

Physiological and behavioural characteristics and needs of pigs Sus scrofa domesticus

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This dossier is a compilation of materials drawn from current scientific and technical works on the physiological and behavioural characteristics and needs, cognitive abilities, and emotions of pigs. The information it contains allows readers to establish an initial understanding of this topic, but it makes no claims to be comprehensive, as not all the scientific literature in this field has been investigated.

The contents of the dossier are all taken from refereed scientific publications and references are provided. Data from French-language publications cited in the text have been translated into English. To see the originals, please refer to the relevant publications in French. Where a text is summarised, no quotation marks are used but the text is referenced. Where appropriate, to aid understanding, text [in square brackets] has been added by the FRCAW to quotations to provide context.

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Cover illustrations. Front cover: Free-range pig farm. Post-weaning ark with straw bedding. Copyright © Christophe MAITRE INRAE. Back cover (clockwise from top left): Pitman-Moore minipig nestled against its mother. Copyright © Henri FLAGEUL INRAE. Fattening pig rooting for food. Copyright © Michel MEURET INRAE. Pigs with full tails. Copyright © Friedrich-Loeffler-Institute. Yucatan minipig. Copyright © Henri FLAGEUL INRAE.



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# 1. Pigs: their characteristics and needs

## 1.1. Domestication of pigs

We know from molecular genetic evidence that the *Sus Scrofa* species first appeared in South-East Asia between 5.3 and 3.5 million years ago [1]. The domestication of wild pigs by humans began in many independent locations in Eurasia around 9000 years ago. Our modern European species are descended from the wild pig populations of central Europe and were crossed with Asian pigs from the eighteenth century onwards. These pig populations evolved initially through natural selection (without human intervention) and then through genetic selection until the contemporary domestic pigs and wild boar occurred alongside this evolution, particularly in Europe [1]. Contemporary domestic pigs vary greatly in their size, morphology and behaviour [2, 3].

Domestication has influenced the behaviour of pigs, making them less alert to predators and more receptive to human contact. Genetic selection has accelerated since the 1970s, driven by the search for improvements in reproductive capacity, growth rates, feed efficiency and physical conformation, to the detriment of behavioural activities [3-5]. Currently, the vitality/viability of piglets at birth and maternal behaviour have also become traits of interest [4]. Scientific studies have shown that certain social characteristics, such as aggressiveness, have a genetic component, opening up pathways for further future selection [6].

Changes in farming practices and living environments that have been introduced only very recently in the evolutionary history of pigs can lead to welfare problems where they fail to match a pig's environment to its behavioural needs. The study of the free/unconstrained behaviour of domestic pigs in natural or semi-natural environments can provide valuable insights into the range and roles of pig behaviours [3,7]. Care must, however, be taken to factor in the considerable variation between breeds and the impacts of human selection on the natural behaviours of current breeds.

Where there are differences between behaviours in the wild (see **Erreur ! Source du renvoi i ntrouvable.**) and in a farmed environment, this may indicate features of a pig's behaviour that are either being prevented, or for which insufficient stimulation is provided. Domestic pigs can adapt to living conditions that are similar to those in the wild. This suggests that, despite intensive genetic selection, domestic pigs have retained their behavioural capacity to adapt to life in the wild [3].

#### Box 1 Definitions of 'natural', 'semi-natural' and '(semi-)free' behaviours and environments

'Natural' behaviour describes the behaviour of wild boar, domestic pigs or feral pigs (i.e., domestic pigs returned to the wild), as observed in studies conducted 'in the wild'. [8]. Authors variously describe their studies as having been conducted either:

- 'in the wild', where wild boar or feral pigs have lived in the wild for many generations ([8-11], or
- 'in a semi-natural environment' [12], where pigs are either 'semi-free ranging' [13] or 'freeranging' [14]. Here, domestic pigs are kept in enclosed natural environments and have access to shelters (arks with straw) for all or part of the year.

In the remainder of this document, the phrase 'in semi-freedom' has been selected to describe the latter situation.



## 1.2. Reproduction [2, 15]

Reproduction is seasonal and linked to the number of daylight hours.

*Oestrus* is the phase of the reproductive cycle during which the female is fertile and seeks to mate. In the wild and in semi-freedom, oestrus in sows is synchronised, they conceive in autumn and on occasion, when food is plentiful, again in late spring, giving birth (farrowing) around February-March and August-September. On conventional modern farms, pigs reproduce all year round ([7], p. 35).

Oestrus lasts approximately 72 hours ([7], p.35). The presence of an adult male stimulates ovulation in sows via visual, auditory, tactile and olfactory cues, including pheromones, the signal-carrying chemical substances secreted by other individuals [16]. The signs of oestrus in all environments are: red and swollen vulva, mucus discharge, loss of appetite, a particular form of grunting, nervousness, increased activity and interest in social contacts, increased interest in the boar as well as 'standing heat' (catatonia) and characteristic erect positioning of the ears ('popping') when pressure is applied to the back.

If the sow is not impregnated, she returns to oestrus after 3 weeks. Following gestation and lactation, the sow returns to oestrus around 8 days after weaning.

For breeding, fertilisation is most often carried out by artificial insemination, but the presence of a boar is generally necessary so that the farmer can detect sows in oestrus on the basis of their behavioural response to the passage of the boar outside the pen [17]. If fertilisation fails on several consecutive occasions, the sows are culled.

*Puberty* occurs at varying ages depending on the breed, but generally occurs between 160 days (5 months 10 days) and 265 days (8 months 15 days) in females, with an average of 190 days (6 months 10 days) for European breeds ([7], p.34). Puberty is reached when the behavioural signs of oestrus synchronise with ovulation ([7], p.34). Male puberty occurs at between 5 and 7 months. This is the age at which, in the wild, young males leave the group in which they have grown up to live on their own or in pairs. They will re-join the females only for the breeding season ([7], p.38).

In males, puberty is accompanied by increased production of steroid hormones, particularly the two steroids, androsterone and scatol, and this gives the meat an odour considered unpleasant by some consumers [18]. It is to avoid these sexual odours that male piglets are frequently castrated during their first week of life<sup>1</sup>.

*Gestation (pregnancy)* lasts from 113 to 117 days in sows (commonly expressed simply as 3 months, 3 weeks and 3 days) ([19]; [7], p.35). Sows give birth to young that are already autonomous in sensory and motor terms (unlike rabbits, rodents or primates).

*Development* (i.e., from birth to maturity, having reproduced at least once) takes around 1 year.

*Sow longevity*: In 2015 in France, conventionally-farmed sows produced an average of 4.8 litters [20]. Even though some sows can produce 20 litters, early culling is still common, with a quarter of sows being removed from the herd before their third farrowing [20]. These figures can be explained by the productivity of the sows (prolificacy levels), losses caused by breeding accidents, and management choices made by farmers [20]. The technical recommendation for sow herd demographics is to maintain an age pyramid, with 20% of sows in their first pregnancy [21]. This calls for a fairly rapid renewal of sow generations. Data on the maximum lifespan of a sow are rare, but this probably exceeds 15 years [2].

<sup>&</sup>lt;sup>1</sup> In France, the live castration of piglets has been banned since 1 January 2022. Only surgical castration with anaesthesia and analgesia and without tearing the tissue is permitted. The alternatives for farmers are to raise whole males or males vaccinated against boar taint, provided that the abattoir they supply accepts this type of animal.



*The prolificacy level* is the average number of piglets born (alive or dead) per litter. Under natural conditions, feral pigs are estimated to produce litters of 3 to 6 piglets on average [3], although older studies on domestic pigs in semi-freedom have suggested higher prolificacy rates than this (**Erreur ! Source du renvoi introuvable.**). In conventional farming, the p rolificacy level is considerably higher. In France in 2021, the average number of piglets born alive per litter was 15.1 [22]. Prolificacy depends on the breed and has significantly increased with genetic selection: in 2020, on livestock selection farms, an average of 16.7 piglets were born alive per litter to Large White sows, while the average for Piétrain sows was 10.5 [23]. This increase in litter size has been accompanied by an increase in the complexity of the rearing environment for suckling sows in an attempt to limit piglet mortality by crushing. This increased environmental complexity causes restricted movement, general discomfort, deterioration in body condition and injuries [24].

# Table 1 Prolificacy figures for semi-free-range sows based on studies published between 1985 and 1992

Publication	Breed	Number of litters	Piglet stage of development	Number of	piglets/litter
Fublication	Dieeu	studied	at counting	Average	[Minium- Maximum]
[25]	Swedish Landrace (SLR)	9	Newly born (live births)	9.5	[6-11]
[26]	SLR	5	Newly born (live births) At weaning (16 weeks)	10.6 7.6	[7-12] [7-9]
[27]	SLR	10	Up to 9 weeks old	7.1	ND
[28]	Large White	7	Up to 10 days old	9	[2-13]

## 1.3. Sow lactation and pre- and post-natal piglet development

#### Neonatal survival

Because of the large number of piglets born per litter, there is a risk of perinatal mortality and morbidity and of competition for teats. The average pre-weaning mortality rate for live-born piglets on French farms was 14.6% in 2019 [29]. More than two-thirds of the mortalities recorded during the lactation period occur in the first three days after birth. This mortality rate is mainly due to piglet hypothermia caused by insufficient colostrum consumption. Hypothermia induces lethargy, which in turn leads to the death of the piglet through malnutrition or crushing [30]. Livestock farmers often set up a nesting area within the pen and equip it to keep the piglets warm with, for example, mats, partitions and heating devices such as lamps.

#### Pre- and post-natal development (from Pond et al. [2] and Nielsen et al. [7]):

The fetal environment affects post-natal development. The gestating sow's food intake influences the weight and viability of newborns. There is great variability in the weight of neonates born in semi-freedom (from 400 g to 2 kg) and on conventional livestock farms (ranging from 600 g to 2.4 kg in Quiniou et al. [31] for example). Average newborn weight decreases and in-litter weight variation increases with the number of pups per litter, and the chances of piglet survival in the days following birth correlate with birth weight [24].

Piglets are born with 4 incisors and 4 canines. These teeth are very sharp and can cause injuries to the mother's teats and to other piglets [32, 33]. It is possible for livestock farmers to remove the canines and upper and lower lateral incisors, but this is subject to regulatory restrictions because of its detrimental effect on the pig welfare [34, 35]. Complete milk dentition



comprises 28 teeth and permanent dentition 44 teeth. The age at which the different teeth appear is shown in Table 2.

In adult males, the canines grow outside the mouth.

Tooth	Milk teeth	Permanent teeth	
Incisor 1	2-4 weeks	12 months	
Incisor 2	2-3 months	16-20 months	
Incisor 3	before birth	8-10 months	
Canine	before birth	9-10 months	
Premolar 1	5 months	12-15 months	
Premolar 2	5-7 months	12-15 months	
Premolar 3 and 4			
upper	4-8 days	12-15 months	
lower	2-4 weeks	12-15 months	
Molar 1	-	4-6 months	
Molar 2	-	8-12 months	
Molar 3	-	18-20 months	

## Table 2 Age of appearance of teeth in pigs (cited in [36])

#### Lactation

Newborn piglets typically find their mother's teats within 30 minutes of farrowing and ingest colostrum within a few hours ([7], p. 36). Within 16 hours of birth, they develop a cyclical behavioural pattern, suckling every 40 to 60 minutes and resting in between. In the first few days of life, piglets will develop a fixed order of access to the mother's teats, with a given piglet generally always suckling at the same teat or pair of teats. Suckling consists of several phases: during the initial massage phase of about 40 to 60 seconds, piglets massage the teats with head movements, triggering the milk ejection phase, which lasts about 20 seconds and is followed by a final massage phase of highly variable duration, ranging from 30 seconds to 10 minutes [3].

A sow's milk production increases with litter size and depends on various factors relating to the sow (litter number, lactation stage), the piglets (birth weight, interval between feedings), and the ambient environment (day length, noise and temperature levels). The hyperprolific sows now increasingly found on farms produce more than 10-12 kg of milk per day [37], allowing piglet weight gain for the litter of between 1 and 4 kg per day, depending on litter size [38], which may represent as much as 16 kg of milk in a day [37, 39]. The composition of the milk changes during lactation, but is very little influenced by nutritional factors, apart from the lipid fraction, which is influenced by the level and nature of lipids in the feed. A nutritional deficiency in energy or amino acids does not affect milk production as long as the sow is able to compensate for the deficit by drawing on her bodily reserves [37].

#### Need for colostrum

A piglet's colostrum intake during the first few hours of life is very important. It provides the energy required to maintain body temperature and to suckle. It also provides the piglet with the factors from the mother's immune system needed to protect it during its first weeks of life. This is known as 'passive' immunity [30].

As in all mammals, the immune system in piglets is not fully developed at birth, providing poor protection against the microorganisms in their environment [40] and leaving newborn piglets open to infection by various pathogenic agents (digestive, respiratory or systemic) to which they are not yet able to respond appropriately. Unlike primates and rodents, for example, pigs cannot transmit immunoglobulins from maternal to fetal blood via the placenta. This means



that a piglet's passive immune protection during its first weeks of life is strongly dependent on how much colostrum it ingests in the first 10 hours after birth, since, as stated above, this colostrum contains important immune factors (maternal antibodies and immune cells, antimicrobial agents), some of which will pass into the piglet's blood [41]. Once this period immediately after the onset of farrowing has passed, the colostrum is replaced by milk and the piglet's intestinal wall loses its permeability, at which point the antibodies and antimicrobial compounds contained in the milk protect only the piglet's digestive system (through local action).

#### Weaning

In semi-freedom, weaning is gradual [42]. Weaning is considered to be complete when the udders are clearly involuted and the piglets are no longer seen suckling. Different studies have reported the completion of weaning to be from 8 to nearly 20 weeks after farrowing. [28, 42]. In conventional farming in France, piglets are most commonly weaned at 3 or 4 weeks of age, in accordance with the regulations. These prohibit weaning before a piglet is 28 days old, except for health reasons, but allow weaning up to 7 days earlier if operational measures are taken to reduce 'as far as possible the risk of disease transmission to the piglets' [43]. The practice of weaning on conventional farms involves physical separation from the mother, the mixing of litters unfamiliar to each other, a change in physical environment (sometimes associated with transport to a different farm), and the abrupt withdrawal of maternal milk, requiring adaptive changes to the digestive system. Weaning is considered to be a particularly stressful event in a pig's life ([3], [7], p.37). A number of practices are available that help pigs adapt to weaning. These include the provision of solid feed in addition to maternal milk and early socialisation (allowing contact between piglets from different litters).

In organic farming, the minimum age for weaning is 40 days, as required by the European Union regulations [44, 45]. This encourages the introduction of solid feed to the ration from 3-4 weeks of age [46], thereby stimulating the ability to digest this type of feed [47]. When reared outdoors, piglets start to consume solid feed earlier and in greater volumes than their counterparts reared under cover from three weeks of age [48].

A piglet's acquisition of behavioural, digestive and immunological maturity is gradual and the process is not yet complete at 28 days [49]. For example, with regard to behaviour, one study has shown that an increase in age at weaning from 19 to 28 days significantly reduces the prevalence of belly-nosing behaviour in piglets during the three weeks following weaning [50]. This behaviour is considered to be a sign of stress in the post-weaning period caused by the loss of contact with the mother [50]. Equally, a study of the digestive tract in piglets has observed this organ's morphological development and function to be less mature in piglets weaned at 14 days than in those weaned at 28 days [51].

While studies vary widely in their conclusions concerning the impact of age at weaning on piglet welfare, 21 days emerges as a pivotal age below which there is a significant impact on welfare ([7], p. 225). Few studies of the welfare consequences of weaning beyond 28 days have been conducted, but it would appear that, subject to good rearing conditions and practices, the benefits of weaning beyond 28 days are marginal ([7], p. 225).

## 1.4. Feeding and watering

Pigs are monogastric, omnivorous and opportunistic. As a result, they can be reared in a variety of environments and adapt their diet to available foodstuffs ([7], p.33).

In the wild, pigs have a varied diet consisting mainly of grasses, fruit, nuts, mushrooms, leaves, insects, sap and roots [52]. Plants form up 90% of their diet, with the remaining 10% comprising animal products such as worms, crustaceans, insects, small amphibians, reptiles and rodents [3]. Foraging essentially involves rooting and nosing in the soil, but pigs may also graze and browse above-ground vegetation.



In semi-freedom, this activity is carried out during the day and evening, but feral pigs may shift their foraging to night time in response to the pressures of hunting by humans [3]. Under semi-free range conditions, domestic pigs spend 6 to 8 hours foraging for food, even when fed a full ration of commercial feed ([7], p.33).

