

Review

Assessment of positive emotions in animals to improve their welfare

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Abstract

It is now widely accepted that good welfare is not simply the absence of negative experiences, but rather is primarily the presence of positive experiences such as pleasure. However scientific investigation of positive emotions has long been neglected. This paper addresses two main issues: first, it reviews the current state of scientific knowledge that supports the existence of positive affective states in animals and, second, it suggests possible applications of this knowledge that may enhance quality of life under animal management conditions. In the first part of the paper, recent advances in psychology and neuroscience are reviewed to provide pragmatic frameworks based on cognitive processes (such as positive anticipation, contrast and controllability) for further investigations of positive emotions in animals. Thereafter, the neurobiological bases of positive emotions are highlighted in order to identify behavioral and physiological expressions of positive experiences in animals. Monitoring both the autonomic nervous system (via heart rate and its variability) and the immune system could offer relevant tools to better assess emotional states in animals, complementary to classical adrenocortical measures. In the second part of the paper, useful strategies for enhancing positive experiences (such as physical, social and cognitive enrichment or putative genetic selection) are outlined. Then this paper emphasizes practical applications for assessing and promoting positive emotions that may help in providing animals with a better quality of life. Play, affiliative behaviors and some vocalizations appear to be the most promising convenient indicators for assessing positive experiences in laboratory and farm animals under commercial conditions.

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1. Introduction

In the last decades of the 20th century, there was a surge of interest in animal sentience. Animal welfare scientists quickly realized that welfare problems can be better addressed with an understanding of how animals could feel. It is now widely accepted that animals can feel pain and suffering, and methods to assess pain and suffering have been developed. However, there is still no agreement on how to assess positive experiences although these are suggested to be a core component of good welfare [1,2]. Nevertheless, animals that have successfully obtained commodities such as food or social contact are known to display signs that are reminiscent of pleasure in humans. Therefore, a central issue is to be able to assess whether and under what circumstances animals experience positive emotions. This issue is far more than merely theoretical; it also has ethical and practical importance for animal welfare. It has been pointed out that well-being is not simply the absence of negative affects, but also (and even predominantly) the presence of positive affects [3,4]. That means it is better to ensure joyful and contented behaviors rather than focusing on behaviors that represent needs that have to be fulfilled to avoid suffering [5]. In addition, the absence of signs of pleasure or positive affect may be an indication on its own of a state of affective discomfort. Indeed anhedonia, which is the inability to experience pleasure, is one of the core symptoms of depression. Therefore, a new challenge for animal welfare science is to better understand the

link between the ability to express positive emotions and a more persistent positive affective state, such as happiness. Moreover, applied ethology deals with a wide range of animal species, having different emotional repertoires and different behavioral patterns. Another challenge is thus to describe the range of putative positive emotions in each of the laboratory and farm animal species.

From an evolutionary perspective, emotions are considered as adaptive programs designed through repeated encounters that are intended to either direct other physiological programs or to directly solve adaptive problems faced by a species over time. One of the key factors explaining the phylogenetic success of emotions is that they would favor adaptive cognition and action. According to evolutionary psychology, emotions are considered as super-ordinate mechanisms allowing the whole organism to operate in a homogenous way when the individual is confronting relevant triggering conditions or situations. They are adaptations that have arisen in response to the adaptive problem of mechanism orchestration [6]. Generally speaking, the situations where emotions play a role are those that recurred ancestrally, those that could not be dealt with without a governing program, and those in which an error would have resulted in large fitness costs [7]. However, given the very nature of emotional self-experience, there is ultimately no way to know if animals experience emotions similar to humans. However, behavior, structure, and brain chemistry are similar in humans and in a large number of animal species. It is therefore likely that they feel as we

do, including not only well-studied negative emotions, but also positive ones.

Study of emotions in animals has received a growing interest in the past few decades, as testified by the emergence of a new discipline referred to as *Affective Neuroscience* [8]. However, despite the efforts of pioneering authors such as Colin Allen, Jaak Panksepp, Michel Cabanac or Kent Berridge, relatively little has been done to further the understanding of positive emotions by comparison to their negative counterparts such as fear. Such an imbalance does not seem to be unique to animal studies. Indeed, the study of emotions in humans suffers the same bias. As in animal studies, the human psychological study of well-being has long been dominated by stress studies. The primary reason for this bias is presumably that the expressions of negative experiences are far more intense than positive affects and therefore easier to study. These latter experiences are commonly considered as less significant since they are more labile and their expression is more subtle. Nevertheless, in the last few years, new disciplines such as *Positive Psychology* have been growing in order to explore positive emotions as primary components of subjective well-being [9,10].

The present paper does not claim to re-equilibrate the balance by itself but to contribute to promote the promise of studying positive emotions in animals. It addresses two main issues. It is intended first to review the current state of knowledge regarding the biological foundations of positive emotions, and second to indicate some possible applications for improving the quality of life of animals under management conditions. The presentation of the biological background of positive emotions successively deals with the cognitive, neurobiological, behavioral, and physiological aspects that support the existence of positive emotions in animals. Following this review, the practical applications in animal welfare are outlined. These applications include useful approaches for enhancing positive experiences and on-going more persistent affective states, as well as a discussion of the most promising positive indicators that may be used to monitor animal welfare in both laboratory and farm animals.

2. Biological processes underlying positive emotions

There is abundant literature from both biology and psychology on the concept of emotion. Whereas there is not a general definition, an emotion can be defined as an intense but short-lived affective response to an event, which is associated with specific body changes [11]. The duration of an emotion is a much-debated question, but briefness seems widely accepted. Emotions refer to processes, which are likely to have evolved from basic mechanisms that gave the animals the ability to avoid harm/punishment or to seek valuable resources/reward [12,13]. Contemporary approaches to study emotions vary according to whether they emphasize a classification of the various emotions (dimensional approaches such as pleasant/unpleasant valence or weak/strong excitation), whether they focus on the eliciting mechanisms (neural circuit models and basic emotion models), or whether they emphasize the different components of an emotion. In componential approaches, an

emotion is classically described as including a behavioral component (a posture or an activity), an autonomic component (visceral and endocrine responses) and a subjective component (emotional experience or feeling) [reviewed by [11]].

2.1. Cognitive aspects of positive emotions

2.1.1. Emotions and feelings

Although it is claimed that animals are sentient creatures, it is paradoxical that there is no exact knowledge of what their emotional experiences are about. Rollin [14] calls attention to the paradox that scientists are reluctant to attribute emotions, such as anxiety or suffering, to animals, while at the same time considerable experimental work is manifestly being done to stop pain or to relieve anxiety in animals. Using the term emotion in animals is often considered unscientific and implicating anthropomorphic assumptions of human-like subjective experience.

As pointed out by LeDoux [15], “a subjective emotional experience, like the feeling of being afraid, results when we become consciously aware of an emotion system of the brain, like the defense system”. In other words, to feel afraid it is necessary to have access to consciousness that allows awareness of the internal state. Damasio [16] claims that the consciousness of an emotion corresponds to the knowledge of the ability to experience emotions. Perceptive (or anoetic) consciousness is usually defined in terms of the capacity to be aware of feelings, sensations, thoughts and emotions [17]. There is a vigorous debate as to whether feelings of consciousness are present in non-human animals, and if so in which species [reviewed by [8,18,19]]. The common assumption is that the more cognitively complex an animal is, the more likely it is to be conscious. However, why should increasing cognitive complexity necessarily be linked to the emergence of consciousness or *vice versa*? The approach of using complex cognitive capabilities as potential indicators of the presence of conscious experience in animals has rightly been criticized [reviewed by [20]]. Recently, Alexandrov and Sams [21] proposed a unified concept of consciousness and emotions. It is not our purpose to discuss the links between cognition and consciousness [reviewed by [22]], but we want to stress the usefulness of cognitive science for research on emotions in animals and thus for animal welfare.

Feelings require some cognitive abilities to establish temporal and instrumental contingencies. These abilities allow anticipation or prediction of events whereas emotional responses involve coping with the situation. Learning temporal contingency refers to the ability to relate the occurrence of one stimulus to another when the two occur in succession, the first one becoming a predictor for the second. Learning an instrumental contingency refers to the ability to assess the consequences of one's response to the situation. In this context, affects provide the “common currency” [23] with which animals can balance conflicting demands of avoiding bad things and approaching better ones, and can evaluate the priority to be given to one over the other [24].

2.1.2. Cognitive components of emotional processing

All the previously reported studies emphasize the relationship between emotions and cognition. They describe how an

emotional system in the brain is operating and the minimum mental operation it requires. Cognition has to do with information processing, and refers to the range of processes involved in the acquisition, storage, and manipulation of information [25]. Whereas the relationship between emotions and cognition has received little attention in animal studies, it has been extensively investigated in human psychology. For most psychologists, there cannot be any emotion without some form of cognition [reviewed by 26], and several theories stress the generative role of cognition in the expression of emotional states. For Lazarus [27], an emotional state requires a primary appraisal of the emotional stimulus, which is responsible for the action planning and execution; the consequences of this action are then evaluated through a secondary appraisal. Cognitive theories of emotion contend that the individual's cognitive appraisal of the stimulating event determines the quality of emotion [28–31]. Although labeled as cognitive, the appraisals are not thought to result from complex analytical reasoning. Instead, they are presumed to be relatively effortless, intuitive and automatic evaluations that are sensitive to events related to survival (e.g. threat) and opportunities (e.g. forming attachments). Various forms of evaluative processings, ranging from rapid to subtle, occur to differentiate the emotional experiences. Appraisal may be influenced by innate automatic responses that probably evolved over many generations (e.g. response to a snake), and by learning and memory of previous encounters with stimuli during the individual's lifetime [15].

