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Delay discounting task in pigs reveals response strategies related to dopamine metabolite

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HIGHLIGHTS

- We develop a novel delay discounting task to investigate impulsive choice in pigs.
- Outcome impulsivity is unrelated to coping style and aggression at weaning.
- Two discounting strategies are adopted, namely 'Switchers' and 'Omitters'.
- Omitters have higher basal levels of urinary homovanillic acid (HVA) than Switchers.
- HVA positively correlates with indecisiveness and frustration during choosing.

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ABSTRACT

We developed a novel delay discounting task to investigate outcome impulsivity in pigs. As impulsivity can affect aggression, and might also relate to proactive and reactive coping styles, eight proactive (HR) and eight reactive (LR) pigs identified in a manual restraint test ("Backtest", after Bolhuis et al., 2003) were weaned and mixed in four pens of four unfamiliar pigs, so that each pen had two HR and two LR pigs, and aggression was scored in the 9 h after mixing. In the delay discounting task, each pig chose between two levers, one always delivering a small immediate reward, the other a large delayed reward with daily increasing delays, impulsive individuals being the ones discounting the value of the large reward quicker. Two novel strategies emerged: some pigs gradually switched their preference towards the small reward ('Switchers') as predicted, but others persistently preferred the large reward until they stopped making choices ('Omitters'). Outcome impulsivity itself was unrelated to these strategies, to urinary serotonin metabolite (5-HIAA) or dopamine metabolite (HVA) levels, aggression at weaning, or coping style. However, HVA was relatively higher in Omitters than Switchers, and positively correlated with behavioural measures of indecisiveness and frustration during choosing. The delay discounting task thus revealed two response strategies that seemed to be related to the activity of the dopamine system and might indicate a difference in execution, rather than outcome, impulsivity.

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1. Introduction

Impulsivity is a multifaceted construct consisting of several independent, interacting factors associated with different aspects of behaviour and influenced by different underlying biological mechanisms [1]. Due to its structural complexity, a single widely agreed definition of impulsivity does not currently exist, but animal studies commonly focus on two major features: impulsive action (i.e., the inability to inhibit a motor response) and impulsive choice (i.e., the modification of decision making processes [2]). The present study investigates a measure of impulsive choice, namely outcome impulsivity. This can be defined as the propensity to choose a less valuable and immediate outcome over a more valuable and delayed outcome [1,3]. Value here is taken as obtaining the greatest amount of food reward in the shortest possible time. Outcome impulsivity revolves around the inability to deal with delay of gratification, and has been researched in the contexts of substance abuse, gambling, attention deficit hyperactivity disorder (ADHD) and aggression [4–6]. In humans, outcome impulsivity has been investigated through questionnaire based measures [7–9], whereas in rodents and birds, it has been studied through operant conditioning paradigms [6,10–12] which is the approach also adopted here.

The aim of our experiment is to shed light on whether outcome impulsivity in pigs is linked to (a) serotonin and dopamine levels as it is in other species, and (b) to their coping style in response to stress, their growth rate and aggressiveness as predicted from previous findings.

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To this end we adapted and developed a delay discounting task, which is one of the standard operant conditioning paradigms for testing outcome impulsivity in rodents [6,10,13,14], for use with pigs.

In commercial pigs, aggression at weaning represents a major welfare, health and economic concern [15–17]. Piglets are usually weaned at about four weeks of age and regrouped with unacquainted pigs of similar weight [18] into unfamiliar pens, leading to a relatively short yet intense fighting period, until hierarchy relationships are formed [19,20]. As impulsivity can affect the speed and appropriateness of decisions to behave aggressively or competitively [21,22] a better understanding of the causes and correlates of impulsivity in pigs should help in the management of welfare-relevant behaviour. In addition, impulsivity levels in humans are positively correlated to some stress-related psychological states (e.g., anxiety or depression; [23,24]). Knowing an individual pig's impulsivity level could thus be a useful means to predict its susceptibility to suffer from specific and potentially stressful husbandry events and conditions such as its feeding expectations not being met or routine husbandry procedures being delayed.

Individual pigs vary in how they respond to mixing after weaning as they do to other social and physical challenges. Such individual variation is influenced by both genetic differences and differences in their pre- and postnatal environments [25–27]. Of interest here is whether individual differences in growth rates and aggressiveness commonly seen in response to mixing correspond to differences in outcome impulsivity.