In livestock farming, pig feeding behaviour is essentially dictated by feed distribution schedules. Feed is largely formulated from plant-based raw materials (cereals, oils, molasses, soya or rapeseed cakes, pulses, milling by-products, etc.). Pigs are generally fed *ad libitum* or in a similar system, with the exception of pregnant sows, whose ration is restricted to prevent them from becoming too obese towards the end of gestation and to avoid problems during farrowing. This dietary restriction can lead to oral stereotypies [53] if the sow has no source of fibre (via the feed or straw bedding).

The amount of water ingested varies according to physiological stage and the individual concerned. For growing animals, water consumption is considered to represent on average 10% of live weight, i.e. 1 to 4 L/day during post-weaning and 4 to 12 L/day during fattening; the calculation for sows is 15 to 20 L/day during pregnancy and 20 to 35 L/day during lactation [54].

According to Ramonet et al. [55], water intake follows a nychthemeral (24-hour) rhythm closely linked to the pattern of feed consumption: 90% of water is ingested in the period from 10 minutes before to 10 minutes after a meal. A thermoneutral growing pig that is being fed dry feed and water *ad libitum* consumes between 2.1 and 2.7 L of water per kg of feed ingested, a proportion that doubles when the ambient temperature exceeds 30°C [55].

'Only permanent access to drinking water enables the animal to meet its physiological needs at all times. [...] If water intake is deferred, physiological needs are not met at certain times, but this has no impact on the pig's physiology, provided that the body's water content does not fall by more than around 1%. However, this decrease introduces a prolonged sensation of thirst, negatively affecting its well-being.' [55]

## 1.5. Space: requirements and uses

#### Use of space

In the wild, except during farrowing, pigs choose to lie in groups in particular areas that offer shelter where possible and allow good visibility of their surroundings [56]. A study carried out on captive wild boars in a zoo enclosure with different areas (including a wooded area, a mud pool, a pond, two shelters, areas of soft ground and areas of hard ground) showed that they used all the areas, associating particular uses with each [57].

Indoors, pigs prefer to rest and sleep in a dedicated area, in contact with a wall, and leave the central part of the pen free to move around [2]. If the weather is hot, they will choose to lie at a distance from each other, on fairly cool floors, for example in the shade or in a pen if they live outdoors, or on slatted floors or concrete if they live inside. If the weather is cold, they will choose to lie close together on warmer ground, for example in the sun or in a bed of straw or an alternative available substrate.

Pigs keep their living quarters as clean and dry as possible, adding or removing bedding regularly ([7], p.33). Given the opportunity, pigs defecate in well-defined places, often close to a wall or a corner, and always in the least comfortable part of their stall. In semi-freedom, they choose a site a short distance from their lying area but well separated from their feeding area [2]. Thus, if pigs are lying in their own excrement, this indicates a problem: either they are too hot and are wallowing in their excrement to cool down, or they lack the space to maintain a dedicated dunging area [58].

Pigs need sufficient and enriched space to correctly perform what are highly motivated behaviours, including exploration, socialisation, lying down, play behaviours and escape from aggressors ([7], p. 226).



#### Floor area

The posture of resting pigs depends largely on thermal conditions [59]. Pigs lie on their sides (lateral position) in warm conditions (27°C) and on their bellies (sternal position, or prone) in cold conditions (18°C). In a thermoneutral situation, 60% of pigs lie on their sides, in a lateral recumbent position [60]. In this position, they occupy more space than in the sternal position, which itself takes up more space than the standing position ([60] cited in [7], p.156). The surface area required for lateral recumbency in a 100 kg pig is calculated to be 0.76 m<sup>2</sup> per animal [60]. Other factors contribute to a pig's lying surface area requirements, such as group size and floor type, and these interact with the thermal conditions.

To protect the pigs' welfare, the total surface area must meet resting requirements, but must also take into account social distance, giving pigs the opportunity to isolate themselves or interact, and the use of space for other activities such as accessing resources (feed, water, cool area in summer, etc.) and disposal of excreta [61, 62]. Insufficient space can thus affect animal behaviours.

For pregnant sows, *Figure 1* demonstrates the links between the surface area available to the sow and the expression of various behaviours [7].



Figure 1 Postures and behavioural activities of sows as a function of the surface area of their accommodation

This figure was created using information from Tables 46 (p 169) and 66 (p. 268-269) of EFSA's Opinion on the Welfare of Pigs on Farm (2022) [7].



# 2. Sensory perception

Studies on hearing, smell, taste and vision in pigs are scarce and some are based on just a handful of individuals. The latter's results should therefore be treated with caution. It can nevertheless be stated that the most important senses for pigs are hearing and smell. Although domestic pigs are active during the day, their ancestors were nocturnal forest animals, so it is natural for them to communicate using acoustic and olfactory stimuli [2]. Smell and taste are necessary for foraging and are critical for social contact [63]. For example, a piglet recognises its mother by the scent of her urine, faeces and udders, and will use its sense of hearing to recognise her vocalisations should they become separated [64].

Pigs use their olfactory and visual memory, as well as their spatial memory, in their search for food and as they move around [65]. They use hearing, touch (particularly via the snout) and sight to recognise humans, who themselves use sight and hearing to interact with animals [33].

## 2.1. Hearing

This sense is highly developed in pigs, who can perceive frequencies ranging from 42 to 40,500 Hz (compared with 31 to 17,600 Hz in humans). Pigs are better equipped than humans to hear high-pitched sounds and can perceive ultrasound. As a result, they can be vulnerable to sounds that, while painful to them, are imperceptible to humans ([63] and *Figure 2*).



## Perceptible frequency range [Hertz – Hz]

Figure 2 Comparison of sound perception in different species. Reproduced from [66] Figure 2

Pigs are highly sensitive to frequencies below 1500 Hz, which lie within the human vocal spectrum [67]. They also appear sensitive to the harmonic structure of music. A recent experiment has assessed the valence of the emotional states of piglets exposed to music with varying harmonic structures, establishing positive and negative emotional indices. The value of these indices was quantitatively increased by listening to all types of music tested and varied qualitatively according to the harmonic structure of the music [68].

Hearing is also used in communication [63]. Pigs have a wide vocal repertoire with different acoustic structures. These vary according to the circumstances in which an animal finds itself [69] and its emotional state [70]. For example, acoustic signals play an important role in regulating the suckling behaviour of piglets [2]. Sows distinguish the vocalisations of their piglets from those of other litters [71]. In semi-freedom, as in conventional rearing, piglets' distress cries immediately attract the mother [15].

Pigs undergoing negative experiences generally emit high-pitched vocalisations (i.e. squeals), at frequencies of between 3000 and 5000 Hz [2]. They may also express their negative emotions using long grunts [70].



## 2.2. Smell and pheromone perception

In pigs, a total of 1113 genes relate to olfaction, explaining why they have one of the largest repertoires of functional olfactory receptors among mammals, being at least equivalent to that of dogs ([72, 73], see *Figure 3* for comparative numbers in other species).

Like all mammals, pigs have a vomeronasal organ in their nasal cavity that specialises in the detection of pheromones.



Figure 3 Comparison of the number of genes involved in olfaction in different mammals. Reproduced from [66] Figure 3.

The olfactory structures in a pig's brain are organised in a similar way to those of other mammals but they are comparatively far more highly developed [74]. This suggests very acute olfactory capacities, although there is a lack of functional studies on the pig olfactory system. Smell is an important sense in this species, being involved in social recognition, the determination of physiological status, and social hierarchy [33, 66].

Olfactory signals contribute to emotional contagion (transmission of stress [75, 76] or appeasement). Studies have shown that the use of synthetic appeasing pheromones reduced social stress and agonistic interactions in pigs [77, 78]. During agonistic interactions between prepubescent pigs, pheromones are released at the end of the fight to signal submission [79]. In a study on a conventional farm, 83% of pigs displayed inflammation of the vomeronasal organ, which could be linked to exposure to contaminants in the air on the farm [80] (it is suggested elsewhere that this inflammation is probably associated with sensitivity loss, see [81]). The study also reported the involvement of pheromones in regulating agonistic interactions in pigs [80].

## 2.3. Taste

Pigs have over 15,000 taste buds, twice as many as humans, suggesting an excellent sense of taste in this species [82]. They perceive the saltiness of sodium chloride<sup>2</sup>, bitterness and acidity [83]. They have a strong liking for umami, associated with glutamic acid, and can detect the tastes of other amino acids [82]. They are strongly attracted to the sweet taste of sucrose, lactose and glucose, but do not perceive that of aspartame [82,84].

#### 2.4. Vision

The anatomical structure of a pig's eye (absence of cones that receive waves associated with red [85]) suggests that this animal has dichromatic vision in blues and greys [33]. Blue is the only primary colour distinguished by pigs [86] and their preferred colour [87]. Pigs have a wide

<sup>&</sup>lt;sup>2</sup> but note very well, which distinguishes it from other mammals



field of vision of 310° (see Figure 1 of [66]), including 50° binocular vision [88]. This enables them to monitor their environment continuously. However, a pig's visual acuity is low, with little discrimination of detail except for moving objects, and it finds it difficult to estimate distances [63]. Pigs can only see what is in front of them well, and are myopic at distances greater than 1.5 m.

A pig's visual system allows it to adapt to a wide range of light intensities [89]. Light intensity preferences appear to vary with age. For example, several studies have shown that young pigs housed indoors and aged between 4 and 7 weeks seem to prefer areas of low light intensity (2.4 lux) for resting and sleeping, while choosing to defecate and being more active in areas of higher light intensity (40 to 400 lux) [90, 91]. By contrast, a study conducted on 1-week-old piglets showed that they disliked being in the dark (5 lux) and tended to seek out areas of intense artificial light (2100 lux) [92]. Last, a study conducted in an abattoir has shown that pigs weighing 90 to 113 kg tended to move from shade to light under artificial lighting, unless they had been reared in a dark atmosphere [88].

Studies do not agree on the effects of the experimental manipulation of photoperiod (daylight length) on physiological parameters, feed intake and weight gain in pigs at different stages of production, leading some authors to conclude that pigs are less sensitive than other species to changes in photoperiod [61].

## 2.5. Touch

Touch is an important sense in pigs. Tactile stimulation is detected by afferent nerve endings in the skin and subcutaneous tissues [2].

The snout is particularly well-provided with mechanoreceptors, transmitting information from tactile signals to the somatosensory cortex, most of which is dedicated to receiving information from the snout [2]. Pigs use their snouts to explore their environment by rooting, sniffing, biting, chewing [63] and nosing. They also use their snouts to make contact with other pigs, particularly on the latter's heads or snouts [93].

#### 2.6. Pain perception in pigs

Pigs have sufficient cognitive and emotional capacity to experience negative affective states such as pain [15]. One of the major criteria used to determine the existence of pain in animals is whether analgesics or anaesthetic techniques can counteract physiological and behavioural responses to a particular condition involving tissue damage. Many examples of this are available for pigs. For example, in one study, behavioural changes after castration were reduced in piglets that had received a pre-operative injection of an anti-inflammatory drug compared with those that had not [94].

There are many sources of pain in pigs, relating to either husbandry practices, injury or disease [95]. For example, in 2013, it was estimated that 8.8% to 16.9% of sows reared in the European Union suffered from lameness and that the associated pain affected their quality of life [96].

Despite this, the behavioural signs of pain in pigs are not always obvious, making detection difficult at times. To assess pain correctly, the combined use of several indicators is therefore necessary. Many indicators of pain are available (see [15], pp. 335-345). These include spontaneous behavioural responses (prostration, rubbing of the painful area, avoidance of contact with the painful area), induced behavioural responses (withdrawal in response to manipulation of the painful area), vocalisations, abnormalities observed through clinical examination, and facial expressions. A grimace scale has been proposed for piglets [97] and has been used successfully to assess the pain associated with piglet castration [97, 98]. Physiological and anatomopathological measurements can also be used to quantify the level of pain (see Table 3).



Pain assessment scales are available for specific situations. A composite scale has recently been proposed and validated for the assessment of acute pain following castration of young pigs under anaesthesia [99]. It is based solely on the observation of behaviours, which makes it suitable for routine use.

Chronic pain can be viewed as a form of chronic stress, measurable indirectly by increases in heart rate, blood pressure, body temperature, respiratory activity or pupil dilation [15]. The severing of nerve fibres can lead to lasting changes in the pain detection and perception system, both locally and in the brain [103]. It may lead to loss of sensitivity or, conversely, to hyperalgesia or chronic pain. For example, it has been shown that caudectomy in piglets over two months of age, which resembles a severe tail bite, causes hypersensitivity of the area around the tail for up to 4 months post-surgery [104].

Table 3 Examples of physiological and behavioural pain criteria for pigs. Translated from [100], itself adapted from [101 and 102]

Physiological criteria	Behavioural criteria	
Hormone concentrations (blood, urine or saliva)	Vocalisations	
Corticotropic axis: CRH, ACTH, glucocorticoids	Number and duration of cries	
Sympathetic system: adrenalin, noradrenalin	Intensity of cries	
Blood metabolites	Spectral component of cries	
Glucose, lactate		
Free fatty acids	Postures and movements	
Neuro-vegetative responses	Pain-avoiding posture	
Heart rate	Tonic immobility	
Respiratory rhythm	Locomotion	
Blood pressure	Escape	
Internal, skin or eye temperature		
Pupil dilation	General behaviour	
Sweating	Loss of appetite	
Inflammatory response (blood)	Agitation	
Haptoglobin, fibrinogen etc.	Prostration	
Brain activity	Isolation	
Electroencephalogram (EEG)	Aggression	

# 3. Behaviour and behavioural needs

## 3.1. Behavioural repertoire and activity time budget for pigs

In their natural habitat, wild boar alternate between long periods of sleep and long periods of activity. They have two activity peaks, one in the morning and the other in the late afternoon and evening [3]. The distribution of active periods depends in part on hunting pressures, with heavily hunted populations having more nocturnal rhythms, but also on weather conditions.

The activity time distribution of groups of pigs comprising young and adult pigs in semi-freedom has been studied and is shown in Figure *4*. The authors calculated that these pigs in semi-freedom spent 75% of their active time during the day in activities related to exploration, foraging and feeding.

Younger pigs differed from the adults in that they spent less time foraging (7% of the time compared with 27% for adults) and moved around more (22% compared with 11%) [105].



In indoor rearing, the diurnal activity pattern of domestic pigs depends mainly on feeding times ([7], p. 33). A study of growing and finishing domestic pigs (young castrated males and gilts) showed that they spent 82.5% of their time lying down, 7.8% of their time standing up and 9.7% of their time feeding [107]. A different study has examined the behavioural repertoire of growing and finishing pigs [(Landrace x Yorshire) x Hampshire] housed in groups of 4, where different quantities of straw were provided as an enrichment material [108]. Their behaviours are shown in *Figure 5.* 



Figure 4 Distribution of daytime activity time for groups of pigs (young and adult, male and female) in semi-free range (expressed as percentages of total time) (after Stolba et al. [105])

Agonistic behaviour = an act of threat, aggression, combat or submission [106]. Marking = an animal senses an element in its environment and rubs its head against it. Observations were carried out by *scan sampling* (in which the entire group was scanned and the behaviour of each individual was recorded regularly) and by *focal sampling* (in which a single individual was observed and all behaviours (included in a more complete ethogram) observed over a given period were recorded).



Figure 5 Breakdown of activity times for pigs [(Landrace x Yorkshire) x Hampshire] housed in groups of 4 (expressed as a percentage of total time). Figure created from data provided in [108] Table 2.



Redirected behaviour: mounting, nibbling/biting a conspecific; biting a conspecific's tail or ear. Observations were made using *focal sampling* from video recordings over a period of 1 hour in the morning (between 9 and 10 am) and 1 hour in the afternoon (between 3 and 4 pm).

A recent study on Large White x Piétrain piglets in the suckling period, housed in maternity pens, showed that neutral or positive social interactions were very brief but very frequent, whereas aggressive behaviour accounted for 8 to 12% of all social interactions [109].

## 3.2. Experiencing and exploring the environment

In pigs, exploratory behaviour is highly developed [110 111], constitutes a need, and is stimulated by novelty [111]. A pig explores its environment by rummaging, rooting, sniffing, digging, and biting and chewing on food or non-food products [111]. Its motives to explore are to find food and a comfortable place to lie down, and to obtain information about the environment either out of curiosity or to relieve boredom [111]. In the wild, pigs find food sporadically in their environment and spend much of their time searching and exploring their surroundings [111]. In a confined or impoverished environment, if a pig cannot fulfil this need to explore, it then redirects it towards its fellows or its environment ([112-116] cited in [7]). The absence of a manipulable substrate is one of the chief contributing causes to undesirable oral behaviours such as tail biting or chewing on the ears of conspecifics [3, 117].

