain, where the individual measures are not taken in isolation but assessed together as they represent an increasing complexity of pain responses that go beyond what can be achieved by reflex responses and begin to demonstrate a level of complexity that would require some form of experience (e.g., Mason & Mendl, 1993; Nicol et al., 2009; Sneddon 2004, 2009, 2011, 2013; Weary et al., 2006; Flecknell et al., 201; Elwood, 2012). The value of triangulation is directly dependent on the quality of the evidence that is included, i.e., for it to be indicative, the evidence (i.e., anatomical, physiological and behavioural responses) must be consistent with demonstrating primary consciousness, i.e., reactions that SPUD organisms do not exhibit (Mason & Lavery, 2022). To determine the validity of such evidence for pain experience across different species, where sufficient evidence exists, a rigorous and systematic meta-analysis is necessary.

CONCLUSION

Currently, there is strong and widely accepted evidence to suggest that mammals and birds experience pain. However, for the other classes of vertebrates and invertebrates, there appears to be a limited consensus regarding the value of the existing evidence, or the evidence remains scant compared to that of higher vertebrates. So, this leads to the fundamental question: '*Where do we draw the line in terms of which species experience pain, and which do not?*' However, before considering this, an equally important question we should consider is: *'Is there really a line?'*. After all, animals (including humans) have evolved along a continuum, and therefore consciousness and emotions (including pain) will have developed along this continuum, like all other biological traits. We know that in humans, primary and access consciousness appear not to be simply present or absent, but instead graded, meaning they occur in degrees, which is likely to be true across different animal species due to evolution (e.g., Dawkins, 1980; Bateson, 1991). By accepting that consciousness is graded across species, this 'magic' line becomes arbitrary, and so our ability to effectively identify the presence of the emotional component of pain and assess its severity becomes crucial; otherwise, we cannot appreciate when animals experience pain and to what degree. To quote Bateson (1991), "*The fuzziness of the boundary between those animals that are judged to feel pain and those that are not does not invalidate the process of assessment*". Ultimately, we may never know whether another species experiences emotional states, including pain, as consciousness is currently inaccessible, leading to arguments that cannot be resolved at this time (Elwood 2019). Ultimately, when assessing whether pain can be experienced in a species that cannot verbally report its experience, we rely on ‘proxy’ indices. Until we have more direct assessments of pain and other emotional states, we should add the most weight to the evidence that is only explained in terms of conscious cognitive processes, rather than non-conscious explanations (Mason & Lavery, 2022).

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Stichting
ANIMALES

De Stichting Animales werd op dertien november 1997 opgericht met als oorspronkelijke doelstelling “het verlenen van hulp aan bedreigde dieren in de ruimste zin des woords”. Het werkterrein van de stichting was vooral gericht op Latijns Amerika, met name Venezuela, omdat twee van de toenmalige bestuursleden daar enige tijd beroepsmatig werkzaam waren. In verband met de verslechterde politieke situatie aldaar, werd in 2014 besloten de stichting om te vormen tot een vermogensfonds met ANBI-status en de doelstelling te wijzigen in “het bevorderen van dierenwelzijn bij voorkeur in Nederland, alles in de ruimste zins des woords”. De stichting tracht haar doel te bereiken door:

a. Het stimuleren van op dieren gericht wetenschappelijk onderzoek op het gebied van welzijn, zoals bijvoorbeeld voeding, medisch handelen en cognitie en emotie.

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c. Het bij voorkeur jaarlijks organiseren van een “Animales-Voordracht” om het belang van dierenwelzijn onder de aandacht te brengen.

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Matt Leach, PhD, works as the Director of the Comparative Biology Centre (CBC) at Newcastle University. CBC supports all in-vivo research at the University and is a recognised centre of excellence for 3Rs innovation, education, and training across a broad range of research species. Matt leads a dedicated team of highly skilled technical and veterinary staff who strive to ensure the highest animal welfare and ethical standards are applied, while balancing this with the requirements of our research community.

Matt is an experienced research scientist whose work focuses on the health and welfare of a range of laboratory animal species. Matt currently leads a small specialist team of researchers (Pain and Animal Welfare Group) who focus on developing and validating new methods of assessing health and welfare in a wide range of laboratory and farm animal species. The group and their work have been successfully supported by both UKRI and industry funding in both the UK and Europe.

Matt is an experienced educator who focuses his teaching on laboratory animal welfare and ethics, and on experimental design in in vivo research. Matt also collaborates with Flaire Consultants to provide cutting-edge e-learning resources that are currently used by organisations worldwide.

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