A simple framework based on cognitive evaluation can be employed for the study of emotions in animals. Events can be appraised according to whether they are rewarding or punishing [12,32]. Presentation of rewards leads to positive emotions such as pleasure, while omission of rewards leads to frustration or anger. Likewise, Lazarus [27] suggested two simple steps of appraisal. The first step appraises whether the current situation alters the well-being of the individual (if not, there is no emotional arousal). The second step appraises the meaning of the alteration. When the alteration reduces well-being, it leads to a negative emotion whereas when the alteration increases well-being, it leads to a positive emotion. The behavioral and physiological profiles recorded under these conditions could be used as indicators of putative emotional states. When a specific internal state is the only discriminating stimulus available to the animal, it can use the said internal state as a cue to select the appropriate operant response in order to get a reward. One might say the animal perceives the internal representation of its state within its central nervous system in a way that contributes to or determines its actions. As a behavioral outcome the animal will choose what seems most pleasurable [23]. Measures of cognitive processes, such as anticipation, can provide information about animal emotion. Indeed, anticipatory behavior measured in a Pavlovian conditioning paradigm has been identified as a potential indicator of emotion [33].

Recent developments in human psychology of emotions could help to create a more complete framework for categorizing emotions in animals. According to Scherer [34], emotions are determined on the basis of a limited number of elementary evaluative criteria: (i) the novelty of the event, (ii) its intrinsic pleasantness,

(iii) its goal significance, (iv) the coping potential of the individual, and (v) the relevance to social norms. The novelty of the event, which breaks down into suddenness, familiarity and predictability, and its intrinsic pleasantness are used to evaluate the relevance of the event. The goal significance concerns the consequences of the event relative to the individual's expectations. The coping potential indicates how well the individual can control and adapt to the event. Finally the relevance to norms concerns how the response fits the personal and social norms. Scherer [34] postulates that the type of emotion results from the particular combination of elementary criteria used to evaluate the eliciting situation. Scherer's model appears useful for trying to describe in very objective terms the types of emotion that are accessible to different animals; it makes it possible to infer an animal's subjective component and to predict responses according to the evaluation process [35,36]. Most of the elementary criteria defined by Scherer [34] are likely to be perceived and used by animals, and the range of emotions that animals can access may be estimated by investigating to what degree they can distinguish among elementary criteria and respond to them. By presenting animals with test situations for which one (or several) likely evaluative criterion has been experimentally manipulated, and at the same time recording their resultant cardiac and behavioral reactions, direct relationships between presumed appraisal and measurable emotional outcomes can be established. Using such an approach, Désiré and collaborators [37] have demonstrated that lambs produce differential emotional responses to suddenness (startle and tachycardia) and unfamiliarity (behavioral orientation and increase heart rate variability). In addition, as would be assumed from the dynamic sequential organization of appraisal in Scherer's model [34], the combination of suddenness and unfamiliarity criteria enhances behavioral and cardiac responses that are specific to one or the other criterion [38]. The *a priori* framework proposed by Désiré and collaborators [36], which directly considers the cognitive component of emotional processes, helps in mapping behavioral and physiological responses in animals to particular emotional states, including positive ones. For instance, an event evaluated as being pleasant, of moderate predictability, and not sudden should trigger a positive emotion.

Whatever the *a priori* framework, it is now time to integrate theories and techniques from cognitive science in order to develop new approaches to understanding emotions in animals. Emotional processing must now be regarded as comprised of not only behavioral, physiological, and subjective components but also a cognitive component.

2.1.3. Emotion and mood: acute and long-term evaluations

As was previously reported, cognitive processing is involved in determining emotional experience. However, there is evidence in humans that causal links between emotions and cognition occur in both directions, with cognitive manipulations influencing felt emotion and emotional manipulations influencing cognitive processing [39]. For instance, the emotional state can lead to changes in cognitive functioning such as an increased tendency to attend to threatening stimuli during fear, or an enhanced memory for an unhappy event during sadness [40].

Recently, Paul and collaborators [39] reviewed the variety of alterations of cognitive processing due to emotions in humans. They classify these cognitive biases into three categories: attention, memory and judgment biases. For instance, anxiety has been argued to represent an attentional shift towards potential threats. Likewise, negative emotions are associated with a heightened ability to memorize negative events. Judgment processes may be affected by current emotions in a number of ways: emotion may directly alter the judgment or risk assessment process, or act indirectly through biases in the attention and memory processes that pertain to it. Such emotional modulations of cognitive processes can be interpreted to have adaptive value by helping a fearful or anxious individual to attend to, to memorize and to make judgments about threatening circumstances. The few studies on animals show that such effects are not restricted to humans. In rodents, the startle response induced by exposure to a sudden event tends to occur faster and with greater amplitude under negative emotional states [41]. Rats housed in conditions designed to induce a persistent negative mood are less ready to respond to an ambiguous stimulus as signaling the delivery of a good event [42]. Likewise, rats housed under social stress or isolation exhibit a reduced frequency of “behavioral transitions” between the presentation of a conditioned stimulus predicting sucrose reward and the arrival of that reward, indicating a reduced anticipatory behavior due to judgment difficulties [43]. Developing similar approaches in farm animals could help to develop new indicators of persistent emotional states (*i.e.*, bad or good moods), such as an enhanced expectation of positive events [33]. All these studies demonstrate how cognitive approaches can be used in animals to probe emotions (as short-term affective experiences) and moods (as persistent affective experiences).

2.1.4. What are positive emotions?

Except for a few approaches, such as the ones developed by Wemelsfelder and Farish [44] and by Burghardt [45] that emphasize positive as well as negative states, studies of negative emotions are generally far more numerous than those of positive emotions. A number of signs can indicate positive experience in animals—for example, successful coping, reward, and wanting resulting in goal-directed behavior. Positive emotions can be separated into three temporal categories: i) past (*e.g.* post-consummatory satisfaction), ii) present (*e.g.* pleasant sensory activity), and iii) future (*e.g.* positive expectation, anticipatory joy). Focusing on present positive emotions, three categories of pleasure have been proposed in humans [4]: sensory pleasures, higher pleasures (*i.e.* non-homeostatic sensory experiences), and gratifications (*i.e.* inner intellectual experiences), with at least the first and presumably the second categories being candidates for animal investigations.

Hedonism refers in its narrowest sense to pleasure or positive affect [46]. Hedonism can also have a broader meaning referring to a general affective disposition, either positive or negative. The presence of behavioral and physiological signs of pleasure reminiscent of human euphoria has been demonstrated in animals. Such signs can be induced both as a result of natural rewards and in models for addiction resulting from treatment with rewarding drugs such as heroin, other opioids, or dopa-

minergic drugs [47]. Animals that are about to obtain food or are engaged in play often have a typical behavioral pattern characterized by short, abrupt, and quickly changing movements (Section 3.4). The behavioral and physiological homology between natural rewards and drugs is striking. The brain mechanisms involved in mediating rewards have been functionally related to motivational aspects of natural behaviors and behaviors of addiction. Classically motivated behaviors can be divided into two components: appetitive and consummatory behaviors. Interestingly, the appetitive component has also been neurobiologically dissociated from the consummatory aspects. Scientific evidence demonstrates similarity in underlying mechanisms for rewards provided by addictive substances and by natural commodities such as foods (Section 2.2). Preventing a behavior that is mainly motivated by internal causal factors is a proposed cause of poor welfare of animals kept in captivity [48–50]. Thus, one might propose an approach to assessing and improving animal welfare that focuses on signs of pleasure instead of post hoc signs of displeasure or of other negative emotional states. After having drawn the neurobiological basis of positive affects, the next sections of this review should help to better assess positive emotional states in animals by validating behavioral and physiological expressions of positive emotions.

2.2. Neurobiological bases of positive emotions: the “emotional 433 brain”

2.2.1. Actions on the reward system

There is now substantial evidence that emotions are based on neural activity in the limbic forebrain, *i.e.* the prefrontal, insular and cingulate cortex, the hippocampus, the amygdala and the septal nuclei. While the cortical areas do not have direct homologues in non-mammalian vertebrates, the others are ubiquitous in at least all tetrapods [51]. Two sensory systems have shortcut access to the limbic system: i) olfactory nuclei projecting directly to the amygdala, and ii) afferents from the medial geniculate body, the thalamic relay of acoustic signals [52]. In mammals, all other sensory modalities also reach the limbic centers, including the amygdala, after being processed in their respective sensory cortical areas [53]. Emotional states are distributed among limbic centers. Various emotions have been attributed to neural activity and the action of several neurotransmitters and modulators in these areas in humans and laboratory animals. Basically, the main players for positive emotional states, such as reward and appetitive behavioral motivations and actions (Section 2.3), are the amygdala complex and, most important, the nucleus accumbens septi as a terminal site of the dopaminergic mesolimbic axis originating in the midbrain ventral tegmental area (VTA) [reviewed by 54,55]. It is noteworthy in this context that opioids act on the mesolimbic axis either indirectly by stimulating dopaminergic VTA neurons or directly by increasing dopamine at the level of the nucleus accumbens, supporting the view that mesolimbic dopamine is closely linked with rewarding stimulation and action [56,57], including positive anticipatory behavior [33,58]. Berridge [59] has suggested that, at least in the context of feeding behavior, the positive emotional valences “wanting” (appetite, incentive

motivation) and “liking” (pleasure) can be dissociated, as they are apparently mediated by different transmitter systems in the brain, that is dopamine and opioids, respectively.