## 3.3. Feeding behaviours

#### Foraging and food intake

On farms, pigs generally receive their feed freely in the form of a ready-prepared mix, delivered either freely, on demand or as meals. It has been shown that the frequency and duration of feed intake by pigs fed *ad libitum* in the post-weaning and fattening stages depends on access to the feeder. Thus, when provided with greater floor space per animal, pigs come to feed more often and divide up their meals more. With less floor space per animal, pigs under an *ad libitum* feed regime choose fewer but larger meals [118].

Foraging in itself is rewarding for pigs, but becomes even more so when it is associated with food intake [119]. In a conditioned place preference test, it was shown that Large White x Landrace pigs in the post-weaning period preferred to search for feed hidden in straw rather than having the feed available in a separate trough [120]. Even when they were fed ad libitum, they preferred to root for feed concealed in a substrate rather than manipulate substrate containing no feed [120, 121]. One study reported that diversification of a piglet's diet before weaning strongly stimulated food exploration and food consumption from an early age and improved pre-weaning growth. It concluded that dietary diversity encourages suckling piglets to eat, thereby improving their performance and, potentially, their welfare before weaning [119]. In semi-freedom, family groups forage together for food, which is distributed unevenly in terms of location and time of consumption [122]. In a study carried out on Swedish Landrace piglets under a semi-free range regime, the piglets began to explore their environment from the first days after birth, rooting, biting, chewing and sniffing objects throughout their first month as they became familiar with their environment. They began to browse during the fourth week and gradually increased their browsing time to reach 42% of their activity time at 8 weeks of age [123].

#### Watering

In pigs, three quarters of watering takes place at the same time as feed intake, and watering follows a stable pattern within a group. This pattern can nevertheless be modified according to the ambient temperature, the proper functioning of watering points, competition for watering points where the latter's numbers are insufficient, and the state of health of the animals [124].



Permanent access to water helps prevent the emergence of behavioural deviations (frustration, competition) or health problems (physical depletion, dehydration, etc.) [55].

### 3.4. Thermoregulation

Pigs have limited hair growth and are fairly sensitive to cold. Their high surface-to-mass ratio and thin subcutaneous fat layer make piglets particularly susceptible to hypothermia. Meanwhile, older pigs find it particularly hard to adapt to heat. Because they lack sweat glands, they cannot evacuate heat by sweating. Thermoregulation therefore mainly involves behavioural adaptations. They lower their temperature by panting and adopting other thermoregulatory behaviours such as voluntarily reducing their food intake and seeking cooler places, such as a wallow [2,125].

In semi-freedom, in order to regulate their temperature in hot weather, pigs seek shade, adapt their periods of activity to the coolest times of the day and roll on the ground or in water to promote heat loss by evaporation; in cold weather, they huddle together, build nests and increase their activity during the day [3].

In hot weather, sprinklers or misters can be used, depending on the type of floor. In the event of high temperatures, heat-stressed pigs may show behavioural and physiological changes, such as a rise in body temperature and higher respiratory and heart rates [126], affecting welfare and growth.

The thermal comfort zone for pigs according to age is shown in Figure 6. The thermal environment is generated by the interaction of air temperature, humidity and air circulation. In buildings, these factors are in turn influenced by a wide variety of other factors such as the size and number of animals, the degree of insulation in the building, the physical condition of the pigs, the presence or absence of bedding and other physical characteristics of both the animals and their housing [83].



Figure 6 Indoor thermal comfort zone plotted by age. Reproduced from [127].



## 3.5. Behaviour of sows in the peripartum period and of piglets after farrowing

In semi-freedom, a female will isolate herself from the group to give birth and may travel kilometres to find a partially enclosed area where she can build a nest. Nest building involves a set of highly active behaviours expressed by all sows in the 12 to 24 hours before farrowing ([128] cited in [7], p.77; [129]). It is characterised by rooting with the snout (movements of the snout on the ground or manipulation of substrate), digging with the legs, chewing, turning and carrying of substrates ([130] cited in [7] p. 58). This nest-building behaviour can be observed in all environments [129]. However, in the absence of suitable substrates, the sow continues to build her nest once farrowing has begun.

Just before giving birth, the sow lies on her side and exposes her teats. After giving birth, she does not lick her new-borns but observes them before touching their snouts with her own, placing them in the nest and lying back down on her side [15]. These behaviours cannot be fully expressed when the sow is restrained, which is the case on most conventional farms.

Under natural or semi-free range conditions, during the first 2 weeks of life, sows limit their movements around the nest and piglets remain close to each other and to their mother [3]. Mother and young leave the nest after 10 days and join the group where the piglets are socialised; they are grouped together by litter to suckle, while the suckling periods are initiated simultaneously by the different sows [42]. Play behaviour in piglets (simulated fighting, racing) peaks around the fourth week after birth.

## 3.6. Interactions with conspecifics

The pig is a highly gregarious species, living in very stable social groups, with hierarchies that are mostly linear in small groups and more complex in large groups [7,131]. Hierarchies are based on dominance/subordination relationships that are linked in particular to the age and size of the animals [7, 132]. On the vast majority of conventional farms, farmers group their pigs into homogeneous age groups that do not fit with their natural social structure, creating lack of stability. There are, however, some extensive free-range farms and farms with alternative buildings where sows are kept in small groups with their litters until weaning and groupings are maintained until slaughter, allowing social structures to develop that more closely resemble that of pigs in their natural state.

In semi-freedom [2], sows live with their piglets in a small group of related females. Adult males are generally solitary but may also form relatively unstable groups ([7], p.38). Adult males join groups of females in the autumn for the breeding season.

#### Establishment of social structure

The first social structure in a pig's life is the order of suckling, established during early feeding. Each piglet will be assigned to a specific teat, following a few fights. The front teats are the most sought-after, probably because they produce more milk. The allocation of teats among piglets gradually stabilises during the first four days of life [133,134]. This teat order is the first social hierarchy for piglets and is established within the sibling group [135].

After weaning, the mixing of animals, the introduction of unfamiliar pigs and, to a lesser extent, changes in the structure of the group (removal of animals) will lead to fights between some of the animals, generally one-on-one, during the first day. It is possible to identify the dominant animal in the group within an hour. The dominant animals behave most aggressively and intimidatingly towards those in the rank below them. The basic structure of the hierarchy is formed by all the strong and stable dominance relationships that appear to develop between animals immediately adjacent to each other in the social hierarchy [136].

Aggression during grouping is a major animal welfare problem. Such aggressive interactions lead to skin lesions and stress [137]. When groups are not stable, the need to continually reestablish the social structure results in higher levels of aggression than in stable groups.



Previous familiarity between the animals may shorten the time it takes to reorganise the social structure and relies on the animals' social memory [138].

#### Positive social behaviour

In pigs, positive social behaviours include social sniffing and snout-to-snout contact, which are thought to contribute to the recognition of individuals, the maintenance of social relationships and group cohesion [109].

Social sniffing in pigs is not related to aggressive behaviour or dominance relationships [93]. Pigs sniff each other for social recognition, to show affiliative behaviour, to obtain olfactory signals or to satisfy an intrinsic need to sniff [137].

#### Play

Pigs are playful animals. It is possible to distinguish three categories of play: locomotor play (jumping, sprinting, shaking the head, pivoting), play involving interaction with objects (carrying, moving, shaking objects) and social play (between mother and offspring, between littermates and between different litters) [139].

Young domestic pigs are particularly playful, and play is important to their social and cognitive development. It helps them to acquire the social skills necessary to resolve conflict and recognise individuals, and to create strong social bonds that endure after regrouping, thus contributing to social cohesion [109]. The expression of playful behaviour is essential for the healthy development of young animals. It mitigates the emergence of detrimental behaviour, and can serve as a welfare indicator [139].

Piglet play behaviours peak between 2 and 6 weeks of age [140]. They decrease sharply but transiently just after weaning, returning to pre-weaning level 5 days after weaning. Early experience of play leads to greater social play after weaning [141].

Environmental enrichment and changes in enrichment can stimulate play behaviour in piglets before weaning and can reduce chronic post-weaning stress and aggression. Also, in object recognition tests, piglets with the most playful behaviours performed better [142].

#### Agonistic interactions

Agonistic interactions have been defined as 'any social interaction or engagement, which involves threatening behaviour, aggression, fighting, or submission' [106, p. 1]. In the wild, agonistic interactions can occur as part of competition for food, but also between boars in the context of sexual competition during the mating season [3,105].

Piglets may bite their litter mates to gain access to the most productive teats. They may behave aggressively towards their siblings, usually during play sequences, but are mostly aggressive towards piglets from other litters, for example when a farmer regroups animals at weaning time [143]. 'Agonistic behaviour in pigs especially occurs when unacquainted pigs are mixed with groups of acquainted ones. Fighting often results in the accumulation of skin lesions which can have detrimental effects on the welfare and longevity of the animals' [144].

Nevertheless, the absence of fighting is not synonymous with the absence of social tension, and an integrated approach may therefore be needed to assess welfare in groups of pigs [137].

## 3.7. Interactions with humans (human/animal relationships)

'Interactions between humans and pigs can be described as positive, neutral or negative from the animal's point of view. This classification depends on the nature of the interaction and how the animal perceives it.' [145]. Interactions with humans involving fear and trust are described in **Erreur ! Source du renvoi introuvable.**.

'In conventional piggeries, opportunities for neutral or positive interactions are less and less frequent due to the automation of feeding and other tasks, as well as the use of slatted floors, which reduces cleaning time. As a result, the proportion of negative interactions in the direct



experiences of pigs with their caretakers is becoming higher and higher.' [145]. In 2009, it was estimated that in France, a farmer spent less than 4 hours in contact with each sow and her piglets during a complete reproductive cycle [145].

In addition to fear or trust, a pig's curiosity concerning humans should also be taken into account in the pig/human relationship and can be classed as an enrichment factor in the animal's environment. In a study of uncastrated pigs, animals reared in an enriched environment were less interested in an unfamiliar human's presence in a test pen than pigs reared in a non-enriched environment. The authors hypothesized that pigs in an unenriched environment viewed the arrival of the human as an enrichment, as a new situation to explore [146].

In experiments on piglet-human interactions, it has been shown that weaned piglets are able to learn and remember previous interactions, develop a 'positive' or 'negative' perception of individual humans, distinguish between and recognise familiar humans and react appropriately to each familiar human on the basis of their previous experience with them [33].

Piglets have also demonstrated the ability to interpret signals given by a human such as pointing a finger in an object choice task [147].

Box 2 A pig's fear and trust in relation to humans. Reproduced and translated from [33].

#### Fear of humans

This is a strong emotion triggered by the perception of the human as a threat. It induces behavioural and physiological reactions that enable the individual to deal with the situation by confronting it (attacking the human), avoiding it (retreating slowly) or fleeing from it (retreating quickly and sometimes running in an uncoordinated way). An animal that is afraid of humans will avoid contact and will therefore be difficult to handle. Fear is detrimental to animal welfare and human work.

#### Trust in humans

Defined as the acceptance of being approached and handled by a human. It reflects both an absence of fear and a positive attraction to humans, a desire for contact. Trust is conducive to animal welfare and safe human work.

#### Link between fear and trust

Fear of and trust in humans are closely linked [...] Numerous studies show that in cases where the animals have not been handled by a human or have been handled in a negative manner, this makes it difficult for humans to approach the animal. By contrast, appropriate handling of the animal (handling that is perceived positively, such as simple presence, gentle tactile contact and feeding) makes it easier for humans to approach and handle the animal'.

#### Effects of positive interactions

The following are examples of instances where positive interactions between humans and pigs have been recorded, as summarised by Hayes et al. (2021)[148] in their introduction:

- Patting and stroking piglets during suckling on the first day of life reduced durations of escape behaviour during tail docking at 2 days of age and during capture at 15 days of age, compared with non-handled piglets [149].

- Caressing and talking softly induced an optimistic cognitive bias in piglets [150] (see section 5.4 below).

- Talking to and patting sows for 3 minutes a day when they approached reduced the physiological stress response associated with tether housing<sup>3</sup> [152].

- Talking to, stroking and rubbing pregnant sows for one minute a day improved ease of handling, reduced fear of humans and shortened farrowing times [153].

- Scratching the backs of lactating sows and playing music reduced pre-weaning piglet mortality [154].

<sup>&</sup>lt;sup>333</sup> Article published prior to the French Order of 20/01/1994 [151] prohibiting the practice of tether housing from 31/12/2005.



- Patting or scratching sows for 2 minutes a day reduced avoidance of the farmer during routine practices such as pregnancy monitoring and vaccination [148].

#### Effects of negative interactions

'Studies assessing the impact of handling on pigs have demonstrated that frequent negative interactions, such as shouting, slapping and hitting, increase pigs' fear of humans and can induce both acute and chronic stress. Reduced growth, feed conversion efficiency and reproduction have all been reported in pigs following aversive handling.' [148]. Inconsistent handling that the animal cannot predict, even if the majority of interactions are positive, induces fear of humans on a permanent basis, so that any interaction will be perceived as negative [155]. The practices of tail docking, tooth resection, tattooing or branding, and surgical castration [banned without anaesthesia in France from 1 January 2022] performed on very young animals are sources of stress and pain that are likely to affect their relationship with humans and lead them to develop a lifelong aversion to the latter [156].

Pig behaviour as described in this section will vary within a group because it depends on individual personalities (*Erreur ! Source du renvoi introuvable.*).

#### Box 3 Behaviour and personality

No real consensus exists on the definition of personality in animals. That used here is 'a correlated set of individual behavioural and physiological traits that are consistent over time and contexts' [157].

Pigs have stable individual behavioural and emotional characteristics that form a complex personality [146]. It is fairly common to classify pigs according to two personality types: 'reactive' animals, who are generally shyer, more passive and adaptable to change; and 'proactive' animals, who are generally more aggressive, more active and less adaptable [158].

# 4. Cognitive skills

There are many definitions of cognition. That used here is by Sara Shettleworth, as quoted in [159]: 'Cognition refers to the mechanisms by which animals acquire, process, store and act on information from the environment.' Pigs have significant cognitive abilities that enable them to adapt to their environment and, in particular, make efficient use of food sources [160]. Their cognitive abilities can be divided into two types: non-social and social. They are used for purposes of learning and anticipation.

#### 4.1. Non-social cognition

This category of cognition refers to an animal's perception, mental representations and conceptualisation of its physical environment [161]. It includes problem solving, object discrimination, spatial cognition, perception of time, etc.

#### Object discrimination and categorisation

Discrimination is the ability to distinguish between items on the basis of their sensory attributes (colour, smell, etc.) and temporal characteristics. It forms the basis of categorisation, which can be defined as the discrimination of categories of objects, for example food versus toys. Pigs have the ability to discriminate between objects in their environment. They will then remember these objects, which calls for both sensory and recall skills. For example, a pig will not respond in the same way to different enrichment objects in its enclosure, thereby



demonstrating discrimination [162]. Pigs can discriminate between black and white geometric shapes [163], enabling them to use these as building blocks for learning. Additionally, when presented with a new object, they will spend more time exploring it than a familiar object presented 10 minutes, 1 hour or 24 hours previously [164]. They can remember objects and will recognise them. They are therefore capable of categorising both unfamiliar and familiar objects and adapt their behaviour accordingly.

One study has shown that domestic piglets can remember a previously encountered object for 5 days [165], while another reported that young Kune Kune pigs could remember the solution for opening a box 5 months after learning it, demonstrating that their long-term memory is good [166]. This ability should be taken into account in the provision of enrichment materials to pigs, which should be varied regularly to maintain their attractiveness over time [165].

Pigs are able to discriminate between different types of food during foraging by remembering their smell and colour, using visual, auditory and olfactory cues [65, 167]. Farmed pigs can also discriminate between sites where food is present based on the amount of food at each site and will show a preference for the site with the most food [168]. Their quantification and categorisation skills have yet to be determined, particularly outside the domain of food.

#### Perception of time

There is little convincing evidence that pigs can perceive time, although some studies suggest that this is the case. For example, sows given a choice of two pens in which they had been isolated for different lengths of time (30 minutes or 240 minutes), chose the pen where they had spent less time. Their choice seemed to be based on the use of sensory cues to distinguish between the two pens [169].

#### Spatial learning and spatial recall

Pigs have good spatial cognitive abilities. They are able to find their bearings in space, remember food locations and remember locations they have already visited. This enables them to avoid returning to these locations and instead forage in unexplored areas [114, 155]. They seem to have the capacity to conceptualise object permanence, i.e., that an object no longer in their field of vision still exists. However, they find it hard to apprehend the movement of hidden objects (e.g., moving a pot containing a reward) [171]. Pigs are capable of finding food in locations of varying complexity that offer 2 or more pathways (in the shape of a T or a Y) to explore, reminiscent of a maze [172].