The notion that non-human animals can adopt different stable strategies to cope with challenging events has been initially introduced in rodent studies [28–30], and then extended to other species, including pigs [31]. Individuals can show different "coping styles", defined as temporally stable and coherent sets of behavioural and physiological stress responses [31]. Animals with a "proactive" coping style are prone to develop routines, are persistent in the face of change and are relatively more aggressive, compared to "reactive" animals, which are more flexible in their behavioural response style and react continuously to subtle environmental changes [31–35]. In pigs, an early manual restraint test named "backtest" has been used in several studies to classify piglets as high (HR) or low (LR) resistant [36–39] with HR pigs being considered to have a proactive coping style and LR pigs a reactive coping style [31].

We used the backtest here to classify individuals by coping style, and then relate their coping style to outcome impulsivity. Proactively coping animals, having a lower behavioural flexibility, are not only expected to show more aggression (e.g., short attack latencies) but also more impulsive choice behaviour than reactively coping animals [21,22,40]. Proactively coping rodents have also been found to have lower serotonergic activity in the prefrontal cortex [41], to have higher dopamine D1 and D3 receptor binding in the nucleus accumbens [42], and to be more susceptible to addiction [43], compared to reactively coping rodents. In our study we tested the hypothesis that proactive pigs show higher outcome impulsivity, lower serotonin metabolite (5-HIAA) and higher dopamine metabolite (HVA) levels than reactively coping pigs.

Although neurotransmitters undergo several processes before reaching the bladder, and some of their metabolites can be synthesised also in peripheral areas [44–46], previous studies have shown that urinary levels of their metabolites as used here may be valid proxy measures for the corresponding levels in the brain (for serotonin metabolite 5-HIAA, e.g., [47]; dopamine metabolite HVA, e.g., [48–50]). Serotonin and dopamine have been shown to play an important role in the control of impulsivity [1,3,51,52]. In rats serotonin depletion in the forebrain increases outcome impulsivity [14,53] as assessed in delay discounting tasks by making the animals hypersensitive to delays [52]. Humans with reduced central serotonin levels resulting from dietary tryptophan depletion showed steeper delay discounting (i.e., higher outcome impulsivity) compared to control subjects with normal serotonin levels [54]. Dopamine is involved in the processes of reinforcement and motivation for reward-oriented behaviour [55,56]. Selective lesions of the nucleus accumbens core, to which dopaminergic (and serotonergic) afferents project, increase outcome impulsivity as assessed in delay discounting tasks in rats [57]. Administration of dopamine receptor antagonists has the same effects [58,59]. In addition, psychostimulants such as amphetamine and methylphenidate have been found to reduce outcome impulsivity both in rats [59] and humans [60]. They increase dopamine activity in the brain by inhibiting the reuptake of the neurotransmitter from the synaptic cleft and/or by increasing their release [61,62]. However, the same psychostimulants had opposite effects in other studies [13,63], where they reduced the choice of the large delayed reward (impulsivity was increased).

The main aims of this study thus are: (i) to develop a novel delay discounting task for pigs; (ii) to assess if basal urinary levels of serotonin and dopamine metabolites are linked with outcome impulsivity and coping style; (iii) to investigate the relationships between outcome impulsivity, aggressiveness at weaning, growth and coping style.

2. Methods

2.1. Animals and housing

Fig. 1 shows the experimental design including subjects and timeline. Subjects were 16 Duroc × Large White × Landrace female pigs born to six multiparous sows at Harper Adams University College, Newport, UK. The farrowing pens measured 1.8–2.0 × 2.4 m and had partially slatted floors, with a small quantity of sawdust provided on the solid part. All sows were confined in a farrowing crate throughout lactation, and piglets were provided with a heating lamp and a dedicated feeder. Piglets were tail-docked at 1 d after birth. Initially, 31 female

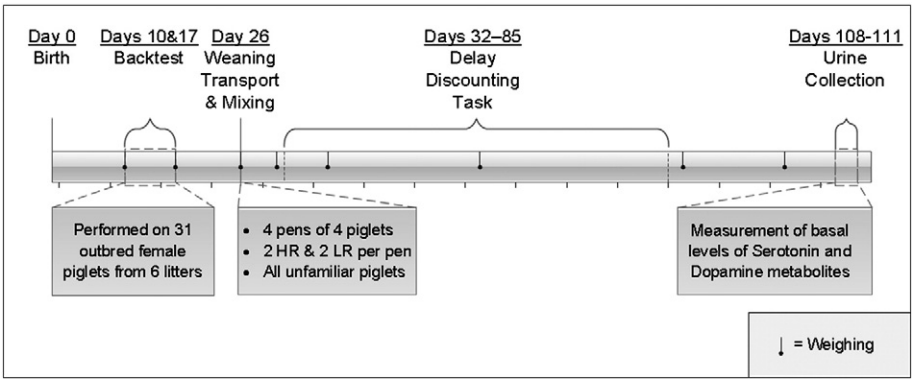

Fig. 1. Experimental design.

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