Amygdala activity has been correlated to negative emotions such as fear and anxiety, where its role is well established [15,60]. In humans the amygdala complex is involved in the understanding of emotional facial expressions [61] and in the perception of perceived or expected negative stimuli as revealed by imaging techniques [62]. However, there is now evidence that the amygdala complex is also involved in positive emotions. Pleasurable music has been found to activate the amygdala and the ventral striatum as well as orbitofrontal centers in humans [63], and it was recently reported that in monkeys single amygdala neurons respond in anticipation of fruit reward [64]. Hence, it seems that subpopulations of amygdaloid neurons exist that respond differently to the emotional value of a stimulus. These findings indicate that this area is likely not a center that mediates judgment of negative events exclusively. Together with thalamic centers the amygdala has also been found to be a relay of oxytocin-mediated social recognition and attachment [65,66]. It now seems evident that, in mammals, brain oxytocin together with vasopressin plays an important role in positive social bonding, mainly, though not exclusively, between mates and between mothers and their offspring [67,68]. Besides acting at amygdaloid sites, oxytocin also acts at the mesolimbic axis, the nucleus accumbens in particular, where it triggers dopamine release in the context of social bonding [69]. The main structures, neuromodulators, sites of origin, and actions are summarized in Table 1.

Within the appraisal framework, the hippocampal and parahippocampal systems have been found to be involved in the detection and evaluation of new events that are embedded in semantic, temporal or local relations [80,81]. The detection of novelty requires perceptual identification and attempts to match actual sensory input to stored items. If this matching attempt remains unsuccessful, the situation is perceptually new and may demand increased effort. Consequently, coping with enriched environments requires activity and exercise, and such environments favor hippocampal neurogenesis and synaptic plasticity [82,83]. This view is supported by the involvement of the hippocampal system in the mediation of stress reactions [84], including the startle response [85]. When there is nothing new and demanding, however, the hippocampus exerts an inhibitory influence on the stress axis. More and more neurobiological evidence has now become available indicating that in fact two

aspects of reward systems must be distinguished. These aspects relate to the previously mentioned appetitive and consummatory behaviors, which are in turn linked to wanting and liking respectively. Combined, these two aspects are involved in a cost–benefit analysis that subjects make in relation to rewards and may reflect the effort that individuals are willing to exert to collect rewards [86].

2.2.2. Dopamine reflects intensity of wanting while opioids determine what is wanted

The meso-accumbens dopamine system is involved in the disposition to act upon previously “liked” rewards, *i.e.* in wanting [47]. Behaviorally, wanting is expressed as changes in transitions of goal-directed behavioral patterns, such as locomotor and investigatory behavior, prior to obtaining rewards. These patterns are labeled as anticipatory or appetitive behavior [33]. Depending on species and test conditions, behavioral changes either increase or decrease [rats: [43,58], mink: [87]]. These changes may be related to the role of dopamine in integrating cue- and context-associated details of the response to be displayed or in other words integrating neuronal inputs from the hippocampus and amygdala in the output of the nucleus accumbens [88].

The meso-accumbens dopamine system has a high degree of plasticity, which underlies its role in the organization of the efficacy of behavior. Highly rewarding incentives may sensitize the system, since it seems adaptive in the long term that what was once “liked” to a certain extent should be “wanted” in the future to the same extent. A seemingly contradictory finding is that stressors such as short-lasting social isolation or poor rearing conditions [58] also increase anticipatory activity for sucrose as a reward due to the fact that stress sensitizes this system [33,89]. Hence it seems that under conditions of apparent loss of control animals must increase their appetitive attempts to improve the perceived affective state.

Stimulation of mu-opioid receptors in the VTA, the origin of the meso-accumbens dopamine system, enhances dopamine release in the accumbens [reviewed by [90]]. It was shown in rats that the expression of anticipatory activity to rewards is blocked by the mu-opioid antagonist naloxone [33, 91]. This point was further demonstrated in mice lacking the mu-opioid receptor in a schedule-induced food-anticipation behavior paradigm [90]. These data show that the meso-accumbens dopamine system is under control of the opioid system, and suggest that the opioid system is important in adjusting the activity of the meso-accumbens dopamine system to challenges from the environment. Opioids in a low dose stimulate the onset of motivated behavior. They elicit feeding [92], social interaction, and play in young animals [93], depending on the context. By their stimulation of motivated behavior and simultaneous suppression of pain *etc.*, they allow the animal to start obtaining commodities. The opioid system is thus related to the consummatory, liking aspect of motivation, whereas dopamine, which is the interface between emotion and motion, would be a system mediating motivation for reward in a broad sense, including relief from stress, rather than reward *per se*. In contrast to states of motivation, where reward is sought and eventually gained, very little is known about the neuronal basis of satisfaction. In mammals this state of fulfilled

Table 1
Structures and neuromodulatory substances involved in positive emotions

Origin	Substance	Site	Effect	References
VTA	Dopamine	NAc	Expect reward Act for reward	[70–73] [70]
NArc, Pit	μ-Opioid	VTA, NAac	Facilitate dopamine response	[74,75]
Pit	Oxytocin	NAc	Facilitate dopamine response Promote social behavior	
		CA	Inhibit negative affect	[76–79]

CA: central amygdala; NAc: nucleus accumbens; NArc: nucleus arcuatus; Pit: pituitary; VTA: ventral tegmental area; μ-Opioid: receptor agonist.

needs and cessation of drive for further rewarding sensations seems to be characterized by reduced activities in a considerable network of forebrain structures, including the hypothalamus, amygdala, and frontal and insular cortex [94]. Shedding more light on the neuronal base of this important state of welfare will be necessary in future in order to have the full picture of well-being.

2.3. Behavioral aspects of positive emotions

2.3.1. Behavioral needs

Being aware of the fact that various perspectives on motivation exist, here we follow the perspective described in behavioral neuroscience, which is strongly supported by ethological and neurobiological evidence. In the literature on reward, addiction and affect [47,19], a close link has been made between neuronal structures and the components of motivation (*e.g.* appetitive or consummatory) [33]. The function of reward systems could be to weigh costs *versus* benefits of obtaining a commodity. The outweighing of costs by benefits would coincide with the experience of pleasure. A number of needs are dealt with autonomously, such as temperature, heart rate *etc.* However behaviors that need integration in space and time and that use previously acquired sensory information require focused attention of the highest emotional and cognitive brain centers. Selection of the most pressing need is executed by reward systems based on expectations. Ventral tegmental dopamine has been called the interface between motivation and movement [95] and links the specific requirement of a particular need with expected satisfaction of that need and activates higher cognitive processing. At least in humans one might say that the reward appraisal centers in combination with the nature of the need are experienced as affective consciousness. Affective consciousness probably occurs in animals as well though it will depend upon the cognitive capacity of the animal [19].

Two types of behavioral needs can be distinguished. First, needs that induce behavioral patterns can be evaluated by their direct physiological consequences for the underlying motivational system. For instance, hunger requires eating of food, which affects blood glucose, leptin levels and other parameters representing the metabolic status of the individual and influencing food regulation centers in the brain. Second, Jensen and Toates [96] defined a behavioral need as a specific behavioral pattern that the animal apparently has to perform, irrespective of the environment or of the animal's physiological needs. In other words, needs that involve the display of typical behaviors lack direct physiological consequences and thus also lack direct feedback from regulatory physiological mechanisms. It seems as though the biological relevance of regular performance of those behaviors lies in their long-term benefits for the individual animal or its offspring, *e.g.* behaviors concerning reproduction, foraging and grooming. The motivation to perform these essential behavioral patterns is governed by the display itself rather than to meet short-term physiological needs [48]. The mechanism underlying the regular display can be understood when it is assumed that the display itself, rather than its immediate effects, has rewarding properties. Long-term effects are then a probable outcome of the display, but beyond

what can be monitored by the individual animal. The impact of the display on reward guarantees its regular occurrence. The absence of such rewarding behavior coincides with the absence of an important source of reward [33].

2.3.2. How can behavioral needs induce pleasure and why do they make the animal vulnerable?

Appetitive behaviors with low probability of success or with a long time interval between onset and eventual consummatory responses would benefit from a regulating mechanism like that just described for behavioral needs. The animal can never stop looking for food, safety, and reproductive opportunities, even following unsuccessful attempts; in other words investing for the future must have direct rewarding consequences. Behaviors, which serve as an investment for collecting a necessary incentive, *e.g.* food or social companionship, may be self-rewarding in order to maintain these types of “searching” behaviors. Other examples are hunting in predators, exploration in a number of species, rooting in pigs, *etc.* Appetitive or seeking behaviors (motivational states of wanting) have been associated with mesolimbic dopamine, whereas consummatory behaviors (liking or hedonic motivational states) have been more associated with opioids [97,19,47,33]. Social behavior [98,19], reproductive behavior [98], play [99], autogrooming [100] and dust-bathing [101,102] are supposed to have rewarding properties.