#### 4.2. Social cognition

This category of cognition relates to a pig's understanding of the social environment in which it spends its life, identification of other pigs, communication, particularly with humans, and adaptation of its responses to social contexts.

#### Ability to discriminate between conspecifics and between humans

Pigs live in structured social groups. This social organisation requires the establishment and maintenance of a hierarchy and involves the ability to discriminate between familiar and unfamiliar conspecifics [173, 174] from an early age [175]. It has been demonstrated that young farmed pigs can discriminate between their conspecifics and show a preference for familiar individuals over strangers [176]. Sows can discriminate between their own piglets and those of other sows [177] but to date there is no evidence that they can identify individual piglets. With regard to human discrimination, pigs are able to distinguish a familiar human from a stranger [178, 179].

#### Perspective-taking and social context

In psychology, perspective-taking refers to the ability to put oneself in someone else's shoes in order to understand their point of view, even if it differs from one's own [180]. In animals,



this concept has been studied mainly in primates, but experimental data suggest perspectivetaking abilities, particularly visual perspective-taking, in many species, including pigs. A small number of studies have suggested that pigs may well use body cues to distinguish between the different attentive states of conspecifics (in need of further validation, reviewed in [160]). This ability would enable pigs to develop strategies that are adapted to the situation. For example, in two studies, young domestic pigs were shown to be capable of developing complex foraging strategies. It was shown that a pig could deduce the location of a food source from the behaviour of an informed conspecific. The latter then appeared to modify its behaviour to deceive the uninformed pig, only approaching the food source when the uninformed pig was not present [181,182]. Farmed pigs also adapt their behaviour, for example their foraging speed, to the presence of other pigs, particularly when the other pig is dominant [183].

#### Self-awareness

Self-awareness is the component of cognition that relates to an individual's perception of themselves. Self-awareness implies being able to recognise oneself physically and to analyse one's own thoughts, feelings and sentiments [161]. This ability is traditionally tested using the mirror test. To date, it has not been proved that pigs can recognise themselves in a mirror. They are, however, able to use a mirror to locate a food source that is hidden by an opaque screen but visible in the mirror [184].

## 4.3. Learning

Learning corresponds to a change in an individual's behaviour based on information stored from previous experience; it necessarily involves recall capacities [185]. The process of learning allows animals to acquire information about their environment and update it when conditions change, making it possible for them to adapt to the change in circumstances.

Pigs can master different types of learning: associative, non-associative, discriminative and social [186]. There are two modes of social learning: vertical learning, when a young pig learns by mimicking adults [187] and horizontal learning, when an animal learns by observing its peers [188].

Associative learning, for example, has been demonstrated in mini-pigs, who can acquire tasks by following coloured signs indicating the action to be performed [189]. Likewise, miniature Vietnamese pigs have demonstrated the ability to discriminate between and understand visual symbols of objects (Frisbee, ball, stick) and verbal and gestural cues for actions (sit, fetch, jump), and to learn to combine an object with an action [190].

Associative learning can take place even *in utero*. Piglets whose mothers had been conditioned to the sound of distinct human voices in situations of positive or negative emotions during gestation showed distinct behaviours in response to the same contrasting auditory stimuli in the postnatal period [191].

At the time of weaning, vertical and horizontal social learning are particularly important. It has been shown that piglets learn to feed by imitating their mothers [187] and will go more readily to a foodstuff if a familiar conspecific is eating it [188].

Pigs are also able to learn to use objects such as a video game joystick to control the movements of a cursor and make it move to aim at targets on a screen. This type of learning requires conceptual understanding of the task [192].

#### 4.4. Cognitive enrichment

Cognitive enrichment is defined as a particular form of enrichment involving the stimulation of the cognitive abilities of captive animals through tasks to be completed in their environment. Completion of the tasks may or may not result in a reward (e.g., food) that the animal finds satisfying. Performance of the task can thus enable the animal to regain a degree of control



over its environment. One example of this type of enrichment is the use of an auditory signal to call individual pigs to a feeding station. Ten-week-old pigs provided with this sort of cognitive enrichment displayed less anxiety during feeding, more exploratory behaviour and fewer fear reactions in stressful situations [193].

## 4.5. Anticipation

Anticipatory behaviours are expressed at a time t on the basis of events expected to occur in the near future and information processed in the past [194]. Few studies exist on anticipatory behaviour in pigs. Two studies have shown that 10 to 12 week-old farmed pigs displayed minor differences in their behavioural reactions (vocalisations, tail position) when anticipating events that they considered either positive or negative [195, 196]. A third study showed that farmed post-weaners expressed their anticipation of social events (arrival of familiar conspecifics or familiar humans) with different grunts depending on the type of anticipation [197]. A final study has demonstrated that weaned piglets anticipate their entry into a play area, and therefore a play activity, following a learning period [198].

## 5. Emotional states

There is a direct link between a pig's emotional state and its welfare. While negative emotions (fear, pain) have long been attributed to pigs, the latter have now been shown to experience positive emotions (joy, satisfaction) and these should be encouraged on farms.

Table 4 provides examples of sources of emotion in pigs.

As stated in [199], the study of animal emotions is challenging because emotions can only be measured indirectly using neural, behavioural and physiological indicators.

Sources of positive emotio	ns	Sources of negative emotions		
Human intervention as a source of pleas feeling of security	ure or a	Human intervention as a source of stress or fear		
Stroking the belly	[149, 150]	Painful procedures [199]		
Scratching the back	[152]	Castration of males		
Speaking softly to the animal	[150, 151]	Caudectomy (tail docking)		
Approaching the animal slowly	[33]	Tooth resection		
Using gentle, slow movements	[33]	Ear-tag fitting		
nvironmental enrichment [205]		Fitting a nasal ring		
Physical enrichment		Tattooing		
Manipulable objects/toys	[207]	Iron injection		
Straw or other manipulable substrate	[206, 208]	Vaccination		
Foodstuffs	[117, 118]	Sudden or rough handling [33, 149]		
Social enrichment		Break-up of social structure		
Finding familiar conspecifics	[207, 209]	Grouping with unfamiliar conspecifics [200, 204		
Reunion of a sow and her piglets	[64]	Separation from the dam before and at [201, 20] weaning		
Encountering a familiar human	[208]	Social isolation of piglets or adults [203]		
Cognitive enrichment	[212, 213]			

#### Table 4 Examples of sources of emotion in pigs



## 5.1. Definitions

#### Emotions

Definitions of the term 'emotion' vary, but they share common elements (for a review, see [200]). We here use a definition derived from [201]: an emotion is a generally intense and fleeting response to a stimulus or triggering event; this response has several components (subjective, physiological, behavioural and cognitive). Emotions are characterised by their valence (positive/negative, pleasant/unpleasant) and their intensity or the degree of arousal they induce in the animal (low or high).

#### Mood

Mood is an emotional state that lasts longer than an emotion and is of low to moderate intensity. Mood is a latent state that is generally not linked to any particular stimulus [202].

#### Emotional states

The term 'emotional state' is often used as a synonym for mood, or even as a generic term encompassing emotion and mood. It has also been used to designate the subjective element of emotions and has also been applied to personality.

## 5.2. Physiological expression of emotional states in pig

#### Physiological indicators of negative emotional states

Stress can be defined as an adaptive response resulting from an individual's subjective assessment of the challenges of their environment [203]. By measuring an animal's stress response, it is possible to deduce its emotional state. Stress is studied via the activity of the autonomic nervous system and the hypothalamic-pituitary-adrenal (HPA) axis (or corticotropic axis).

The activity of the autonomic nervous system can be measured through reference to cardiovascular parameters such as heart rate and its variability. This makes it possible to measure the intensity of an emotional response, but not its valence.

*The corticotropic axis* is stimulated by aversive situations. Its stimulation is commonly assessed by measuring cortisol levels, particularly in circulating blood, saliva or hair. Impaired functioning of the corticotropic axis, for example excessive reactivity to stress [204] or a disturbed nychthemeral rhythm of cortisol secretion [205] may indicate situations of chronic stress. However, cortisol is not a specific measure of negative emotional states and, given that no linear relationship exists between cortisol and stress, it is also a poor indicator of stress intensity [203]. This indicator should therefore be used in combination with others.

The functioning of the immune system in pigs can be modified by responses from the autonomic nervous system and the corticotropic axis. The effects of social stress on inflammatory responses in pigs have been examined and reviewed [206]. They include changes in the distribution of different types of leukocytes, cytokine secretion, lymphocyte proliferation and antibody production, and immune responses to viral infections or vaccination.

#### Physiological indicators of positive emotional states

Several physiological parameters have been explored as potential animal-based indicators of the intensity and positive valence of emotions in pigs. Thus far, though, the results, which are sometimes contradictory, have yet to be validated.

Even though a *rise in heart rate* is associated with high emotional intensity, this marker gives no indication of the valence of the emotion. *Heart rate variability*, which is a measure of the variation in the temporal intervals between two consecutive heartbeats, has been proposed as an indicator of emotional states in pigs [203]. In a cognitive environmental enrichment test,



which the authors linked to a positive emotional state, young pigs showed an increase in heart rate variability [207].

Activation of the endogenous opioid system modulates an individual's subjective hedonic experience of reward, while the *dopaminergic system* influences motivation to obtain a reward. A preliminary study in pigs has shown that the provision of a form of cognitive enrichment altered the expression of opioid receptors in the amygdala, the part of the brain that processes reward-related stimuli [208].

*Brain oxytocin* is involved in the regulation of social bonds. In pigs, a study showed that positive interactions with humans led to an increase in the secretion of oxytocin in the cerebrospinal fluid [209]. However, the difficulty oxytocin has in crossing the blood-brain barrier makes a relationship between central and peripheral changes in oxytocin levels highly unlikely, meaning that this this indicator is of little practical interest.

*Brain-derived neurotrophic factor* (BDNF) is a growth factor for certain neurons in the central and peripheral nervous systems. In rodents, BDNF is implicated in cognitive function and resilience to stress. The measurement of BDNF in blood has recently been proposed as a means to identify positive mental states in pigs, since its concentrations were observed to increase when pigs were housed in an enriched environment [210].

Despite the above, studies on physiological indicators in pigs remain few and far between and their findings are sometimes contradictory.

## 5.3. Behavioural expression of emotional states in pigs

Certain pig behaviours have been associated with a positive emotional state while others are linked to a negative emotional state. The most significant of these are summarised in Box *4*.

Box 4 (adapted from [33,195, 211]) : Behaviours associated with negative and positive emotional states in pigs

#### In a negative emotional state, a pig may:

- become agitated (moving around a lot) or unable to move (petrified)
- move away from the source of the emotion
- show little tendency to explore its environment
- be highly alert (motionless, ears pricked)
- look towards the source of emotion, when at a safe distance
- emit long vocalisations resembling cries and squeals, very frequently if the emotion is very strong
- increase the frequency with which it urinates and defecates.
- In a positive emotional state, a pig may:
- move only a little or not at all (the animal lies down)
- move towards the source of emotion
- explore its environment
- point its ears forward
- have a relaxed tail with side-to-side motions
- emit short vocalisations resembling growls and barks, very frequent if the emotion is very strong
- play.

#### Vocalisations

Pigs express their emotions through the type (grunts, cries, squeaks, barks), duration and frequency of the vocalisations they emit. For example, piglets emit short, low growls when they anticipate the arrival of a familiar conspecific, a highly positive situation, and longer growls



when they anticipate the arrival of a human, these longer growls having previously been shown to be a sign of frustration [197]. Pigs express high-pitched long cries when they are in negative mental states, for example when they feel pain or fear. Using a small number of acoustic features, it is possible to associate a vocalisation with a given emotional valence and rearing situation [70].

#### Playing

Pigs are more playful in enriched and stimulating environments. Play is a potential indicator of a positive emotional state because it generally occurs when an animal's other needs are met and ceases when the animal feels threatened [212]. However, play can also help pigs to cope with difficult situations. Whether or not play expresses positive emotions in the individual performing it still has to be proved and is the subject of ongoing research.

#### Facial expressions and posture

Facial expressions and posture have been studied as indicators of emotion and emotional valence in pigs. Research has focused mainly on the movements and position of the ears and tail. For example, a hanging, relaxed, slightly wagging tail has been associated with a positive emotional state and low arousal in pigs [213]. Miniature pigs at play exhibited less frequent and slower ear movements than control conspecifics whose environment was not enriched with toys [214].

One study has demonstrated that, during agonistic encounters between two pigs, certain facial measurements can be used to distinguish negative emotional states. These measures

are the distance between the eye and the nose, nose disc length, ear angle with the eyenose line, and the length/width ratio of the eye [215] (



Figure 7).

Figure 7 Facial measurements. Reproduced from [215]

Left: Red dots indicate the fixed points from where measures were taken. Black lines indicate the measurement of the eye-nose length, nose disc length and ear angle. Right: measurement of the eye height/width ratio.

The posture of the back can provide information about a pig's emotional state. A rounded back with a low head position has been associated with negative situations in pigs [216]. There are also pain grids for assessing muscular tension in the pig's head and distinguishing painful episodes for piglets [98, 99] (see **Erreur ! Source du renvoi introuvable.** above).



## 5.4. Effects of emotional states on cognitive performance

Emotional states can lead to bias in various cognitive processes, including biased judgement, attention and memory. A cognitive bias occurs when an individual's personality affects their cognitive functions such as learning, remembering and decision-making [217]. Cognitive bias has been identified in pigs [218, 219]. The study of cognitive bias makes it possible, among other things, to evaluate the mood and personality of individuals [219].

#### Judgement bias

Both negative and positive bias in perceptions of the situation have been demonstrated in newly weaned piglets as a function of their previous repeated experiences of humans [150]. An animal's emotional state or mood will alter the way it perceives a stimulus or situation. For example, if one stimulus (black square) is associated with a reward and another (white square) with punishment, the animal will react differently to an ambiguous stimulus (grey square) depending on its mood. An animal in a positive mood will react as if the stimulus were positive, and an animal in a negative mood will react as if the stimulus were negative [203]. Enriched environments and positive relationships with humans encourage positive cognitive bias compared with impoverished environments and the absence of positive contact with humans [150, 219].

#### Attention bias

Attention bias as it relates to an affective state can be defined as the propensity for increased vigilance or attention to novel or negative aspects of the environment in individuals experiencing a negative affective state such as fear or depression [200]. In pigs, housing conditions are thought to change the degree of attention paid to a sound stimulus, particularly in proactive animals [220].

#### Memory bias

Memory bias in relation to affective states takes the form of a propensity to remember particular objects or events that are consistent with an individual's current affective state. To our knowledge, no memory bias test has been conducted in pigs.

#### 5.5. Emotional contagion

Emotional contagion is defined in [221] as a simple form of empathy in which only the emotional state of the other is shared, without cognitive perspective. 'Naïve' farmed sows, i.e. sows that have had no experience known to affect their emotional state either positively or negatively, have been shown to be subject to emotional contagion; when placed in the presence of conspecifics in either a positive or negative emotional state, their own emotional state became attuned to that of the conspecifics [221, 222]. Negative emotional contagion has also been demonstrated in piglets [223].

## Conclusion

This dossier has explored the welfare of pigs from the point of view of the animals themselves, starting with the physiological and behavioural needs that are closely linked to their cognitive and emotional capacities. These concepts are at the heart of the ANSES definition of animal welfare: 'The welfare of an animal is the positive mental and physical state associated with the satisfaction of its physiological and behavioural needs and also with its expectations. This state varies according to the animal's perception of the situation' [224].



This approach complements that of the EFSA opinion published in 2022 on the welfare of pigs [7]. EFSA's opinion identifies, for each stage of production, the consequences for animal welfare of the main European farming systems and practices; it proposes animal-based indicators and makes recommendations from the animal's point of view (for more information, see the summary of the EFSA opinion by FRCAW, in preparation). These recommendations are given for optimal farming conditions, and not all are directly applicable to the most prevalent farming systems.

In practice, in order to take better account of the animal's point of view, reliable, effective and routinely practicable welfare assessment methods are called for that can take into account all the dimensions of welfare and move between individual and herd levels. Such methods have yet to be developed and constitute a challenge for research. Current assessment methods, based on the 'five freedoms'<sup>4</sup>, are complex and time-consuming to put into practice, and take little account of positive emotions, which remain hard to identify.

Last, the improvement of livestock welfare must be properly and fully incorporated into the economic and working conditions of farmers, into how they deal with food safety, environmental protection and climate change and, more generally, the sustainable development of livestock farming. To remedy the non-availability of multicriteria evaluation methods for the environmental impacts of livestock farming that fully incorporate welfare issues [225], a number of research projects are underway, including the European partnership on animal health and welfare<sup>5</sup> and the Multibov, Multiporc and Multipoul projects<sup>6</sup>.