To be self-rewarding, a specific behavior should activate the mesolimbic system, for instance by the release of endorphins, which then exert a positive feedback on this behavior, resulting in a longer lasting, on-going behavioral bout. Taking this process into account, one would expect that opioids may induce such behaviors, while opioid antagonists would counteract their display. One would expect self-rewarding behaviors to interact – cross sensitization and cross tolerance – with drugs of addiction or rewarding stimuli such as food. The opportunity to display may itself act as a reinforcer and can be used as an incentive in conditioned place preference studies. Being deprived of opportunities to perform specific behaviours resulting from these behavioral needs produces signs of withdrawal paralleling those observed in deprivation of an addictive drug [19,23,47,95,98]. Exploration in rodents, when modeled by wheel-running behavior, shows such interaction (cross sensitization) with mesolimbic dopamine and cross tolerance with morphine [103], an interaction similar to those observed for drugs of addiction. Cross sensitization between food and drugs of abuse has also been shown, and this phenomenon could be counteracted by an opiate antagonist [104]. Social behavior, play and self-grooming can be induced by endorphins and counteracted by naloxone [98–100].

A drawback of this efficient mechanism regulating the motivation of those behaviors that represent animals' behavioral needs is that self-rewarding behaviors may run out of control when dopaminergic systems are sensitized by stress [105–107]. If some stressors amplify animals' wanting for rewards when no external rewards are immediately available, they may instead look for compensation by performing self-rewarding behavior [108,109]. Thus, depending on the species and circumstances, stressed individuals may display excessive locomotion, sexual

activity, or self-grooming. Because highly motivated behaviors are so rewarding, being deprived of them is a severe stressor. At the same time some of them do not have an immediate high priority because they have a long-term payoff. Play for instance only occurs when other needs are met. Therefore, occurrence of play behavior or typical signs of satisfaction indicate that the animal is not deprived of important sources of pleasure and that other needs are being met. That is why such behaviors are good candidates for welfare indicators (Section 3.4).

2.4. Physiological markers of positive emotions

2.4.1. Sympathetic and parasympathetic balance

The autonomic nervous system (ANS) is an important efferent of the limbic system. It is primarily amygdala output, acting via hypothalamic centers, that influences autonomic brainstem nuclei controlling the activity of sympathetic and parasympathetic systems. The relative level of activity of these two systems is an indicator of an organism's general physiological state (action or digestion). Though this relative activity depends on homeostasis, it is also determined to a great degree by current emotions. Hence, measures of heart rate (HR) are broadly accepted as a valid index of stress in many vertebrate species as they give an impression of the activity of the ANS [110–112]. Interpretations have often been based on the assumption that HR reflects the activity of the sympathetic branch of the ANS and therefore can be used as an indicator of the sympatho-adrenomedullary stress response. However, the heart is also under parasympathetic control, and HR at every point in time is the result of non-additive effects of the interaction between the two branches of the ANS [113]. Thereby, the effects of emotional perceptions on cardiac activity are mediated via direct innervations of the sino-atrial node of the heart by sympathetic and parasympathetic fibers [114,115].

As a consequence of these permanent regulatory functions, HR is never constant but varies from beat to beat, hence the concept of heart rate variability (HRV). HRV is mediated by either an increase/decrease of sympathetic tone or an increase/decrease of parasympathetic tone. Hence, analyzing HRV helps to identify which branch of the ANS is actually mediating heart rate and to assess the sympatho-vagal balance of an organism [116]. The assumption underlying the assessment of HRV is that, as a peripheral measure of ANS activity, it serves as a proxy for vagal tone, vagal reactivity and sympatho-vagal balance that otherwise could only be measured by hard-to-perform invasive techniques [115,117]. A certain degree of HRV is a characteristic of any healthy vertebrate [118].

In recent years, cardiac vagal tone assessed by HRV-analysis has received considerable attention as a psychophysiological marker of emotion regulation, and of certain aspects of psychological adjustment in humans [reviewed by 119,120]. Most of the work has focused mainly on negative emotions and emotional disorders, which have been referred to as anger-proneness, irritability, irritable distress, and negative mood. However, cardiac vagal tone may also be an indicator of positive emotional states. Fox [121] found a near significant correlation between infant HRV and positive reactivity during a peek-a-boo

procedure with mothers and strangers. McCraty and colleagues [122,123] reported higher HRV in human adults after self-induced positive emotional states. Recently, Lee and collaborators found higher levels of HRV and reduced HR in humans after the intake of a traditional herbal remedy [124] and during Qi therapy, a Chinese external therapy [125]; this effect was correlated with more pleasant and calm emotions compared to the placebo group. Rainville and collaborators [126] found evidence that distinct patterns of peripheral physiological activity (e.g. HRV) are associated with different emotions like sadness or happiness. Recently, patterns of HRV reduction have been studied in farm animals in reaction to stressors [127–129], behavioral disorders [130] and in the context of cognitive appraisal [37]. For a broader discussion of this topic see also the review on HRV by von Borell and collaborators in this issue.

The potential elements and patterns of autonomic activity have not been exhaustively examined. Moreover, it is possible that emotions or components of emotions could be differentiated on the basis of sympathetic and parasympathetic innervations of the viscera rather than on visceral responses *per se* [131]. However, taken together the data indicate that monitoring activity of the autonomic nervous system, essentially through heart rate and its variability as suggested especially by human studies, may deliver suitable approaches to assess positive emotions in animals when combined with behavioral records [36].

2.4.2. Neuroendocrine activation

The physiological responses of the autonomic nervous and neuroendocrine systems trigger neuronal processes in the brain that influence the way animals cope with the situation. For instance, sustained high cortisol levels are associated with a higher probability of engaging in passive coping (*i.e.* being reactive), whereas high catecholamine levels are associated with a higher probability of engaging in active coping [132]. However, transient activations of the stress axes—*i.e.* the adrenocortical axis (HPA) and the ANS—are regularly coincident with any emotionally triggered activity and cannot be easily differentiated for positive and negative emotions. They might as readily be activated for actions of defense as for reward. Accordingly, in a comprehensive study in pigs it has been demonstrated that individuals with a high success in a dominance intruder test displayed dynamic peripheral responses of the HPA that were virtually the same as in losers [133]. Roughly the same was revealed in the ANS, however with a tendency toward a more rapid decrease after fighting in the high success animals. Further, winners tended to have a higher noradrenalin/adrenalin ratio which, in general, could reflect a less passive behavioral pattern [134]. Hence, intrinsic processes (e.g. fluctuations of hormone concentrations, induced spontaneously or by chronic emotional stress) may cause changes in mood, while sensory inputs may be able to release emotions.

Although experimental evidence is still scarce concerning changes in physiological parameters that accompany positive emotional experiences, some recent studies with human subjects reveal promising leads to follow in animal studies. Taking advantage of recent developments in salivary assay methods, physiological studies of human saliva suggest that its protein

composition could be used as a monitoring tool for the assessment of some emotional/mood states. Indeed, while negative emotions are associated with a decrease in 20–200 kD proteins, in positive emotions an increase in these proteins is observed [135]. It has also been found that salivary alpha-amylase (sAA) levels in humans are increased in response to physiological and psychological stress [136]. Furthermore, it is suggested that the level of this enzyme could be considered as an index of soothing effect or relaxation in humans as sAA levels are significantly decreased by soothing/pleasant video viewing [137]. The detailed mechanism of the amylase decrease remains unclear. However, developing such measures in animals could offer a relevant tool to assess positive emotional states in animals.

2.4.3. Immunological activation

An important literature exists regarding the emotional influences on immune functions, supported by both human and animal studies. Indeed, not only is there an extensive literature on the complex interactions between the HPA-axis and the immune system [138], but also emotional limbic activity has been found to have important effects on immunity [139]. In pigs, positive and negative psychological experiences affected immune system parameters antagonistically, depending on the success of coping [140]. Hence, immune status may be another indicator of long-lasting emotional state (or mood), and immunological parameters may be indicators of frequent positive (or negative) emotions [141]. However, with the present state of knowledge, they are difficult to interpret since the various immune factors constitute a multidimensional vector whose components are mutually interacting and can be easily influenced by non-obvious infections. Unfortunately, experimental evidence linking positive emotional experiences to the immune system is lacking. It is therefore risky to infer that positive emotional stimuli would enhance immune defenses. However, a recent study found that pleasant stimuli in human (*i.e.* humoristic story-telling) induced an increase in secretory immunoglobulin-A (s-IgA) [142]. This confirms results from a pioneering study by Dillon and collaborators [143] in which the salivary IgA concentration was specifically increased after subjects viewed a humorous video sequence. Since s-IgA is considered an indicator of overall immune function, such measures in laboratory and farm animals could offer new insights for the understanding of emotional influence over immunity.

Conversely with brain-to-immune influences, growing evidence reveals that the immune system influences brain functions, including structures involved in emotional processes. In addition to various effects on emotion-related neurotransmitters (*i.e.* serotonin or noradrenalin), immune activation is known to induce HPA activation [138]. When these data are combined with the fact that immune and stress responses have been argued to share common evolutionary defensive properties, immune activation is increasingly considered as a stress response by itself [144]. Moreover, some studies show that immune activation has emotional effects, such as anxiety- or depression-like behaviors [141,145].

Nevertheless, it has recently been shown that rats made sick through the peripheral administration of endotoxin are still able

to respond positively (*i.e.* hedonic facial responses) to palatable taste solutions such as sucrose [146]. However, when subjected to mixed bittersweet solutions, these rats display more aversive and fewer hedonic responses than do controls [146]. Therefore, immune activation cannot be considered to induce anhedonia as had been reported in earlier studies. Rather, these data may illustrate alliesthesia, *i.e.* modification of the affective value (*i.e.* valence) of a specific stimulus related to the subject's physiological status [147]. In other words, it has been proposed that instead of causing a negative emotional state, immune activation would enhance reactivity of subjects to salient negative features of a given situation, thus motivating their defensive repertoire [148,149]. Inflammatory markers could therefore be used as possible indicators of a transitory vulnerability of subjects to external sources of stress, and immune activation could be used as a tool to evaluate the plasticity of the valence (*e.g.* from pleasant to aversive) of specific features of each subject's environment [150]. In conclusion, even if a lot remains to be done to fully validate their use and relevance, heart rate variability as well as alpha-amylase and immunoglobulin-A levels could be interesting physiological parameters for assessing positive emotional states in animals, at least as complements to classical adrenocortical and/or inflammatory measures.

3. Application of positive emotions in animal welfare

Increasing research in the area of positive emotions, in combination with pressure from society that animals should have a “good” life and not just a “not-so-bad” life, is leading to a greater aspiration to apply some of the knowledge described in the first part of this review. The most likely practical applications fall into four broad areas: i) promoting positive experiences as a way to give animals a generally better quality of life; ii) enhancing long-term positive emotional states; iii) highlighting the link between positive emotional states and improving health, and iv) including criteria of positive welfare in on-farm monitoring systems.

3.1. Enhancing quality of life by promoting positive experiences

Here we outline new approaches that might be useful in animal husbandry for inducing positive emotions in animals throughout their lives. Three approaches can be defined—signaling or predicting a reward in advance, giving a higher reward than expected, and enabling the animals to cope with or to control the situation.

3.1.1. Positive anticipation

Investigations of what animals find positively reinforcing and of the animal's behavioral expression during anticipation or expectation of the rewarding result provide a basis for assessing positive emotional states in animals [33]. The period between the signal and the arrival of the reward is the period in which behavioral activity related to dopaminergic activity can be seen (Section 2.3), *i.e.* anticipatory behavior. Anticipatory behaviors are considered to represent biologically significant preparatory

behaviors [151]. When anticipating food rewards, rats [58], mink [152] and pigs [153] show increased locomotor activity and frequent behavioral transitions, *i.e.* anticipatory hyperactivity. More specifically, the behavioral categories reported in rats during anticipation of sucrose rewards include locomotion, grooming, alertness, arousal, scanning, attention, exploration and running [58]. In pigs, signaled positive stimuli such as extra space, food, or straw lead to increased activity due to orientation toward the place where the reward is offered and frequent behavioral transitions, most often combined with play markers, *i.e.* hopping, scampering, pivoting, pawing, flopping, and head tossing [153]. During anticipation of feed rewards, farmed mink showed a general increase in locomotor activity, and they spent more time moving in/out of the nest box, less time in the nest box, more time “nose-poking” around the feeding area, and more time standing and scratching at the cage door [152,154]. Farmed silver foxes anticipating a food reward or playing incentive were more active, had more erect ears and higher body carriage, and spent more time in front of the cage compared to animals that were anticipating aversive stimuli [155]. The predictability of the rewarding stimulus plays a role in behavioral expression during anticipation. Silver foxes anticipating a positive predictable reward (food or play) had more upright ears, whereas for a positive unpredictable reward the ears were more backwards rotated and flat [155].

Sensitivity to dopamine is adapted to the impact of reward and the needs of the animal in the manner that is related to previous experience. Thus, the threshold of the animal to react to a stimulus reflects the sensitivity of the system. In addition, the amount of activity is related to the needs of animals. For instance, if housed in a poor cage environment, rats were more sensitive to signaled positive rewards compared to rats housed in an enriched environment [58]. However, there is a risk of misinterpretation here as the absence of a reaction to a reward may indicate that the animal is in a state either of full satisfaction or of anhedonism, and these are opposite states in terms of welfare. In addition, the intensity of reaction to a small reward has to be calibrated for each species and situation. In silver foxes, anticipatory behavior consisted of high levels of locomotor stereotypical behaviors such as running back and forth in the cage environment [155]. Whether stereotypies during positive anticipation are an expression of enhanced expectation shaped by the environment into repeated movements or a stereotyped behavior due to previous and/or current frustration [156] remains to be seen.

3.1.2. Positive contrast

In a typical positive contrast experiment an animal is first trained to perform a task by giving it a reinforcer of a certain size. The animal is then given a larger reinforcer than they had been given before. If the animal changes its behavior so that its response is faster/more vigorous than that of a control group given the larger reinforcer from the start, a successive positive contrast (SPC) has occurred. In the same way, an animal that has been trained using a large reinforcer, and then shifted to a small one, might react with a decrease in response, bringing it lower than an animal that has always received a small reinforcer,

demonstrating a successive negative contrast (SNC) [reviewed by [157]]. SPC and SNC can be found for both appetitive and consummatory responses. It is the difference between the expected value and the actual value that influences a subject's behavior rather than the exact level of reinforcement. If the animal has a previous experience of a higher value reinforcer, the reaction to a given level of reinforcement is much less pronounced. Any contrast effect is often temporary and disappears over time [*e.g.* [158]]. The fact that the appearance of an unexpected reward makes such a difference to the behavior of the animal has led several authors to suggest that positive contrast corresponds to the emotion elation in humans, while negative contrast might be related to frustration or disappointment [*e.g.* [159,160]].

Overall there are more studies showing a negative than a positive contrast. Negative contrast seems to be a more robust phenomenon and is easier to detect. This is also possibly due to a ceiling effect; for instance, an animal that is running at top speed for a reinforcer is unable to increase its speed even if the reinforcement is increased. Unfortunately this result has meant that the majority of theories of the contrast effect have focused on explaining the negative contrast effect exclusively. Although some of the theories involve emotions *e.g.* elation or disappointment as described above, most are alternative ‘non-emotional’ theories such as generalization decrement [161], incentive averaging [162] or exploration [Elliott, 1928 cited by [157]]. There are nevertheless a number of more specialized emotional theories that do not rely on a general emotional drive, *e.g.* Amsel's frustration theory [163] or Gray's disinhibition theory [29]. Positive contrast has been found in few species of mammals and birds [164–166]. For instance, in his original study, Crespi [159] reported that rats for which the quantity of reward has just been increased run faster towards the food reward than do rats having always received the large quantity of reward. However, the changes in the behavioral responses are generally more pronounced for the negative than for the positive contrasts [164–166]. Due to the relatively small number of studies, further research is needed to confirm the value of a positive contrast model in the study of potential positive emotions and their behavioral expressions.

3.1.3. Coping and controllability

The possibility of controlling the environment and coping successfully with challenges may be another source of positive emotions. Despite some degree of stress being necessary in the initial state of coping to activate alertness and metabolism [167], successful actions with a positive outcome make the animal master of the environment. Successful coping stops the initial stress reactions, independent of the positive or negative value of the stressor, while uncontrollable and, hence, persistent negative stressful stimuli lead to the well-known detrimental effects of chronic stress [84,168–170]. A prerequisite of controllability is predictability, *i.e.* the environmental reactions are (mostly) contingent on the subject's actions. If the environment where a species lives is sufficiently constant during a long period of time, successful behavioral coping strategies may well be acquired during the process of evolution and, then, are innate at the individual level. If there is no innate coping behavior, an

animal may try to learn how to deal with a challenge. Success depends on a number of prerequisites. First, the animal has to have the motor patterns necessary to be able to deal with the challenge with at least some success; eventually these patterns can even be shaped to deal with it better. Second, there must be a kind of random action selector to try out what could be helpful when dealing with the challenge. Third, in the central nervous system there must be the ability to link the sensory and perceptual cues that are coincident with successful behaviors and the challenging context. Fourth, there must be contiguity between the challenge and the behavioral action [171]. If any of these conditions remain unfulfilled the animal will be unable to learn how to cope, a failure that will eventually lead to chronic stress. Hence, inactivity displayed by an animal may be caused by two emotional states: total equilibrium, when everything is at or close to optimum, or learned helplessness, if the subject has the experience that there is no possibility to escape the negative environment [172]. The result is an inactive, depression-like chronic stress state that is often accompanied, *inter alia*, by permanently increased levels of the stress hormone cortisol.

Social and physical challenges can be perceived as positive experiences when exists an adequate coping behavior. Hence, frequent challenges that can always be successfully mastered and eventually enable the animal to reach a desired and rewarding goal may be suitable means to regularly evoke positive emotions. Using an approach of this type, a program of research on the effects of rewarded cognitive processes has been developed [173]. In the studies conducted thus far, each animal out of a group of pigs had to learn an individual acoustic signal as a call to work for food by pressing a button. The demands of this situation were threefold: The animals had to be attentive for their individual acoustic summons, they had to localize its source, and they had to respond to a button with their nose disc in order to be rewarded with a small portion of food. It was shown that the pigs were willing and quite able to cope with these demands. Using this approach it will be possible to analyze the physiological and behavioral effects of a complex but predictable environment presenting positive challenges with which individuals are able to cope.

3.2. Enhancing long-term positive emotional states

3.2.1. Concept of temperament

The emotional sensitivity or temperament of an animal has an important influence on its welfare, and so predisposition to some positive emotional states is a good premise for investigating long-term positive emotional states in animals. The terms and concepts used for defining long-term emotional states differ in the degree of structure they provide, from “individual differences” to the concept of personality.