# References

- 1. Groenen, M.A.M.; Archibald, A.L.; Uenishi, H.; Tuggle, C.K.; Takeuchi, Y.; Rothschild, M.F.; Rogel-Gaillard, C.; Park, C.; Milan, D.; Megens, H.-J.; et al. Analyses of Pig Genomes Provide Insight into Porcine Demography and Evolution. *Nature* **2012**, *491*, 393–398, doi:10.1038/nature11622.
- 2. *Biology of the Domestic Pig*; Pond, W.G., Mersmann, H.J., Eds.; Comstock Pub. Associates, Cornell University Press: Ithaca, N.Y, 2001; ISBN 978-0-8014-3468-6.
- 3. D'Eath, R.B.; Turner, S.P.; Marchant-Forde, J. The Natural Behaviour of the Pig. *The Welfare of Pigs* **2009**, 13–45, doi:10.1007/978-1-4020-8909-1\_2.
- 4. Bidanel, J.P.; Silalahi, P.; Tribout, T.; Canario, L.L.; Ducos, A.; Garreau, H.; Gilbert, H.; Larzul, C.; Milan, D.; Riquet, J.; et al. Cinquante Années d'amélioration Génétique Du Porc En France : Bilan et Perspectives. *50. Journées de la Recherche Porcine* **2018**, *50*, 61–74.
- 5. Dourmad, J.-Y.; Canario, L.L.; Gilbert, H.; Merlot, E.; Quesnel, H.; Prunier, A. Evolution Des Performances et de La Robustesse Des Animaux En Élevage Porcin. *INRA Productions Animales* **2010**, *23*, 53–64, doi:10.20870/productionsanimales.2010.23.1.3287.
- Turner, S.P.; D'Eath, R.B.; Roehe, R.; Lawrence, A.B. Selection against Aggressiveness in Pigs at Re-Grouping: Practical Application and Implications for Long-Term Behavioural Patterns. *Animal Welfare* **2010**, *19*, 123–132, doi:10.1017/S0962728600002323.
- 7. EFSA Panel on Animal Health and Welfare (AHAW); Nielsen, S.S.; Alvarez, J.; Bicout, D.J.; Calistri, P.; Canali, E.; Drewe, J.A.; Garin-Bastuji, B.; Gonzales Rojas, J.L.;

 <sup>&</sup>lt;sup>4</sup> Freedom from hunger and thirst, freedom from discomfort, freedom from pain, injury or illness, freedom from fear and distress, and freedom to express the normal behaviour of the species.
<sup>5</sup> European Partnership on Animal Health and Welfare (EU PAHW):

https://www.efsa.europa.eu/en/funding-calls/european-partnership-animal-health-and-welfare https://www.assolitouesterel.org/nos-travaux/mesures-du-bien-etre-animal-et-evaluation-du-progres/evaluationsmulticritere/



Schmidt, G.; et al. Welfare of Pigs on Farm. *EFS2* **2022**, *20*, doi:10.2903/j.efsa.2022.7421.

- 8. Frädrich, Ha. A Comparison of Behaviour in the Suidae. In *The Behaviour of Ungulates and its relation to management*; UCN Publications new series; International Union for Conservation of Nature and Natural Resources Morges: Switzerland, 1974; Vol. 1, p. 509.
- 9. Howells, O.; Edwards-Jones, G. A Feasibility Study of Reintroducing Wild Boar Sus Scrofa to Scotland: Are Existing Woodlands Large Enough to Support Minimum Viable Populations. *Biological Conservation* **1997**, *81*, 77–89, doi:10.1016/S0006-3207(96)00134-6.
- Mauget, R. Behavioural and Reproductive Strategies in Wild Forms of Sus Scrofa (European Wild Boar and Feral Pigs). In *The Welfare of Pigs: A Seminar in the EEC Programme of Coordination of Research on Animal Welfare held in Brussels, November 25–26, 1980*; Sybesma, W., Ed.; Springer Netherlands: Dordrecht, 1981; pp. 3–15 ISBN 978-94-011-9574-4.
- 11. Leaper, R.; Massei, G.; Gorman, M.L.; Aspinall, R. The Feasibility of Reintroducing Wild Boar (Sus Scrofa) to Scotland. *Mammal Review* **1999**, *29*, 239–258, doi:10.1046/j.1365-2907.1999.2940239.x.
- 12. Wood-Gush, D.G.M.; Jensen, P.; Algers, B. Behaviour of Pigs in a Novel Semi-Natural Environment. *Biology of Behaviour* **1990**, *15*, 62–73.
- Nota, G.; Berretti, R.; Ascoli, D.; Barberis, D.; Ravetto Enri, S.; Pittarello, M.; Motta, R.; Battaglini, L.M.; Lombardi, G.; Lonati, M. Plant Species Selection and Impact on Tree Resprouts by Semi-Free Ranging Pigs in a Temperate Deciduous Forest. *Agroforest Syst* **2023**, *97*, 121–132, doi:10.1007/s10457-022-00792-1.
- 14. Jensen, P. The Weaning Process of Free-Ranging Domestic Pigs: Within- and Between-Litter Variations. *Ethology* **1995**, *100*, 14–25, doi:10.1111/j.1439-0310.1995.tb00311.x.
- 15. *Advances in Pig Welfare*; Špinka, M., Ed.; Woodhead Publishing in food science, technology, and nutrition; Woodhead Publishing, an imprint of Elsevier: Duxford, United Kingdom, 2018; ISBN 978-0-08-101012-9.
- 16. Hemsworth, P.H.; Tilbrook, A.J. Sexual Behavior of Male Pigs. *Hormones and Behavior* **2007**, *52*, 39–44, doi:10.1016/j.yhbeh.2007.03.013.
- 17. *Memento de l'éleveur de porc*; Institut Technique du Porc.; 2000; ISBN 978-2-85969-126-4.
- Parois, S.; Bonneau, M.; Chevillon, P.; Larzul, C.; Quiniou, N.; Robic, A.; Prunier, A. Odeurs Indésirables de La Viande de Porcs Mâles Non Castrés : Problèmes et Solutions Potentielles. *INRA Prod. Anim.* 2018, *31*, 23–36, doi:10.20870/productionsanimales.2018.31.1.2206.
- 19. Pig 333 Pig Glossary Pregnancy (Gestation).
- 20. Badouard, B. La Longévité Des Truies Dans Les Troupeaux Français Analysée à Partir Des Bases de Données Nationales 2020.
- 21. IFIP Fiche Conseil "Porcisanté" N°1 : Conduite et Interventions Truie 2019.
- 22. Badouard, B.; Boulot, S. Survie des porcelets en maternité : utilisation des nouvelles fonctionnalités de l'outil PertMat pour évaluer les pratiques de gestion des porcelets surnuméraires. Presented at the 55es Journées de la recherche porcine, 2023.
- 23. Le Porc Par Les Chiffres 2021-2022 Available online: https://ifip.asso.fr/actualites/ (accessed on 24 May 2022).
- 24. Rutherford, K.; Baxter, E.; D'Eath, R.; Turner, S.; Arnott, G.; Roehe, R.; Ask, B.; Sandøe, P.; Moustsen, V.; Thorup, F.; et al. The Welfare Implications of Large Litter Size in the Domestic Pig I: Biological Factors. *Animal Welfare* **2013**, *22*, 199–218, doi:10.7120/09627286.22.2.199.



- 25. Petersen, V.; Recén, B.; Vestergaard, K. Behaviour of Sows and Piglets during Farrowing under Free-Range Conditions. *Applied Animal Behaviour Science* **1990**, *26*, 169–179, doi:10.1016/0168-1591(90)90096-V.
- 26. Jensen, P. Observations on the Maternal Behaviour of Free-Ranging Domestic Pigs. *Applied Animal Behaviour Science* **1986**, *16*, 131–142, doi:10.1016/0168-1591(86)90105-X.
- 27. Jensen, P.; Stangel, G. Behaviour of Piglets during Weaning in a Seminatural Enclosure. *Applied Animal Behaviour Science* **1992**, *33*, 227–238, doi:10.1016/S0168-1591(05)80010-3.
- 28. Newberry, R.C.; Wood-Gush, D.G.M. The Suckling Behaviour of Domestic Pigs in a Semi-Natural Environment. *Behaviour* **1985**, *95*, 11–25, doi:10.1163/156853985X00028.
- 29. Badouard, B. Analyse des pertes en maternité à partir de la GTTT. In *Bilan d'activité de l'IFIP*; 2021.
- 30. Quesnel, H.; Gondret, F.; Merlot, E.; Farmer, C. Influences maternelles sur la consommation de colostrum et la survie néonatale du porcelet. *INRAE Productions Animales* **2015**, *28*, 295–304, doi:10.20870/productions-animales.2015.28.4.3034.
- 31. Quiniou, N.; Dagorn, J.; Gaudré, D. Variation Du Poids Des Porcelets à La Naissance et Incidence Sur Les Performances Zootechniques Ultérieures. *Techniporc* **2001**, *24*, 11–17.
- 32. IFIP Fiche Conseil "Porcisanté" N°9 : Gestion Des Porcelets Après La Mise Bas 2021.
- Tallet, C.; Courboulay, V.; Devillers, N.; Meunier-Salaün, M.-C.; Prunier, A.; Villain, A. Mieux Connaître Le Comportement Du Porc Pour Une Bonne Relation Avec Les Humains En Élevage. *INRA Prod. Anim.* 2020, 33, 81–94, doi:10.20870/productionsanimales.2020.33.2.4474.
- 34. Directive 2008/120/CE Du Conseil de l'UE Du 18 Décembre 2008 Établissant Les Normes Minimales Relatives à La Protection Des Porcs Available online: https://eurlex.europa.eu/legal-content/FR/TXT/HTML/?uri=CELEX:32008L0120&from=FR (accessed on 13 May 2022).
- 35. Conseil de l'Europe Directive 2001/88/CE Du Conseil Du 23 Octobre 2001 Modifiant La Directive 91/630/CEE Établissant Les Normes Minimales Relatives à La Protection Des Porcs Available online: https://eur-lex.europa.eu/legalcontent/FR/ALL/?uri=CELEX%3A32001L0088 (accessed on 27 May 2022).
- 36. National Hog Farmer Sow Dentistry Available online: https://www.nationalhogfarmer.com/mag/farming\_sow\_dentistry (accessed on 19 December 2022).
- 37. Etienne, M.; Legault, C.; Dourmad, J.Y.; Noblet, J. Production Laitière de La Truie : Estimation, Composition, Facteurs de Variation et Évolution. *Journées Recherche Porcine* **2000**, *32*, 253–264.
- Quiniou, N.; Brossard, L.; Van Milgen, J.; Salaün, Y.; Quesnel, H.; Gondret, F.; Dourmad, J.Y. La Variabilité Des Performances Animales En Élevage Porcin : Description et Implications Pratiques. *INRA Prod. Anim.* 2012, 25, 5–16, doi:10.20870/productions-animales.2012.25.1.3191.
- 39. Noblet, J.; Etienne, M. Estimation of Sow Milk Nutrient Output. *Journal of Animal Science* **1989**, *67*, 3352, doi:10.2527/jas1989.67123352x.
- 40. Lallès, J.-P.; Konstantinov, S.; Rothkötter, H.-J. Bases Physiologiques, Microbiologiques et Immunitaires Des Troubles Digestifs Du Sevrage Chez Le Porcelet : Données Récentes Dans Le Contexte de La Suppression Des Antibiotiques Additifs Alimentaires. *Journées Recherche Porcine* **2004**, *36*, 139–150.
- 41. Salmon, H.; Berri, M.; Gerdts, V.; Meurens, F. Humoral and Cellular Factors of Maternal Immunity in Swine. *Developmental & Comparative Immunology* **2009**, *33*, 384–393, doi:10.1016/j.dci.2008.07.007.



- 42. Jensen, P.; Recén, B. When to Wean Observations from Free-Ranging Domestic Pigs. *Applied Animal Behaviour Science* **1989**, *23*, 49–60, doi:10.1016/0168-1591(89)90006-3.
- Arrêté Du 16 Janvier 2003 Établissant Les Normes Minimales Relatives à La Protection Des Porcs - Légifrance Available online: https://www.legifrance.gouv.fr/loda/id/LEGITEXT000005633899/ (accessed on 24 May 2022).
- 44. Commission européenne Règlement (CE) n o 889/2008 de La Commission Du 5 Septembre 2008 Portant Modalités d'application Du Règlement (CE) n o 834/2007 Du Conseil Relatif à La Production Biologique et à l'étiquetage Des Produits Biologiques En Ce Qui Concerne La Production Biologique, l'étiquetage et Les Contrôles 2008.
- 45. Calvar, C. Le Porc Biologique. Principaux Points de La Règlementation Européenne Available online: https://www.chambres-agriculture-bretagne.fr/synagri/ag-le-porcbiologique---principaux-points-de-la-reglementation-europeenne (accessed on 24 May 2022).
- 46. Bøe, K.; Jensen, P. Individual Differences in Suckling and Solid Food Intake by Piglets. *Applied Animal Behaviour Science* **1995**, *42*, 183–192, doi:10.1016/0168-1591(94)00528-M.
- 47. Choudhury, R.; Middelkoop, A.; de Souza, J.G.; van Veen, L.A.; Gerrits, W.J.J.; Kemp, B.; Bolhuis, J.E.; Kleerebezem, M. Impact of Early-Life Feeding on Local Intestinal Microbiota and Digestive System Development in Piglets. *Sci Rep* **2021**, *11*, 4213, doi:10.1038/s41598-021-83756-2.
- 48. Miller, H.M.; Carroll, S.M.; Reynolds, F.H.; Slade, R.D. Effect of Rearing Environment and Age on Gut Development of Piglets at Weaning. *Livestock Science* **2007**, *108*, 124–127, doi:10.1016/j.livsci.2007.01.016.
- 49. Edwards, S.A.; Turpin, D.L.; Pluske, J.R. 9. Weaning age and its long-term influence on health and performance. In *The suckling and weaned piglet*, Farmer, C., Ed.; Wageningen Academic Publishers: The Netherlands, 2020; pp. 225–250 ISBN 978-90-8686-343-3.
- 50. Faccin, J.E.G.; Laskoski, F.; Hernig, L.F.; Kummer, R.; Lima, G.F.R.; Orlando, U.A.D.; Gonçalves, M.A.D.; Mellagi, A.P.G.; Ulguim, R.R.; Bortolozzo, F.P. Impact of Increasing Weaning Age on Pig Performance and Belly Nosing Prevalence in a Commercial Multisite Production System. *Journal of Animal Science* **2020**, *98*, skaa031, doi:10.1093/jas/skaa031.
- 51. Pluske, J.R.; Kerton, D.K.; Cranwell, P.D.; Campbell, R.G.; Mullan, B.P.; King, R.H.; Power, G.N.; Pierzynowski, S.G.; Westrom, B.; Rippe, C.; et al. Age, Sex, and Weight at Weaning Influence Organ Weight and Gastrointestinal Development of Weanling Pigs. *Aust. J. Agric. Res.* **2003**, *54*, 515, doi:10.1071/AR02156.
- 52. Ballari, S.A.; Barrios-García, M.N. A Review of Wild Boar Sus Scrofa Diet and Factors Affecting Food Selection in Native and Introduced Ranges. *Mammal Review* **2014**, *44*, 124–134, doi:10.1111/mam.12015.
- 53. Lawrence, A.B.; Terlouw, E.M.C. A Review of Behavioral Factors Involved in the Development and Continued Performance of Stereotypic Behaviors in Pigs. *J Anim Sci* **1993**, *71*, 2815–2825, doi:10.2527/1993.71102815x.
- 54. Chambre Régionale d'Agriculture de Bretagne; IFIP; Anses L'abreuvement Des Porcs 2018.
- 55. Ramonet, Y.; Chiron, J.; Etore, F.; Laval, A.; Nielsen, B.; Pol, F.; Prunier, A.; Meunier-Salaün, M.-C. Abreuvement Des Porcs : État Des Connaissances et Conséquences Sur Le Bien-Être Des Animaux et La Gestion Des Effluents Chez Des Porcs Alimentés En Soupe. *Journées Recherche Porcine* **2017**, *49*, 139–150.
- 56. Stolba, A.; Wood-Gush, D.G.M. The Identification of Behavioural Key Features and Their Incorporation into a Housing Design for Pigs. Abstract Europe PMC. *Annales de recherches vétérinaires* **1984**, *15*, 287–302.