The distinction according to the species and the age of the individual between temperament (for animals and human infants) and personality (for children and adult humans) has not been maintained consistently in the literature [174]. Temperament can be defined as the characteristics of individuals that describe and account for consistent patterns of feeling and behaving [175]. Whereas dimensions of personality have generally been discussed in terms of either coping style or fearfulness,

there is currently no method for assessing a propensity to feel and express positive emotions. However, by identifying long-term positive emotional states we can examine whether characteristic behavioral patterns could be linked to particular neuroendocrine states and if they correlate within individuals and over time. From such studies we might be able to predict responses of an animal in one situation based upon its responses in another.

There is no universally accepted definition of “individual variation” or “individual differences”. Erhard and Schouten [176] structured individual variation in animal behavior using the Eysenck [177] description of personality. This approach organizes the different aspects of personality into three levels—“state”, “trait”, and “type”. The term state or mood is used for the behavior that an individual performs at a specific moment in time and in a specific situation. If an individual is repeatedly found to be in similar states in similar situations, we can make assumptions about the underlying personality trait (*e.g.* fearfulness or happiness). Regarding the third level, when several trait dimensions are linked in such a way that an individual’s position on one dimension predicts its position in another, the individual can be categorized by their position in a type dimension.

This approach brings the study of individual differences in non-humans closer to what is done in humans [39,176,178]. Different studies have been carried out to evaluate emotional states in farm animals. For instance, from a combination of the responses to fear and learning tests, three emotional states were established in dairy sheep: non emotive ewes (calm, fear sustainable, reacting adequately in learning tests), emotive ewes (nervous, fear susceptible, reacting inadequately in learning tests) and intermediate ewes [179]. It was further established that the emotional state influenced various adaptive behaviors. The non-emotive ewes revealed a stable maternal care, whereas the anxiety increased in the emotive ewes on the second and third days postpartum [180]. Furthermore, by contrast to the emotive sheep, non-emotive animals usually successfully collect different rewards (appetitive and consummatory behaviors) ensuring successful reproduction and higher production [181]. Personality may have different “dimensions”. This idea was supported by Kilgour and collaborators [182] showing different components of personality in cattle and sheep adapted from human studies: general agitation and avoidance. The hypothesis that calm animals produce better quality milk than nervous animals was supported by the result for protein concentration [183]. Merino ewes of calm temperament can provide better quality milk, indicating that temperament should be considered when selecting dairy animals. Martin and collaborators [184] propose a strategy aiming to maximize offspring survival by a combination of management, nutrition and genetic selection for temperament. From a divergent selection on behavioral reactivity, calm ewes are found to be better mothers than nervous ewes [185]: they spend more time with their lambs, have a short flight distance when disturbed and return to their lambs faster than nervous ewes. In addition to postnatal lamb survival, temperament may influence other aspects of the reproductive process, all of which might be improved by genetic selection for calm temperament. These include the length of the estrous cycle [186], ovulation rate [187], the proportion of ewes mated, and

sexual behavior [188]. Finally, temperament seems to affect other aspects of production such as growth rate [189–191] immune function [191], milk yield [192] and meat quality [193, 194]. All of these outcomes could be used to improve productivity while giving the industry an ethical quality [reviewed by [184]].

3.2.2. Genetic background

Large differences in emotional responses have been reported between breeds in various farm species [195]. In dairy cattle, sire had a significant effect on the reactivity of cows in the milking parlor [196]. Similarly, sheep sired by Romney sires were more reactive when placed in a fearful situation than ewes sired by Suffolk or Columbia rams [197]. Genetic analysis revealed that such emotional responses were due to direct genetic differences and less to direct maternal influence or to heterosis. The estimates of heritability of fear in domestic animals seem to be sufficiently high to allow further selection on fearfulness in attempts to improve herbivore management [reviewed by [198]].

In addition, the development of marker-assisted selection can be useful for psychological states such as fearfulness. Identifying quantitative trait loci for fear has recently been extended to cattle [199]. So far, QTL for reactivity to humans have been identified using linked markers in cattle [200,201]. Such linked markers may be used for marker-assisted selection within sire families once the relationship between the marker and the gene has been determined. The interactions between the genotype of animals and their environment must be seen as a critical determinant of animal welfare that could reconcile production with ethical concerns [198].

3.2.3. Ontogenetic influences

Abundant data demonstrate that stimulation occurring during early life may markedly modulate the development of subsequent emotion processing in a positive direction. It has been demonstrated that some postnatal stimulation have opposite effects to those induced by prenatal stress. For example, adult rats that have received substantial positive stimulation during infancy, such as environmental enrichment or regular handling, are less emotionally reactive to various challenging situations [202–204]. Handling animals during infancy also leads to improved endocrine reactivity in adulthood. For instance, early handling alters neuroanatomical development in rats by increasing the number of hippocampal glucocorticoid receptors or by decreasing CRF mRNA implicated in endocrine regulations occurring under stress [205,206]. Extensive research on the influences of early regular handling has been conducted in domestic animals. For instance, early handled ungulates are generally less fearful of humans than their non-handled counterparts, a pattern shown in goats [207], horses [208], cattle [209], sheep [210] and pigs [211]. Experiences that occur during adulthood may also influence emotional responsiveness, particularly through classical processes of learning and habituation. The exposure of adult animals to enriched environments or handling procedures has been shown to decrease subsequent fear, although the reported effects are generally less marked than those induced by the same treatments occurring during infancy [212].

Taken together these findings indicate that early stimulation and later experiences interact with genetic background through

out the life of the individual to continually modulate emotional reactivity by shaping tendencies to feel secure. Although not all aspects of personality in animals are clear, we can state that emotional traits do exist in animals since emotional reactivity was found to be consistent across time and situation [176,213]. Although most of the studies have been done to reduce negative emotions, the study of emotional traits may also provide good tools to better enhance long-term positive emotional experiences. For instance, social play behavior was more often seen in mink selected for low fearfulness than in those selected for high fearfulness [214].

3.2.4. Enriching the environment or just reducing stressful events?

Environmental enrichment is often proposed as the way to enhance positive experiences in farm and laboratory animals. Unfortunately, most studies on environmental enrichment are actually only adding resources or features to an impoverished setting [215], suggesting the term “housing supplementation” might be better for such practices [216]. The beneficial effects of supplementation are usually represented by a reduction in the indicators of poor welfare (*e.g.* fewer stereotypies, less aggression) rather than an increase in indicators of good welfare. It is argued that the term “enrichment” should be reserved for environments that are truly enriched beyond basic needs [217], and it is this meaning of the term that is adopted here. This enhanced quality of life could be achieved by physically enriching an already varied environment with new resources or by cognitive means. The methods for achieving such enrichment are presented throughout this review, *i.e.* by creating a situation where there is anticipation of a positive reward, by offering more space to promote play, and by providing opportunities for positive contrast situations, for improving coping abilities, and for information gathering. Some concrete examples of where these methods have been tried are given by Moe and collaborators [155] and Ernst and collaborators [173], and other examples include the work by Wood-Gush and Vestergaard on seeking novelty and its relation to play [218], problem solving in cattle [219] and stroking animals [220]. Nevertheless, in all cases it is necessary to confirm that the enrichment is having the desired effect, which is not as easy as might be proposed. At present, the enhancing effect is usually taken to be an increase in those behavior patterns scientists think are positive. However this approach entails a risk of circularity in reasoning, *i.e.* we change an environment to promote exploration and play, and then say it is enriched because we see more exploration and play.

Another practical application of positive emotions in enhancing overall quality of life is that they can be used to prevent or reduce the development of negative emotions, so leading to a net benefit. This effect may be achieved by associating an event, *e.g.* taking a blood sample, with a positive one, *e.g.* getting a food reward, [221] or by making negative events, *e.g.* a veterinary procedure, less negative beforehand by habituating the animal to being handled [222]. Although these are examples of reducing negative emotions rather than enhancing positive ones, the net benefit to welfare is positive. If this argument can be used to reduce the effects of short duration negative events, the question

of whether positive events can be used to offset negative ones over the course of a lifetime can be raised. Although theoretically justifiable using a preference utilitarian philosophical approach, we propose that this summing up of earlier positive experiences is not applicable to animals living mainly in the present as do most farm animals. Neither should we justify poor long-term housing and management because we sometimes give animals short-term positive experiences. If we want to maximize welfare, then the aim must be to give the animals as good quality of life as possible all the time. Since it has been shown that anticipatory behavior followed by the consummatory act has beneficial effects compared to the provision of the mere reward alone, there is the possibility to manage animals in a way which stimulates the activation of these systems, while at the same time giving as good housing and management as we can. The caveat is of course that a certain degree of sensitization is necessary for induction of pleasure but not to the extent that the period of need for reward outweighs the satisfaction. This balance should be explored further. Promoting play in young animals and stroking animals (or alternatively promoting social licking) are also probably feasible methods to promote positive emotions in practice and so enhance overall quality of life in systems that are usually regarded as acceptable from an animal welfare point of view. Finally, in relation to the “active” behavioral expressions of positive emotions (Section 3.4), like play, allogrooming and exploration, another class of behavioral expressions of positive emotions should be mentioned here, namely those expressing full comfort and satiation, *i.e.* the fulfillment of biological needs.