- 57. Blasetti, A.; Boitani, L.; Riviello, M.C.; Visalberghi, E. Activity Budgets and Use of Enclosed Space by Wild Boars (Sus Scrofa) in Captivity. *Zoo Biology* **1988**, *7*, 69–79, doi:10.1002/zoo.1430070108.
- 58. Nannoni, E.; Aarnink, A.J.A.; Vermeer, H.M.; Reimert, I.; Fels, M.; Bracke, M.B.M. Soiling of Pig Pens: A Review of Eliminative Behaviour. *Animals* **2020**, *10*, 2025, doi:10.3390/ani10112025.
- 59. Ducreux, E.; Aloui, B.; Robin, P.; Dourmad, J.-Y.; Courboulay, V.; Meunier-Salaün, M.-C. Les porcs affichent leurs préférences vis-à-vis du type de sol en fonction de la température ambiante. *Journées Recherche Porcine* **2002**, *34*, 211–216.
- 60. Ekkel, E.D.; Spoolder, H.A.M.; Hulsegge, I.; Hopster, H. Lying Characteristics as Determinants for Space Requirements in Pigs. *Applied Animal Behaviour Science* **2003**, *80*, 19–30, doi:10.1016/S0168-1591(02)00154-5.
- 61. Hill, G.; Lay, D.C.J.; Radcliffe, S.; MacNeil, M.D. Chapter 9: Swine. In *Guide for the care and use of agricultural animals in research and teaching*; Federation of Animal Science Societies, 2020; p. 227 ISBN 978-0-9634491-5-3.
- 62. AHAW Panel Opinion of the Scientific Panel on Animal Health and Welfare (AHAW) on a Request from the Commission Related to Welfare of Weaners and Rearing Pigs: Effects of Different Space Allowances and Floor. *EFSA Journal* **2005**, *268*, 1–19, doi:10.2903/j.efsa.2005.268.
- 63. Adamczyk, K.; Górecka-Bruzda, A.; Nowicki, J.; Gumułka, M.; Molik, E.; Schwarz, T.; Earley, B.; Klocek, C. Perception of Environment in Farm Animals – A Review. *Annals* of *Animal Science* **2015**, *15*, 565–589, doi:10.1515/aoas-2015-0031.
- 64. Horrell, I.; Hodgson, J. The Bases of Sow-Piglet Identification. 2. Cues Used by Piglets to Identify Their Dam and Home Pen. *Applied Animal Behaviour Science* **1992**, *33*, 329–343, doi:10.1016/S0168-1591(05)80070-X.
- 65. Croney, C.C.; Adams, K.M.; Washington, C.G.; Stricklin, W.R. A Note on Visual, Olfactory and Spatial Cue Use in Foraging Behavior of Pigs: Indirectly Assessing Cognitive Abilities. *Applied Animal Behaviour Science* **2003**, *83*, 303–308, doi:10.1016/S0168-1591(03)00128-X.
- 66. Courboulay V, Depoudent C, Ramonet Y, Villain N, Kling-Eveillard F, Barbier P, Pol F, Vermeil de Conchard R, Delion M, Paboeuf P, Boivin X, Tallet C La Méthode RHAPORC : Apprécier Les Facteurs Qui Modulent La Relation Homme-Animal Pour l'améliorer Available online: https://docs.ifip.asso.fr/default/digitalCollection/DigitalCollectionAttachmentDownloadH andler.ashx?parentDocumentId=119&documentId=10860&skipWatermark=true&skipC opyright=true (accessed on 15 April 2022).
- 67. Bensoussan, S.; Tigeot, R.; Lemasson, A.; Meunier-Salaün, M.-C.; Tallet, C. Domestic Piglets (Sus Scrofa Domestica) Are Attentive to Human Voice and Able to Discriminate Some Prosodic Features. *Applied Animal Behaviour Science* **2019**, *210*, 38–45, doi:10.1016/j.applanim.2018.10.009.
- 68. Zapata Cardona, J.; Ceballos, M.C.; Tarazona Morales, A.M.; David Jaramillo, E.; Rodríguez, B. de J. Music Modulates Emotional Responses in Growing Pigs. *Sci Rep* **2022**, *12*, 3382, doi:10.1038/s41598-022-07300-6.
- Tallet, C.; Linhart, P.; Policht, R.; Hammerschmidt, K.; Šimeček, P.; Kratinova, P.; Špinka, M. Encoding of Situations in the Vocal Repertoire of Piglets (Sus Scrofa): A Comparison of Discrete and Graded Classifications. *PLOS ONE* **2013**, *8*, e71841, doi:10.1371/journal.pone.0071841.
- Briefer, E.F.; Sypherd, C.C.-R.; Linhart, P.; Leliveld, L.M.C.; Padilla de la Torre, M.; Read, E.R.; Guérin, C.; Deiss, V.; Monestier, C.; Rasmussen, J.H.; et al. Classification of Pig Calls Produced from Birth to Slaughter According to Their Emotional Valence and Context of Production. *Scientific Reports* **2022**, *12*, 1–10, doi:10.1038/s41598-022-07174-8.



- 71. Illmann, G.; Špinka, M.; Schrader, L.; Šustr, P. Acoustical Mother-Offspring Recognition in Pigs (Sus Scrofa Domestica). *Behaviour* **2002**, *139*, 487–505, doi:10.1163/15685390260135970.
- 72. Nguyen, D.T.; Lee, K.; Choi, H.; Choi, M.; Le, M.T.; Song, N.; Kim, J.-H.; Seo, H.G.; Oh, J.-W.; Lee, K.; et al. The Complete Swine Olfactory Subgenome: Expansion of the Olfactory Gene Repertoire in the Pig Genome. *BMC Genomics* **2012**, *13*, 584, doi:10.1186/1471-2164-13-584.
- 73. Weisslinger, M. Fiche espèce- Tout savoir sur le porc ! Chaire bien-être animal 2022.
- 74. Brunjes, P.C.; Feldman, S.; Osterberg, S.K. The Pig Olfactory Brain: A Primer. *Chem Senses* **2016**, *41*, 415–425, doi:10.1093/chemse/bjw016.
- 75. Vieuille-Thomas, C.; Signoret, J.P. Pheromonal Transmission of an Aversive Experience in Domestic Pig. *J Chem Ecol* **1992**, *18*, 1551–1557, doi:10.1007/BF00993228.
- 76. Amory, J.R.; Pearce, G.P. Alarm Pheromones in Urine Modify the Behaviour of Weaner Pigs. *Animal Welfare* **2000**, *9*, 167–175, doi:10.1017/S0962728600022508.
- 77. Temple, D.; Barthélémy, H.; Mainau, E.; Cozzi, A.; Amat, M.; Canozzi, M.E.; Pageat, P.; Manteca, X. Preliminary Findings on the Effect of the Pig Appeasing Pheromone in a Slow Releasing Block on the Welfare of Pigs at Weaning. *Porcine Health Management* **2016**, *2*, 13, doi:10.1186/s40813-016-0030-5.
- 78. Yonezawa, T.; Koori, M.; Kikusui, T.; Mori, Y. Appeasing Pheromone Inhibits Cortisol Augmentation and Agonistic Behaviors During Social Stress in Adult Miniature Pigs. *jzoo* **2009**, *26*, 739–744, doi:10.2108/zsj.26.739.
- 79. McGlone, J.J. Olfactory Cues and Pig Agonistic Behavior: Evidence for a Submissive Pheromone. *Physiology & Behavior* **1985**, *34*, 195–198, doi:10.1016/0031-9384(85)90105-2.
- 80. Asproni, P.; Mainau, E.; Cozzi, A.; Carreras, R.; Bienboire-Frosini, C.; Teruel, E.; Pageat, P. Is There a Link between Vomeronasalitis and Aggression in Stable Social Groups of Female Pigs? *Animals* **2022**, *12*, 303, doi:10.3390/ani12030303.
- 81. Mechin, V.; Asproni, P.; Bienboire-Frosini, C.; Cozzi, A.; Chabaud, C.; Arroub, S.; Mainau, E.; Nagnan-Le Meillour, P.; Pageat, P. Inflammation Interferes with Chemoreception in Pigs by Altering the Neuronal Layout of the Vomeronasal Sensory Epithelium. *Front. Vet. Sci.* **2022**, *9*, 936838, doi:10.3389/fvets.2022.936838.
- 82. Hellekant, G.; Danilova, V. Taste in Domestic Pig, Sus Scrofa. *Journal of Animal Physiology and Animal Nutrition* **1999**, *82*, 8–24, doi:10.1046/j.1439-0396.1999.00206.x.
- 83. Jones, J.B.; Carmichael, N.L.; Wathes, C.M.; White, R.P.; Jones, R.B. The Effects of Acute Simultaneous Exposure to Ammonia on the Detection of Buried Odourized Food by Pigs. *Applied Animal Behaviour Science* **2000**, *65*, 305–319, doi:10.1016/S0168-1591(99)00063-5.
- 84. Kennedy, J.M.; Baldwin, B.A. Taste Preferences in Pigs for Nutritive and Non-Nutritive Sweet Solutions. *Animal Behaviour* **1972**, *20*, 706–718, doi:10.1016/S0003-3472(72)80142-8.
- 85. Hendrickson, A.; Hicks, D. Distribution and Density of Medium- and Short-Wavelength Selective Cones in the Domestic Pig Retina. *Experimental Eye Research* **2002**, *74*, 435–444, doi:10.1006/exer.2002.1181.
- 86. Tanida, H.; Senda, K.; Suzuki, S.; Tanaka, T.; Yoshimoto, T. Color Discrimination in Weanling Pigs. *Nihon Chikusan Gakkaiho* **1991**, *6*2, 1029–1034, doi:10.2508/chikusan.62.1029.
- 87. Klocek, C.; Nowicki, J.; Brudzisz, B.; Pabianczyk, M. Colour Preferences in Pigs. *Animal Science and Genetics* **2016**, *12*, 123–129, doi:10.5604/01.3001.0013.5420.
- 88. Grandin, T. Pig Behavior Studies Applied to Slaughter-Plant Design. *Applied Animal Ethology* **1982**, *9*, 141–151, doi:10.1016/0304-3762(82)90190-0.



- 89. Zonderland, J.J.; Cornelissen, L.; Wolthuis-Fillerup, M.; Spoolder, H.A.M. Visual Acuity of Pigs at Different Light Intensities. *Applied Animal Behaviour Science* **2008**, *111*, 28–37, doi:10.1016/j.applanim.2007.05.010.
- 90. Agriculture and Horticulture; Development Board Lighting in Pig Buildings: The Principles 2019.
- 91. Taylor, N.; Prescott, N.; Perry, G.; Potter, M.; Sueur, C.L.; Wathes, C. Preference of Growing Pigs for Illuminance. *Applied Animal Behaviour Science* **2006**, *96*, 19–31, doi:10.1016/j.applanim.2005.04.016.
- 92. Tanida, H.; Miura, A.; Tanaka, T.; Yoshimoto, T. Behavioral Responses of Piglets to Darkness and Shadows. *Applied Animal Behaviour Science* **1996**, *49*, 173–183, doi:10.1016/0168-1591(96)01039-8.
- 93. Camerlink, I.; Turner, S.P. The Pig's Nose and Its Role in Dominance Relationships and Harmful Behaviour. *Applied Animal Behaviour Science* **2013**, *145*, 84–91, doi:10.1016/j.applanim.2013.02.008.
- 94. Keita, A.; Pagot, E.; Prunier, A.; Guidarini, C. Pre–Emptive Meloxicam for Postoperative Analgesia in Piglets Undergoing Surgical Castration. *Veterinary Anaesthesia and Analgesia* **2010**, *37*, 367–374, doi:10.1111/j.1467-2995.2010.00546.x.
- 95. Ison, S.H.; Clutton, R.E.; Di Giminiani, P.; Rutherford, K.M.D. A Review of Pain Assessment in Pigs. *Front. Vet. Sci.* **2016**, *3*, doi:10.3389/fvets.2016.00108.
- 96. Heinonen, M.; Peltoniemi, O.; Valros, A. Impact of Lameness and Claw Lesions in Sows on Welfare, Health and Production. *Livestock Science* **2013**, *156*, 2–9, doi:10.1016/j.livsci.2013.06.002.
- 97. Viscardi, A.V.; Hunniford, M.; Lawlis, P.; Leach, M.; Turner, P.V. Development of a Piglet Grimace Scale to Evaluate Piglet Pain Using Facial Expressions Following Castration and Tail Docking: A Pilot Study. *Front. Vet. Sci.* **2017**, *4*, doi:10.3389/fvets.2017.00051.
- 98. Di Giminiani, P.; Brierley, V.L.M.H.; Scollo, A.; Gottardo, F.; Malcolm, E.M.; Edwards, S.A.; Leach, M.C. The Assessment of Facial Expressions in Piglets Undergoing Tail Docking and Castration: Toward the Development of the Piglet Grimace Scale. *Front. Vet. Sci.* **2016**, *0*, doi:10.3389/fvets.2016.00100.
- Luna, S.P.L.; de Araújo, A.L.; da Nóbrega Neto, P.I.; Brondani, J.T.; de Oliveira, F.A.; Azerêdo, L.M. dos S.; Telles, F.G.; Trindade, P.H.E. Validation of the UNESP-Botucatu Pig Composite Acute Pain Scale (UPAPS). *PLoS ONE* 2020, *15*, e0233552, doi:10.1371/journal.pone.0233552.
- Le Neindre, P.; Guatteo, R.; Guemene, D.; Guichet, J.-L.; Latouche, K.; Leterrier, C.; Levionnois, O.; Mormède, P.; Prunier, A.; Serrie, A.; et al. Douleurs Animales. Les Identifier, Les Comprendre, Les Limiter Chez Les Animaux d'élevage. 2009, doi:10.15454/EYY0-DJ57.
- Mellor, D.J.; Cook, C.J.; Stafford, K.J. Quantifying Some Responses to Pain as a Stressor. In *The biology of animal stress: basic principles and implications for animal welfare.*; Moberg, G.P., Mench, J.A., Eds.; CABI Publishing: UK, 2000; pp. 171–198 ISBN 978-0-85199-359-1.
- 102. Prunier, A.; Hay, M.; Servrière, J. Evaluation et Prévention de La Douleur Induite Par Les Interventions de Convenance Chez Le Porcelet. *Journées de la Recherche Porcine* **2002**, *34*, 257–268.
- Lamont, L.A.; Tranquilli, W.J.; Grimm, K.A. Physiology of Pain. Veterinary Clinics of North America: Small Animal Practice 2000, 30, 703–728, doi:10.1016/S0195-5616(08)70003-2.
- 104. Di Giminiani, P.; Edwards, S.A.; Malcolm, E.M.; Leach, M.C.; Herskin, M.S.; Sandercock, D.A. Characterization of Short- and Long-Term Mechanical Sensitisation Following Surgical Tail Amputation in Pigs. *Scientific Reports* **2017**, *7*, 1–9, doi:10.1038/s41598-017-05404-y.