3.3. *Inducing positive emotions for improving health*

Although research in this area is just developing, there are already some data showing that positive emotions may improve health. Pioneering researchers suggest that there are health benefits in humans of humor and laughter as positive-emotions promoters, especially in coping with a diagnosis of cancer [223]. Although the scientific evidence for this claim is inconclusive [224], humor is being increasingly used as a mean of reducing stress and making patients feel better [225]. Obviously, there are no such studies in animals, but as it is documented in the next section, play and tickle-induced ultrasonic vocalizations have been identified in rats and interpreted as sharing evolutionary relations with primitive laughter in human [226]. Nevertheless, poor health is a well-accepted indicator of poor welfare in animals, and improved conditions for animals usually lead to improved health. It is logical to suggest, therefore, that giving increased opportunities for positive experiences might also have a positive effect on animal health. There is evidence that pigs given the opportunity to show successful adaptation by rewarded cognitive processes recover more quickly from a standard biopsy [221] and have improved carcass quality [227]. However, a central question is whether the effect is a promotion of actual health and fitness or a reduction of chance in health degradation. The terms of the dilemma are the same as for environmental enrichment. That is to say, are we really improving health or are we just counteracting some of the negative health effects of the way we keep animals? In laboratory animals, signaling rewards

can significantly reduce anhedonia [228]. More specifically, signaled rewards counteracted the impairment of anticipatory behavior in socially stressed rats, further supporting the view that eliciting positive affective states has beneficial health effects. However, even in this example the effect is in reducing otherwise negative health effects rather than inducing positive health effects *per se*. In any event, understanding these mechanisms will improve our ability to understand the benefits of positive emotions and also suggest new clinical treatments based on these behavioral mechanisms.

3.4. *Using positive emotions for assessment and monitoring of animal welfare*

3.4.1. *Assessing and enhancing behavioral expressions of positive emotions*

3.4.1.1. *Play behavior:* Play behavior includes elements of well-defined “functional” behavior such as fleeing, fighting, sexual, or predatory behavior as well as specific play behaviors. However, in play the “functional” elements are exaggerated, repeated, more variable, and without the corresponding consummatory act [229–232]. The function of play behavior has been, and still is, the main focus in the scientific study of this behavior. In early studies the function of play behavior was thought to be exclusively long-term benefits. However, studies testing functional hypotheses of play behavior found little evidence of long-term effects. Thus, current theories focus more on short-term benefits to the juvenile and less on long-term benefits, although the two may not be mutually exclusive [232]. Proposed functions of play behavior are training of the skeletal muscles [229] (later refined to include permanent modifications in brain and skeletal muscles [233]), self-assessment of physical and social abilities [234], and training of flexible kinematics and emotional responses to the unexpected events, a hypothesis that predicts both immediate and long-term effects of play behavior [235].

The fact that play behavior may be suppressed in harsh and unfavorable environmental conditions together with the problems of early studies to prove any long-term function of play behavior suggested that play behavior was merely a sign of surplus energy without any motivation of its own. However, there are now several sources of evidence to suggest that play is a rewarding activity [232]. First, animals actively seek out play partners and solicit play behavior [229]. Second, the opportunity to play may be used as a reward in place preference conditioning experiments [236]. Finally, thwarting of play will lead to a rebound when more favorable conditions occur [237].

Conditions intuitively associated with bad welfare, *e.g.* insufficient food supply, suppress play behavior in deer [238] and domestic pigs [239]. Castration eliminates play behavior in lambs [240] and domestic pigs in a semi-natural environment did not play during periods of cold weather [241]. Thus, the presence of the motivation to play may indicate a state of good welfare, *i.e.* that the primary needs of the animals are met.

In calves the two most common types of play are social play and locomotor play. Locomotor play emerges first and is seen as

early as a few hours after birth, and the presence of the mother has been found to stimulate this type of play behavior [242]. Under natural conditions locomotor play behavior occurs within the first weeks of life [243,244]. Increasing the space allowance for group-housed calves has been found to increase the occurrence of play behavior [245]. Furthermore, calves kept with little space showed a large rebound of locomotor play indicating that these calves had built up a larger motivation during the period of confinement [245,246]. In piglets play behavior includes both locomotor and social play behavior, although it may be difficult to distinguish between play fighting and genuine fights [197]. In piglets more locomotor play behavior was seen in larger farrowing crates compared to smaller ones [247]. In addition, different types of farrowing crates placed in pens of equal space affected play behavior [248]. Locomotor play behavior is reduced by mixing of piglets [249] and by social isolation [250,251]. In mink the additional provision of a water bath to mink kits stimulated more play behavior, both solitary locomotor play and social play (e.g. chasing and rough-and-tumble play) [87]. Likewise, the provision of a wooden block in the home cage of mink stimulated accelerated running, interrupted by sham attacks of the object [214]. As outlined above play behavior is a good candidate for an indicator of positive emotions and good welfare. However, caution must be taken when developing play behavior as a positive welfare indicator since social play can end in a fight, as in piglets [248]. This problem may be specific for the juvenile pig, where dominance plays a role from birth, whereas in cattle the tendency for social play to develop into real fights does not increase until the animals reach puberty [252]. However, for all species some elements of play behavior may be better indicators than others, and one way of developing the area further could be to identify and validate so-called “play markers” as signs of true play in the different animal species [241]. Such play markers may be play signals, which communicate a playful mood to potential play partners. Play signals have the advantage that they are often conspicuous and easy to distinguish. Present evidence on play behavior applies only to juveniles of mammalian farm animal species. In these species it will be important to develop and validate measures of play as welfare indicators, both in animals reared for meat or for replacement (weaned piglets, growing pigs, calves, lambs, and goats), and in foals.

3.4.1.2. Affiliative behavior: Affiliative behavior is characterized by maintaining proximity, providing food, protection or allogrooming between specific individuals. In farm animals, affiliative behavior has been much less well studied than social competition and it has only rarely been investigated with regard to affective states. However, terms such as “affiliative”, “sociopositive” or “preferential” relationships already suggest a beneficial effect for the animals involved.

In general, positive effects of affiliative behavior can be attributed to improved group cohesion, building or strengthening of bonds between group mates and reduced aggression [253]. Preferential relationships between group members have been described for cattle [254], horses [255], poultry [256] and pigs [257]. Such relationships occur between genetically related

[254,258] as well as unrelated animals [259,260]; the latter has recently been shown for horses, donkeys, cattle and sheep [261]. Familiarity appears to be one of the main factors in establishing cohesion [262–264]. Stress responsiveness is lower in familiar animals [265–267] whereas mixing of unfamiliar animals is accompanied by an increase in agonistic interactions in pigs [268], cattle [269], poultry [270] and horses [271]. Affiliative behavior may therefore play a major role in achieving a positive mood in animals. It should however be noted that external threats might increase the proximity between animals. Therefore, inter-animal distance cannot be taken as a direct measure of positive emotion level without knowing more about the threats perceived by the animals.

Allogrooming plays a key role with regard to so-called sociopositive interactions. It is common among non-human primates [33]. In farm animals, allogrooming is seen in cattle, horses, pigs and, rather rarely, in sheep. Allogrooming seems to serve both hygienic (body care) and social functions. With regard to the latter, allogrooming is thought to play a major role in reinforcing social bonds and in reducing tension in groups of animals [100,272]. Such an arousal-reduction effect suggests that allogrooming may provide long-term benefits. However, there is also evidence that allogrooming is rewarding in the short term. Soothing effects in terms of a reduction in heart rate have been demonstrated in primates [273,274] and cattle [272]. Grooming stimulation produced similar effects in horses [275,276]. In pigs, heart rate variability was used to assess the effect of grooming simulation [277]. A short-term increase in vagal tone appeared to be contradictory to the behavioral reactions of pigs suggesting relaxation, a finding that was interpreted as “positive strain”; regular grooming, however, increased parasympathetic activity. Increased β -endorphin levels have also been found in primates with intensive grooming relationships [278].

Based on the above-mentioned findings, affiliative behaviors appear to be promising indicators of long-term positive affective states in farm animals. Allogrooming should be further investigated as a key indicator in cattle, horses and pigs. In cattle, social licking is mainly carried out at the head, neck or shoulder of the animals [252]. It is performed spontaneously, after solicitation, or following agonistic interactions. Social licking may also be terminated by agonistic behavior mostly performed by the licked animal. Solicitation of social licking [279] underlines the rewarding function of such behavior, at least for the receiver. Whereas the overall benefits for the receiver are obvious, it is less clear to what extent the actor is positively influenced. While in horses mostly reciprocal grooming (mainly consisting of biting and nibbling the group mate’s neck) between bonded pairs is observed [280], in cattle Sato [281] found that all animals were groomed but that only 75% performed grooming. Reports on the importance of the social position of the groomer are contradictory [252,282,283]. However, subordinate animals might experience performance of the behavior as stressful if licking has been initiated by dominant animals, although they may benefit from a less tense social environment in the long term. The use of allogrooming as an indicator in welfare assessment protocols may be limited

since, for example, in horses social grooming is influenced by season [260], social structure [264] and reproductive state [284] and therefore needs further investigation with regard to reliability issues. In wild boars, regular nose-to-body contacts [285] suggest that allogrooming forms part of the pig's normal behavior. Meynhardt [285] also states that the receiver shows relaxation-related behaviors, a finding that has been confirmed by a grooming simulation study [277]. However, high levels of allogrooming activity may not necessarily reflect positive states of the animal. Pigs in barren environments showed more allogrooming than did those in enriched housing systems that allowed for rooting and exploration [286,287]. On the one hand, increased allogrooming may disturb the receiver. On the other hand, redirected abnormal behaviors may develop such as tail- or ear-biting [255]. Therefore, the level of allogrooming indicative of positive affective states in pigs must be determined before it can be used as a welfare indicator. With regard to animal species showing little allogrooming activity, such as sheep and goats [288], or species in which other affiliative behaviors have to be taken into account (poultry), potential alternative indicators of positive affective states would have to be identified and validated. With these caveats affiliative behaviors and especially allogrooming is a promising candidate for a type of behavior indicative of positive emotions.

3.4.1.3. Self-grooming. Self-grooming is the maintenance of one's own body surface. In mammals this maintenance is achieved through licking, scratching, and rubbing of the fur, as well as through wallowing and bathing. In birds it is through preening and bathing in water or sand. These various forms of self-grooming maintain the body surface by removal of dirt and ectoparasites as well as by thermoregulation.

However, self-grooming may also occur as a displacement activity with an arousal-reduction or relaxation effect [100]. In birds, self-grooming increases in response to a thwarting or a conflict situation [289]. Likewise in mammals, self-grooming is elicited in reaction to a novel or stressful situation [290–292]. Self-grooming is also reported to be higher in animals kept in barren environments. For example, self-grooming occurred less among rabbits kept in cages with a shelter as compared to rabbits kept in barren cages [293]. Self-grooming in animals kept in barren or restrictive environments may be reduced either by the provision of hay, *e.g.* in rabbits [294], or by increasing the space allowance, *e.g.* in dogs [295] or in dairy calves [296,297]. Likewise, the occurrence of self-grooming is decreased under group-housed farming, *e.g.* in calves [298–300] and horses [275]. When kept in groups the animals engage in allogrooming, and the higher level of self-grooming in individually housed animals may be due to the lack of allogrooming that may have an arousal-reducing effect (Section 3.4.1 “affiliative behaviors”). Thus, as outlined above, the relation between the performance of self-grooming and positive emotions is much less clear-cut than it is for allogrooming. The performance of self-grooming may occur as a displacement activity in stressful situations and barren environments. However, self-grooming may also be performed to substitute for social grooming; it is possible that the performance of self-

grooming reduces arousal as has been suggested for social grooming. If these effects of self-grooming can be demonstrated, it would be a potential indicator for positive emotions.

3.4.1.4. Vocalizations. Specific vocalizations could be considered to some extent as direct expressions of positive immediate experiences in animals. While vocalizations have long been used as markers of emotions in animals [301], they have usually concerned negative experiences (*e.g.* distress, fear, aggression, defeat). However, focusing on data obtained in rats, Panksepp and Burgdorf [226] have recently argued that some short chirping ultrasonic vocalizations centered around 50-kHz could signal positive affects. This conclusion is supported by the fact that such vocal signals are produced in “positive” contexts, such as sex, winning fights, play, or manual tickling, and are inhibited by negative situations [226]. Intriguingly, it is proposed that these vocalizations could reflect a positive state in rats analogous to primitive laughter that accompanies social play in human infants. Not only does such a proposal offer a framework to further study evolutionary roots of positive emotions (and especially laughter) in humans, but it could also be extended to other species (*e.g.* domestic species). For example, some vocalizations of domestic cats, such as purring, are well-known to be produced in situations of positive valence, such as mother–kitten interactions, contacts with familiar partner, or during tactile stimulation with inanimate objects as when rolling and rubbing [302]. Therefore, purring can be generally considered as an indicator of “pleasure” in cats. Similar data could be obtained in farm animals. Indeed, low-pitched bleating in sheep has been associated with some positive-valence situations, as they are produced by males as an estrus female is approaching or by lactating mothers while licking and nursing their lambs [288]. Such an approach could be highly beneficial for animal welfare as farm animals' vocalizations could offer easily measurable markers of positive emotions since they are audible sounds for humans and can be monitored automatically [303]. Overall there are findings supporting the hypothesis that at least play behaviors, affiliative behaviors, and some vocalizations can be perceived as indicators of positive affective states in animals.

3.4.1.5. Information gathering. Information gathering or exploration might be relevant for positive affective states for two reasons. The first reason is that it is a behavior that most species of animals are motivated to perform, *i.e.* they are fulfilling a behavioral need. The second reason is that exploration is a behavior that is closely related to and affected by fear. Information gathering is a behavior that seems to be self-reinforcing to some extent. It doesn't satiate in the same way as many other behaviors do, and this property has led some authors to suggest that it might actually be a behavior that is continually on-going and is only interrupted when other, more immediate needs, are present [304]. There are two forms of exploration: the inquisitive exploration in which the animal is looking for a change and the inspective exploration in which the animal responds to a change [305]. If the information primacy interpretation is correct, then exploration, especially inquisitive

exploration, can be regarded as both an indicator of no other immediate needs and a continuous pleasurable activity in itself (since the animal keeps doing it). The maintenance of a behavior might not in itself warrant calling it reinforcing, but combining its flexibility with its self-reinforcing properties makes it hard to avoid that supposition.

In inspective exploration, which typically is investigation in response to a novel object, there is a gradual approach to the novel object similar to that seen in other approach/avoidance situations involving, for example, hunger instead of curiosity. In many of the motivational models of exploration, the response to the novel object is a result of curiosity and fear. The fear either interacts with curiosity, with exploration being the behavioural outcome of that interaction [e.g. [306]], or alternatively fear and exploration are seen as lying along the same axis [e.g. [305,307]]. This close relationship between exploration and fear is further supported by the finding that personality research on animals tends to find a negative correlation between the reaction of the animal in situations that provoke fear and those that measure exploration [e.g. [308]]. However, some caution is needed when interpreting these results since in some cases only a few situations have been measured, and these may make it inevitable that the two motivational systems are intimately linked.

3.4.2. Developing an on-farm monitoring system to assess animal welfare

Consumers are increasingly concerned with the welfare of animals contributing to the products they buy, and there have been several initiatives to develop products marketed according to animal welfare standards. In the main, welfare assessment schemes have consisted of checks that the resources available to the animal are sufficient and of good quality. Nevertheless, there is a consensus among researchers that while this approach is a good way to minimize the risk of poor welfare, the actual assessment of animal welfare must depend on animal-based measures [309]. Unfortunately, as already stated earlier in this section, there are as yet no feasible animal-based measures indicative of good welfare. Instead there are measures of poor welfare, such as injury, body condition, fear *etc.*, and it does not necessarily follow that in the absence of these indicators an animal's welfare is good. It merely means that we have no avoidance that welfare is poor.

“Qualitative” assessment methods have been proposed as a way to characterize global expressive affects in animals using a free choice profiling approach [44,310]. Among the terms chosen by the observers are those usually associated with positive states, e.g. “relaxed”, “friendly”, “affectionate”, “playful”, and “social”. There is difficulty though in validating these potential welfare indicators since new measures are usually validated against existing measures. On the other hand, we know that play is a likely candidate for being associated with a positive affective state and, furthermore, play behavior is probably the indicator of positive emotions that is most easily “readable” by non-professional observers (Section 3.4.1 “play behavior”). Another approach to find animal-based indicators of positive affects is to watch for the occurrence of affiliative behaviors that an animal will only perform when it is feeling

safe, such as allogrooming (Section 3.4.1 “affiliative behavior”). Such an approach may be related to the identification of the terms “relaxed” or “affectionate” used by the observers in the Wemelsfelder and collaborators [44] study. Finally, further studies on vocalizations in farm animals could lead to the identification of reliable vocal markers of positive states in these domestic species (Section 3.4.1 “vocalizations”). These markers would represent easy and convenient tools to assess positive experiences in farm animals. Although only valid measures should be included in monitoring systems, it may be that these are the most valid measures currently available to us if we want to include animal-based measures of positive affective states under commercial conditions.

4. Conclusion

Over the past few years the growing interest in positive emotions in neuroscience and psychology has led to the development of new areas of investigation, both theoretical and experimental. Successful expression of positive emotions typically requires a temporal sequence: a rewarding environment, eliciting a cognitive appraisal in the central nervous system and followed by physiological and behavioral reactions. Repeated or steady positive emotional experiences commonly lead to, and are often referred to, as a global state of “happiness”. The concept of happiness has always been considered one of the greatest philosophical quandaries and this has often detracted from scientific investigations. However, such a concept would be very valuable for the study of animal welfare since it could represent the affective background reflecting maximum well-being. Whereas pleasure is generally assessed in the context of sensory stimulation, such as the hedonic impact of taste, happiness refers to a longer and less intense internal state of feeling, which we argue is closer to the concept of “well-being” or “quality of life”. Although the concept of happiness has been studied very little, there are some theoretical attempts in the evolutionary approach that integrates this concept [311]. Some recent work suggests that happiness could be defined as consisting of both positive emotions and positive activities [4,312]. Animal studies have accumulated a large amount of valuable data regarding sensory pleasure or evaluating the rewarding properties of many agents, but there is a lack of data concerning more persistent affective states in animals. Hence, we must rely on theoretical and human studies to provide stimulating clues to the question of happiness in animals and the developing study of positive emotions must be considered as a first step in addressing the question of stable and less expressive affective states (*i.e.* mood) in animals. Is there such a state as happiness in animals? If so, how can it be reliably assessed? Under what conditions is it maintained? What are its relationships with cognitive abilities?

Supported by the recent interest of neuroscience and psychology, further research into the field of positive emotions and more persistent positive affective states in animals represents a new avenue for increasing our understanding of animal welfare processes. Such development could provide new insights in establishing the bases of real positive well-being in animals.

Research in positive affective states in animals is clearly an ambitious task, but there are promising returns. Promoting positive experiences can be a way to improve health in animals and more generally to give them a better quality of life. Likewise, including criteria of positive affective states in farm or laboratory monitoring schemes can improve welfare assessment beyond the traditional focus on mere absence of disease and distress.

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