- 105. Stolba, A.; Wood-Gush, D.G.M. The Behaviour of Pigs in a Semi-Natural Environment. *Anim. Sci.* **1989**, *48*, 419–425, doi:10.1017/S0003356100040411.
- Young, C. Agonistic Behavior. In *Encyclopedia of Animal Cognition and Behavior*, Vonk, J., Shackelford, T., Eds.; Springer International Publishing: Cham, 2019; pp. 1–6 ISBN 978-3-319-47829-6.
- 107. Gonyou, H.W.; Chapple, R.P.; Frank, G.R. Productivity, Time Budgets and Social Aspects of Eating in Pigs Penned in Groups of Five or Individually. *Applied Animal Behaviour Science* **1992**, *34*, 291–301, doi:10.1016/S0168-1591(05)80090-5.
- Bodin, L.; Algers, B.; Andersson, M.; Olsson, AC.; Botermans, J. The Amount of Straw for Growing-Finishing Pigs Considering the Reduction of Time Spent in Manipulative Behavior. SOJVS 2015, 1, 1–6, doi:10.15226/2381-2907/1/1/00105.
- Clouard, C.; Resmond, R.; Prunier, A.; Tallet, C.; Merlot, E. Exploration of Early Social Behaviors and Social Styles in Relation to Individual Characteristics in Suckling Piglets. *Sci Rep* 2022, *12*, 2318, doi:10.1038/s41598-022-06354-w.
- 110. Fraser, D.; Phillips, P.A.; Thompson, B.K.; Tennessen, T. Effect of Straw on the Behaviour of Growing Pigs. *Applied Animal Behaviour Science* **1991**, *30*, 307–318, doi:10.1016/0168-1591(91)90135-K.
- 111. Studnitz, M.; Jensen, M.B.; Pedersen, L.J. Why Do Pigs Root and in What Will They Root?: A Review on the Exploratory Behaviour of Pigs in Relation to Environmental Enrichment. *Applied Animal Behaviour Science* **2007**, *107*, 183–197, doi:10.1016/j.applanim.2006.11.013.
- 112. Fraser, D. The Effect of Straw on the Behaviour of Sows in Tether Stalls. *Anim. Sci.* **1975**, *21*, 59–68, doi:10.1017/S0003356100030415.
- 113. Petersen, V.; Simonsen, H.B.; Lawson, L.G. The Effect of Environmental Stimulation on the Development of Behaviour in Pigs. *Applied Animal Behaviour Science* **1995**, *45*, 215–224, doi:10.1016/0168-1591(95)00631-2.
- Damm, B.I.; Lisborg, L.; Vestergaard, K.S.; Vanicek, J. Nest-Building, Behavioural Disturbances and Heart Rate in Farrowing Sows Kept in Crates and Schmid Pens. *Livestock Production Science* 2003, *80*, 175–187, doi:10.1016/S0301-6226(02)00186-0.
- 115. Oostindjer, M.; van den Brand, H.; Kemp, B.; Bolhuis, J.E. Effects of Environmental Enrichment and Loose Housing of Lactating Sows on Piglet Behaviour before and after Weaning. *Applied Animal Behaviour Science* **2011**, *134*, 31–41, doi:10.1016/j.applanim.2011.06.011.
- Kelly, H.R.C.; Bruce, J.M.; English, P.R.; Fowler, V.R.; Edwards, S.A. Behaviour of 3-Week Weaned Pigs in Straw-Flow®, Deep Straw and Flatdeck Housing Systems. *Applied Animal Behaviour Science* **2000**, *68*, 269–280, doi:10.1016/S0168-1591(00)00109-X.
- 117. Schrøder-Petersen, D.L.; Simonsen, H.B. Tail Biting in Pigs. *The Veterinary Journal* **2001**, *162*, 196–210, doi:10.1053/tvjl.2001.0605.
- Courboulay, V.; Corrégé, I.; Gaudré, D.; Gourmelen, C.; Guingand, N.; Massabie, P. Le Point Sur Les Effets de La Densité En Post-Sevrage et Engraissement. *Techniporc* 2006, 29, 7–13.
- 119. Middelkoop, A.; van Marwijk, M.A.; Kemp, B.; Bolhuis, J.E. Pigs Like It Varied; Feeding Behavior and Pre- and Post-Weaning Performance of Piglets Exposed to Dietary Diversity and Feed Hidden in Substrate During Lactation. *Front. Vet. Sci.* **2019**, *0*, doi:10.3389/fvets.2019.00408.
- 120. de Jonge, F.H.; Tilly, S.-L.; Baars, A.M.; Spruijt, B.M. On the Rewarding Nature of Appetitive Feeding Behaviour in Pigs (Sus Scrofa): Do Domesticated Pigs Contrafreeload? *Applied Animal Behaviour Science* **2008**, *114*, 359–372, doi:10.1016/j.applanim.2008.03.006.
- 121. Holm, L.; Jensen, M.; Pedersen, L.; Ladewig, J. The Importance of a Food Feedback in Rooting Materials for Pigs Measured by Double Demand Curves with and without a



Common Scaling Factor. *Applied Animal Behaviour Science - APPL ANIM BEHAV SCI* **2008**, *111*, 68–84, doi:10.1016/j.applanim.2007.05.013.

- 122. Mendl, M.; Held, S.; Byrne, R.W. Pig Cognition. *Current Biology* **2010**, *20*, R796– R798, doi:10.1016/j.cub.2010.07.018.
- 123. Petersen, V. The Development of Feeding and Investigatory Behaviour in Free-Ranging Domestic Pigs during Their First 18 Weeks of Life. *Applied Animal Behaviour Science* **1994**, *42*, 87–98, doi:10.1016/0168-1591(94)90149-X.
- Andersen, H.M.-L.; Dybkjær, L.; Herskin, M.S. Growing Pigs' Drinking Behaviour: Number of Visits, Duration, Water Intake and Diurnal Variation. *Animal* 2014, *8*, 1881– 1888, doi:10.1017/S175173111400192X.
- 125. Gómez-Prado, J.; Pereira, A.M.F.; Wang, D.; Villanueva-García, D.; Domínguez-Oliva, A.; Mora-Medina, P.; Hernández-Avalos, I.; Martínez-Burnes, J.; Casas-Alvarado, A.; Olmos-Hernández, A.; et al. Thermoregulation Mechanisms and Perspectives for Validating Thermal Windows in Pigs with Hypothermia and Hyperthermia: An Overview. *Front. Vet. Sci.* **2022**, *9*, 1023294, doi:10.3389/fvets.2022.1023294.
- Cecchin, D.; Ferraz, P.; Campos, A.; Sousa, F.; Amaral, P.; Castro, J.; Conti, L.; Cruz, V. Thermal Comfort of Pigs Housed in Different Installations. *Agronomy Research* 2019, *17*, 378–384, doi:10.15159/AR.19.117.
- 127. Marcon, M. Les Porcs Ne Manquent Pas d'air. Tech Porc 2016, 24–25.
- 128. Jensen, P. Nest Site Choice and Nest Building of Free-Ranging Domestic Pigs Due to Farrow. *Applied Animal Behaviour Science* **1989**, *22*, 13–21, doi:10.1016/0168-1591(89)90076-2.
- 129. Courboulay, V.; Ganier, E.; Boulot, S. Importance d'un matériau de nidification pour la truie et les porcelets. *Journées Recherche Porcine* **2021**, *53*, 71–76.
- Andersen, I.L.; Vasdal, G.; Pedersen, L.J. Nest Building and Posture Changes and Activity Budget of Gilts Housed in Pens and Crates. *Applied Animal Behaviour Science* 2014, 159, 29–33, doi:10.1016/j.applanim.2014.07.002.
- 131. Lanthony, M.; Danglot, M.; Špinka, M.; Tallet, C. Dominance Hierarchy in Groups of Pregnant Sows: Characteristics and Identification of Related Indicators. *Applied Animal Behaviour Science* **2022**, *254*, 105683, doi:10.1016/j.applanim.2022.105683.
- 132. Ewbank, R. Social Hierarchy in Suckling and Fattening Pigs: A Review. *Livestock Production Science* **1976**, *3*, 363–372, doi:10.1016/0301-6226(76)90070-1.
- 133. De Passillé, A.M.B.; Rushen, J.; Hartsock, T.G. Ontogeny of Teat Fidelity in Pigs and Its Relation to Competition at Suckling. *Can. J. Anim. Sci.* **1988**, *68*, 325–338, doi:10.4141/cjas88-037.
- 134. Puppe, B.; Tuchscherer, A. Developmental and Territorial Aspects of Suckling Behaviour in the Domestic Pig (*Sus Scrofa f. Domestica*). *Journal of Zoology* **1999**, 249, 307–313, doi:10.1111/j.1469-7998.1999.tb00767.x.
- 135. Skok, J.; Prevolnik, M.; Urek, T.; Mesarec, N.; Škorjanc, D. Behavioural Patterns Established during Suckling Reappear When Piglets Are Forced to Form a New Dominance Hierarchy. *Applied Animal Behaviour Science* **2014**, *161*, 42–50, doi:10.1016/j.applanim.2014.09.005.
- 136. Meese, G.B.; Ewbank, R. The Establishment and Nature of the Dominance Hierarchy in the Domesticated Pig. *Animal Behaviour* **1973**, *21*, 326–334, doi:10.1016/S0003-3472(73)80074-0.
- 137. Camerlink, I.; Turner, S.P.; Ursinus, W.W.; Reimert, I.; Bolhuis, J.E. Aggression and Affiliation during Social Conflict in Pigs. *PLoS ONE* **2014**, *9*, e113502, doi:10.1371/journal.pone.0113502.
- 138. Spoolder, H.A.M.; Burbidge, J.A.; Edwards, S.A.; Lawrence, A.B.; Simmins, P.H. Social Recognition in Gilts Mixed into a Dynamic Group of 30 Sows. *Proc. Br.Soc. Anim. Sci.* **1996**, *1996*, 37–37, doi:10.1017/S1752756200592394.
- 139. Horback, K. Nosing around : Play in Pigs. *Animal behavior and cognition* **2014**, *1*, 186–196, doi:10.12966/abc.05.08.2014.



- 140. Newberry, R.C.; Wood-Gush, D.G.M.; Hall, J.W. Playful Behaviour of Piglets. *Behavioural Processes* **1988**, *17*, 205–216, doi:10.1016/0376-6357(88)90004-6.
- 141. Donaldson, T.M.; Newberry, R.C.; Špinka, M.; Cloutier, S. Effects of Early Play Experience on Play Behaviour of Piglets after Weaning. *Applied Animal Behaviour Science* **2002**, *79*, 221–231, doi:10.1016/S0168-1591(02)00138-7.
- 142. Martin, J.E.; Ison, S.H.; Baxter, E.M. The Influence of Neonatal Environment on Piglet Play Behaviour and Post-Weaning Social and Cognitive Development. *Applied Animal Behaviour Science* **2015**, *163*, 69–79, doi:10.1016/j.applanim.2014.11.022.
- 143. Petersen, H.V.; Vestergaard, K.; Jensen, P. Integration of Piglets into Social Groups of Free-Ranging Domestic Pigs. *Applied Animal Behaviour Science* **1989**, *23*, 223–236, doi:10.1016/0168-1591(89)90113-5.
- 144. Stukenborg, A.; Traulsen, I.; Stamer, E.; Puppe, B.; Krieter, J. The Use of a Lesion Score as an Indicator for Agonistic Behaviour in Pigs. *Archives Animal Breeding* **2012**, *55*, 163–170, doi:10.5194/aab-55-163-2012.
- 145. Prunier, A.; Tallet, C. Endocrine and Behavioural Responses of Sows to Human Interactions and Consequences on Reproductive Performance. In *The gestating and lactating sow*; Wageningen Academic Publishers, 2015; p. np.
- 146. Tallet, C.; Brilloüet, A.; Meunier-Salaün, M.-C.; Paulmier, V.; Guérin, C.; Prunier, A. Effects of Neonatal Castration on Social Behaviour, Human–Animal Relationship and Feeding Activity in Finishing Pigs Reared in a Conventional or an Enriched Housing. *Applied Animal Behaviour Science* **2013**, *145*, 70–83, doi:10.1016/j.applanim.2013.03.001.
- 147. Nawroth, C.; Ebersbach, M.; von Borell, E. Juvenile Domestic Pigs (Sus Scrofa Domestica) Use Human-given Cues in an Object Choice Task. *Anim Cogn* **2014**, *17*, 701–713, doi:10.1007/s10071-013-0702-3.
- 148. Hayes, M.E.; Hemsworth, L.M.; Morrison, R.S.; Butler, K.L.; Rice, M.; Rault, J.-L.; Hemsworth, P.H. Effects of Positive Human Contact during Gestation on the Behaviour, Physiology and Reproductive Performance of Sows. *Animals* **2021**, *11*, 214, doi:10.3390/ani11010214.
- 149. Muns, R.; Rault, J.-L.; Hemsworth, P. Positive Human Contact on the First Day of Life Alters the Piglet's Behavioural Response to Humans and Husbandry Practices. *Physiology & Behavior* **2015**, *151*, 162–167, doi:10.1016/j.physbeh.2015.06.030.
- 150. Brajon, S.; Laforest, J.-P.; Schmitt, O.; Devillers, N. The Way Humans Behave Modulates the Emotional State of Piglets. *PLOS ONE* **2015**, *10*, e0133408, doi:10.1371/journal.pone.0133408.
- Arrêté Du 20 Janvier 1994 Établissant Les Normes Minimales Relatives à La Protection Des Porcs Available online: https://www.legifrance.gouv.fr/jorf/id/JORFTEXT000000363084 (accessed on 24 May 2022).
- 152. Pedersen, V.; Barnett, J.L.; Hemsworth, P.H.; Newman, E.A.; Schirmer, B. The Effects of Handling on Behavioural and Physiological Responses to Housing in Tether-Stalls Among Pregnant Pigs. *Animal Welfare* **1998**, *7*, 137–150, doi:https://doi.org/10.1017/S0962728600020467.
- 153. English, P.R.; Grant, S.A.; McPherson, O.; Edwards, S.A. Evaluation of the Effects of the Positive 'Befriending' of Sows and Gilts ('Pleasant' Treatment) Prior to Parturition and in Early Lactation on Sow Behaviour, the Process of Parturition and Piglet Survival. BSAP Occasional Publication 1999, 23, 132–136, doi:10.1017/S0263967X00033401.
- Meyer, D.D.; Amalraj, A.; Limbergen, T.V.; Fockedey, M.; Edwards, S.; Moustsen, V.A.; Chantziaras, I.; Maes, D. Short Communication: Effect of Positive Handling of Sows on Litter Performance and Pre-Weaning Piglet Mortality. *animal* 2020, *14*, 1733– 1739, doi:10.1017/S1751731120000427.



- 155. Hemsworth, P.H.; Barnett, J.L.; Hansen, C. The Influence of Inconsistent Handling by Humans on the Behaviour, Growth and Corticosteroids of Young Pigs. *Applied Animal Behaviour Science* **1987**, *17*, 245–252, doi:10.1016/0168-1591(87)90149-3.
- 156. 4. Husbandry Interventions in Suckling Piglets, Painful Consequences and Mitigation | The Suckling and Weaned Piglet Available online: https://www.wageningenacademic.com/doi/abs/10.3920/978-90-8686-894-0\_4 (accessed on 13 April 2022).
- 157. Finkemeier, M.-A.; Langbein, J.; Puppe, B. Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare. *Front. Vet. Sci.* **2018**, *0*, doi:10.3389/fvets.2018.00131.
- 158. O'Malley, C.I.; Turner, S.P.; D'Eath, R.B.; Steibel, J.P.; Bates, R.O.; Ernst, C.W.; Siegford, J.M. Animal Personality in the Management and Welfare of Pigs. *Applied Animal Behaviour Science* **2019**, *218*, 104821, doi:10.1016/j.applanim.2019.06.002.
- 159. Broom, D.M. *Broom and Fraser's Domestic Animal Behaviour and Welfare*; 6th edition.; CAB International: Wallingford, Oxfordshire ; Boston, MA, 2021; ISBN 978-1-78924-983-5.
- 160. Nawroth, C.; Langbein, J.; Coulon, M.; Gabor, V.; Oesterwind, S.; Benz-Schwarzburg, J.; von Borell, E. Farm Animal Cognition—Linking Behavior, Welfare and Ethics. *Front. Vet. Sci.* **2019**, *0*, doi:10.3389/fvets.2019.00024.
- 161. Marino, L.; Colvin, C.M. Thinking Pigs: A Comparative Review of Cognition, Emotion, and Personality in Sus Domesticus. *International Journal of Comparative Psychology* **2015**, *28*.
- Leroux, M.; Ramonet, Y.; Villain, N. Utilisation par les porcs de matériaux d'enrichissement du commerce pour améliorer le bien-être des animaux. *Journées Recherche Porcine* 2021, 53, 77–82.
- 163. Gieling, E.T.; Musschenga, M.A.; Nordquist, R.E.; van der Staay, F.J. Juvenile Pigs Use Simple Geometric 2D Shapes but Not Portrait Photographs of Conspecifics as Visual Discriminative Stimuli. *Applied Animal Behaviour Science* **2012**, *14*2, 142–153, doi:10.1016/j.applanim.2012.10.018.
- 164. Kornum, B.R.; Thygesen, K.S.; Nielsen, T.R.; Knudsen, G.M.; Lind, N.M. The Effect of the Inter-Phase Delay Interval in the Spontaneous Object Recognition Test for Pigs. *Behavioural Brain Research* **2007**, *181*, 210–217, doi:10.1016/j.bbr.2007.04.007.
- 165. Gifford, A.K.; Cloutier, S.; Newberry, R.C. Objects as Enrichment: Effects of Object Exposure Time and Delay Interval on Object Recognition Memory of the Domestic Pig. *Applied Animal Behaviour Science* **2007**, *107*, 206–217, doi:10.1016/j.applanim.2006.10.019.
- 166. Veit, A.; Wondrak, M.; Huber, L. Object Movement Re-Enactment in Free-Ranging Kune Kune Piglets. *Animal Behaviour* **2017**, *132*, 49–59, doi:10.1016/j.anbehav.2017.08.004.
- 167. Nawroth, C.; von Borell, E. Domestic Pigs' (Sus Scrofa Domestica) Use of Direct and Indirect Visual and Auditory Cues in an Object Choice Task. *Anim Cogn* 2015, *18*, 757–766, doi:10.1007/s10071-015-0842-8.
- Held, S.; Baumgartner, J.; KilBride, A.; Byrne, R.W.; Mendl, M. Foraging Behaviour in Domestic Pigs (Sus Scrofa): Remembering and Prioritizing Food Sites of Different Value. *Anim Cogn* **2005**, *8*, 114–121, doi:10.1007/s10071-004-0242-y.
- 169. Špinka, M.; Duncan, I.J.H.; Widowski, T.M. Do Domestic Pigs Prefer Short-Term to Medium-Term Confinement? *Applied Animal Behaviour Science* **1998**, *58*, 221–232, doi:10.1016/S0168-1591(98)00109-9.
- 170. Mendl, null; Laughlin, null; Hitchcock, null Pigs in Space: Spatial Memory and Its Susceptibility to Interference. *Anim Behav* **1997**, *54*, 1491–1508, doi:10.1006/anbe.1997.0564.
- 171. Nawroth, C.; Ebersbach, M.; von Borell, E. A Note on Pigs' Knowledge of Hidden Objects. *Arch. Anim. Breed.* **2013**, *56*, 861–872, doi:10.7482/0003-9438-56-086.



- 172. Gieling, E.T.; Nordquist, R.E.; van der Staay, F.J. Assessing Learning and Memory in Pigs. *Anim Cogn* **2011**, *14*, 151–173, doi:10.1007/s10071-010-0364-3.
- 173. Mendl, M.; Randle, K.; Pope, S. Young Female Pigs Can Discriminate Individual Differences in Odours from Conspecific Urine. *Animal Behaviour* **2002**, *64*, 97–101, doi:10.1006/anbe.2002.3040.
- 174. Parent, J.-P. Stabilité de la hiérarchie sociale chez les porcs femelles en croissance et les truies gestantes. Mémoire pour l'obtention du grade de Maître ès sciences, Université Laval: Québec, Canada, 2012.
- McLeman, M.A.; Mendl, M.; Jones, R.B.; White, R.; Wathes, C.M. Discrimination of Conspecifics by Juvenile Domestic Pigs, Sus Scrofa. *Animal Behaviour* 2005, 70, 451–461, doi:10.1016/j.anbehav.2004.11.013.
- 176. McLeman, M.A.; Mendl, M.T.; Jones, R.B.; Wathes, C.M. Social Discrimination of Familiar Conspecifics by Juvenile Pigs, Sus Scrofa: Development of a Non-Invasive Method to Study the Transmission of Unimodal and Bimodal Cues between Live Stimuli. *Applied Animal Behaviour Science* **2008**, *115*, 123–137, doi:10.1016/j.applanim.2008.06.010.
- 177. Maletínská, J.; Špinka, M.; Víchová, J.; Stěhulová, I. Individual Recognition of Piglets by Sows in the Early Post-Partum Period. *Behaviour* **2002**, *139*, 975–991, doi:10.1163/156853902320387927.
- 178. Tanida, H.; Nagano, Y. The Ability of Miniature Pigs to Discriminate between a Stranger and Their Familiar Handler. *Applied Animal Behaviour Science* **1998**, *56*, 149–159, doi:10.1016/S0168-1591(97)00095-6.
- 179. Brajon, S.; Laforest, J.-P.; Bergeron, R.; Tallet, C.; Devillers, N. The Perception of Humans by Piglets: Recognition of Familiar Handlers and Generalisation to Unfamiliar Humans. *Anim Cogn* **2015**, *18*, 1299–1316, doi:10.1007/s10071-015-0900-2.
- 180. Canizales, D.L. La prise de perspective lors de l'évaluation de la douleur d'autrui : études auprès d'adultes ayant un trouble psychotique d'évolution récente et d'adultes en bonne santé générale, Université Laval: Québec, Canada, 2015.
- 181. Held, S.; Mendl, M.; Devereux, C.; Byrne, R.W. Social Tactics of Pigs in a Competitive Foraging Task: The 'Informed Forager' Paradigm. *Animal Behaviour* **2000**, *59*, 569–576, doi:10.1006/anbe.1999.1322.
- Held, S.; Mendl, M.; Devereux, C.; Byrne, R.W. Foraging Pigs Alter Their Behaviour in Response to Exploitation. *Animal Behaviour* 2002, *64*, 157–165, doi:10.1006/anbe.2002.3044.
- 183. Held, S.D.E.; Byrne, R.W.; Jones, S.; Murphy, E.; Friel, M.; Mendl, M.T. Domestic Pigs, Sus Scrofa, Adjust Their Foraging Behaviour to Whom They Are Foraging With. *Animal Behaviour* **2010**, *79*, 857–862, doi:10.1016/j.anbehav.2009.12.035.
- 184. Broom, D.M.; Sena, H.; Moynihan, K.L. Pigs Learn What a Mirror Image Represents and Use It to Obtain Information. *Animal Behaviour* **2009**, *78*, 1037–1041, doi:10.1016/j.anbehav.2009.07.027.
- 185. Breed, M.D.; Moore, J. *Animal Behavior*, Second edition.; Academic Press: Amsterdam, 2016; ISBN 978-0-12-801532-2.
- 186. Lévy, F.; Darmaillacq, S. *Éthologie animale*; Série LMD; 2ème édition.; de Boeck, 2019; ISBN 978-2-8073-2037-6.
- 187. Oostindjer, M.; Bolhuis, J.E.; Mendl, M.; Held, S.; van den Brand, H.; Kemp, B. Learning How to Eat like a Pig: Effectiveness of Mechanisms for Vertical Social Learning in Piglets. *Animal Behaviour* **2011**, *82*, 503–511, doi:10.1016/j.anbehav.2011.05.031.
- 188. Figueroa, J.; Solà-Oriol, D.; Manteca, X.; Pérez, J.F. Social Learning of Feeding Behaviour in Pigs: Effects of Neophobia and Familiarity with the Demonstrator Conspecific. *Applied Animal Behaviour Science* **2013**, *148*, 120–127, doi:10.1016/j.applanim.2013.06.002.



- Moustgaard, A.; Arnfred, S.M.; Lind, N.M.; Hemmingsen, R.; Hansen, A.K. Acquisition of Visually Guided Conditional Associative Tasks in Göttingen Minipigs. *Behavioural Processes* 2005, *68*, 97–102, doi:10.1016/j.beproc.2004.11.002.
- 190. Croney, C.C. Cognitive abilities of domestic pigs ProQuest, The Pennsylvania State University, 1999.
- 191. Tallet, C.; Rakotomahandry, M.; Guérin, C.; Lemasson, A.; Hausberger, M. Postnatal Auditory Preferences in Piglets Differ According to Maternal Emotional Experience with the Same Sounds during Gestation. *Scientific Reports* **2016**, *6*, 1–8, doi:10.1038/srep37238.
- 192. Croney, C.C.; Boysen, S.T. Acquisition of a Joystick-Operated Video Task by Pigs (Sus Scrofa). *Front. Psychol.* **2021**, *0*, doi:10.3389/fpsyg.2021.631755.
- 193. Zebunke, M.; Puppe, B.; Langbein, J. Effects of Cognitive Enrichment on Behavioural and Physiological Reactions of Pigs. *Physiology & Behavior* **2013**, *118*, 70–79, doi:10.1016/j.physbeh.2013.05.005.
- 194. van den Bos, R. Animal Anticipation: A Perspective. In *Handbook of Anticipation: Theoretical and Applied Aspects of the Use of Future in Decision Making*; Poli, R., Ed.; Springer International Publishing: Cham, 2019; pp. 235–247 ISBN 978-3-319-91554-8.
- 195. Reimert, I.; Bolhuis, J.E.; Kemp, B.; Rodenburg, T.B. Indicators of Positive and Negative Emotions and Emotional Contagion in Pigs. *Physiology & Behavior* **2013**, *109*, 42–50, doi:10.1016/j.physbeh.2012.11.002.
- 196. Imfeld-Mueller, S.; Van Wezemael, L.; Stauffacher, M.; Gygax, L.; Hillmann, E. Do Pigs Distinguish between Situations of Different Emotional Valences during Anticipation? *APPLIED ANIMAL BEHAVIOUR SCIENCE* **2011**, *131*, 86–93, doi:10/fkchq4.
- 197. Villain, A.S.; Hazard, A.; Danglot, M.; Guérin, C.; Boissy, A.; Tallet, C. Piglets Vocally Express the Anticipation of Pseudo-Social Contexts in Their Grunts. *Scientific Reports* 2020, 10, 1–13, doi:10.1038/s41598-020-75378-x.
- 198. Lidfors, L.M.; Farhadi, N.; Anderson, C.; Zupan Šemrov, M. Investigating the Reward Cycle of Play in Pigs (Sus Scrofa). *Front. Anim. Sci.* **2021**, *0*, doi:10.3389/fanim.2021.740778.
- 199. Leliveld, L.M.C; Düpjan, S.; Tuchscherer, A.; Puppz, V. Behavioural and physiological measures indicate subtle variations in the emotional valence of young pigs. *Physiology* & *Behavior* **2016**, *157*, 116-124, doi: 10.1016/j.physbeh.2016.02.002
- 200. Kremer, L.; Holkenborg, S.E.J.K.; Reimert, I.; Bolhuis, J.E.; Webb, L.E. The Nuts and Bolts of Animal Emotion. *Neurosci. Biobehav. Rev.* **2020**, *113*, 273–286, doi:10.1016/j.neubiorev.2020.01.028.
- 201. Paul, E.S.; Mendl, M.T. Animal Emotion: Descriptive and Prescriptive Definitions and Their Implications for a Comparative Perspective. *Applied Animal Behaviour Science* **2018**, *205*, 202–209, doi:10.1016/j.applanim.2018.01.008.
- 202. Berkowitz, L. *Causes and Consequences of Feelings*; 1st ed.; Cambridge University Press, 2000; ISBN 978-0-521-63325-3.
- Murphy, E.; Melotti, L.; Mendl, M. Assessing Emotions in Pigs: Determining Negative and Positive Mental States. In Understanding the behaviour and improving the welfare of pigs; Burleigh Dodds Science Publishing: University of Newcastle, U, 2021; pp. 455–496 ISBN 978-1-78676-443-0.
- 204. Kanitz, E.; Otten, W.; Tuchscherer, M. Central and Peripheral Effects of Repeated Noise Stress on Hypothalamic–Pituitary–Adrenocortical Axis in Pigs. *Livestock Production Science* **2005**, *94*, 213–224, doi:10.1016/j.livprodsci.2004.12.002.
- 205. Janssens, C.J.J.G.; Helmond, F.A.; Weigant, V.M. The Effect of Chronic Stress on Plasma Cortisol Concentrations in Cyclic Female Pigs Depends on the Time of Day. *Domestic Animal Endocrinology* **1995**, *12*, 167–177, doi:10.1016/0739-7240(94)00018-V.



- 206. Gimsa, U.; Tuchscherer, M.; Kanitz, E. Psychosocial Stress and Immunity—What Can We Learn From Pig Studies? *Front. Behav. Neurosci.* **2018**, *12*, 64, doi:10.3389/fnbeh.2018.00064.
- 207. Zebunke, M.; Langbein, J.; Manteuffel, G.; Puppe, B. Autonomic Reactions Indicating Positive Affect during Acoustic Reward Learning in Domestic Pigs. *Animal Behaviour* **2011**, *81*, 481–489, doi:10.1016/j.anbehav.2010.11.023.
- 208. Kalbe, C.; Puppe, B. Long-Term Cognitive Enrichment Affects Opioid Receptor Expression in the Amygdala of Domestic Pigs. *Genes, Brain and Behavior* **2010**, *9*, 75–83, doi:10.1111/j.1601-183X.2009.00536.x.
- 209. Rault, J.-L. Effects of Positive and Negative Human Contacts and Intranasal Oxytocin on Cerebrospinal Fluid Oxytocin. *Psychoneuroendocrinology* **2016**, *69*, 60–66, doi:10.1016/j.psyneuen.2016.03.015.
- 210. Rault, J.-L.; Lawrence, A.J.; Ralph, C.R. Brain-Derived Neurotrophic Factor in Serum as an Animal Welfare Indicator of Environmental Enrichment in Pigs. *Domestic Animal Endocrinology* **2018**, *65*, 67–70, doi:10.1016/j.domaniend.2018.05.007.
- 211. Murphy, E.; Nordquist, R.E.; van der Staay, F.J. A Review of Behavioural Methods to Study Emotion and Mood in Pigs, Sus Scrofa. *Applied Animal Behaviour Science* **2014**, *159*, 9–28, doi:10.1016/j.applanim.2014.08.002.
- Boissy, A.; Manteuffel, G.; Jensen, M.B.; Moe, R.O.; Spruijt, B.; Keeling, L.J.; Winckler, C.; Forkman, B.; Dimitrov, I.; Langbein, J.; et al. Assessment of Positive Emotions in Animals to Improve Their Welfare. *Physiology & Behavior* 2007, *92*, 375– 397, doi:10.1016/j.physbeh.2007.02.003.
- 213. Camerlink, I.; Ursinus, W.W. Tail Postures and Tail Motion in Pigs: A Review. *Applied Animal Behaviour Science* **2020**, 230, 105079, doi:10.1016/j.applanim.2020.105079.
- Marcet Rius, M.; Pageat, P.; Bienboire-Frosini, C.; Teruel, E.; Monneret, P.; Leclercq, J.; Lafont-Lecuelle, C.; Cozzi, A. Tail and Ear Movements as Possible Indicators of Emotions in Pigs. *Applied Animal Behaviour Science* **2018**, *205*, 14–18, doi:10.1016/j.applanim.2018.05.012.
- 215. Camerlink, I.; Coulange, E.; Farish, M.; Baxter, E.M.; Turner, S.P. Facial Expression as a Potential Measure of Both Intent and Emotion. *Sci Rep* **2018**, *8*, 17602, doi:10.1038/s41598-018-35905-3.
- 216. Tallet, C.; Sénèque, E.; Mégnin, C.; Morisset, S.; Val-Laillet, D.; Meunier-Salaün, M.-C.; Fureix, C.; Hausberger, M. Assessing Walking Posture with Geometric Morphometrics: Effects of Rearing Environment in Pigs. *Applied Animal Behaviour Science* **2016**, *174*, 32–41, doi:10.1016/j.applanim.2015.10.008.
- 217. Mendl, M.; Burman, O.H.P.; Parker, R.M.A.; Paul, E.S. Cognitive Bias as an Indicator of Animal Emotion and Welfare: Emerging Evidence and Underlying Mechanisms. *Applied Animal Behaviour Science* **2009**, *118*, 161–181, doi:10.1016/j.applanim.2009.02.023.
- 218. Carreras, R.; Mainau, E.; Rodriguez, P.; Llonch, P.; Dalmau, A.; Manteca, X.; Velarde, A. Cognitive Bias in Pigs: Individual Classification and Consistency over Time. *Journal of Veterinary Behavior* **2015**, *10*, 577–581, doi:10.1016/j.jveb.2015.09.001.
- 219. Asher, L.; Friel, M.; Griffin, K.; Collins, L.M. Mood and Personality Interact to Determine Cognitive Biases in Pigs. *Biol. Lett.* **2016**, *12*, 20160402, doi:10.1098/rsbl.2016.0402.
- 220. Luo, L.; Reimert, I.; de Haas, E.N.; Kemp, B.; Bolhuis, J.E. Effects of Early and Later Life Environmental Enrichment and Personality on Attention Bias in Pigs (Sus Scrofa Domesticus). *Anim. Cogn.* **2019**, *22*, 959–972, doi:10.1007/s10071-019-01287-w.
- 221. Reimert, I.; Bolhuis, J.E.; Kemp, B.; Rodenburg, T.B. Emotions on the Loose: Emotional Contagion and the Role of Oxytocin in Pigs. *Anim Cogn* **2015**, *18*, 517–532, doi:10.1007/s10071-014-0820-6.



- 222. Reimert, I.; Fong, S.; Rodenburg, T.B.; Bolhuis, J.E. Emotional States and Emotional Contagion in Pigs after Exposure to a Positive and Negative Treatment. *Applied Animal Behaviour Science* **2017**, *193*, 37–42, doi:10.1016/j.applanim.2017.03.009.
- 223. Goumon, S.; Špinka, M. Emotional Contagion of Distress in Young Pigs Is Potentiated by Previous Exposure to the Same Stressor. *Anim Cogn* **2016**, *19*, 501–511, doi:10.1007/s10071-015-0950-5.
- 224. CES SABA AVIS de l'Anses Relatif Au « Bien-Être Animal : Contexte, Définition et Évaluation » 2018.
- 225. Lanzoni, L.; Whatford, L.; Atzori, A.; Chincarini, M.; Giammarco, M.; Fusaro, I.; Vignola, G. Review: The Challenge to Integrate Animal Welfare Indicators into the Life Cycle Assessment. *animal* **2023**, 100794, doi:10.1016/j.animal.2023.100794.





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