ARTICLES

Can domestic fowl, *Gallus gallus domesticus*, show self-control?

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An important aspect of cognition is whether animals live exclusively in the present or can anticipate the future. Defined as self-control, the ability to choose a large, remote reinforcer over a small, proximate reinforcer available at the same frequency has been examined in a number of species, often proving difficult to demonstrate. We investigated self-control for food in domestic fowl using a standard two-key operant task and an equivalent two-choice return maze (TCRM) task. When hens chose between a 2-s delay to a 3-s feed access (impulsive) and a 6-s delay to a 7-s feed access (self-control), they appeared unable to discriminate in the TCRM but were impulsive in the operant task. We explored reasons for not choosing self-control in the operant task, first by examining the relation between feed access time and actual feed intake. A second operant experiment examined whether failure to show self-control could be attributed to an inability to combine the delay and access (quantity) reward information associated with choices to reach overall predictions of value. New hens chose between a 2-s delay to a 3-s feed access (impulsive) and either a 22-s delay to a 22-s feed access (standard self-control) or a 6-s delay to a 22-s feed access (jackpot self-control). While hens were impulsive in the standard condition, they showed significant and pronounced self-control in the jackpot condition, eliminating the possibility of an absolute cognitive constraint. Impulsive behaviour can instead be explained by temporal discounting: perceived depreciation of reward value as a function of the uncertainty associated with delay. Implications for welfare are discussed.

Our understanding of the cognitive abilities of livestock has implications for their husbandry, production and welfare. A central assumption of animal welfare is the capacity of animals for basic conscious experience, i.e. subjective awareness of sensations and emotions (Dawkins 2001; Mendl & Paul 2004). Despite justifiable criticism of the perceived link between increasing cognitive complexity and consciousness, hence a greater capacity for suffering (Dawkins 2001), people generally make more positive value judgements regarding animals that show cognitive similarities to humans (Serpall 2004). Demonstration of these attributes is therefore a potentially powerful influence on treatment of animals in society (Mendl &

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Paul 2004). If consciousness is assumed, an animal's cognitive capacities imply circumstances under which its welfare may be jeopardized and potential approaches for mitigation (Bekoff 1994; Nicol 1996). Advancing knowledge in this area could improve confidence in methods of welfare assessment that currently assume various cognitive abilities, for example prediction of the consequences of a response resulting in exposure to a stressor during experiments examining stressors with delayed effects (Abeyesinghe et al. 2001). Furthermore, approaches based on measurement of cognition may provide better indicators of emotion, because the behavioural and physiological measures currently used may dissociate from conscious experience (Harding et al. 2004; Mendl & Paul 2004). Finally, understanding how animals process information about their environment can inform improvements in housing design and management strategies.

Perception and processing of time is an important aspect of cognition with implications for the impact of environmental events on welfare (Duncan & Petherick 1991). For an animal living exclusively in the present,

termination of a stressful event, such as handling, cannot be predicted, rendering it potentially 'all encompassing'. Anticipation of event conclusion may increase predictability and reduce aversiveness (Spinka et al. 1998; Taylor et al. 2002; Mendl & Paul 2004); however, anticipation may also increase vulnerability to pre-emptive stress or anxiety and thwarting of expectations. Perceiving the later consequences of a choice or action grants an animal some control over its environment through informed decision making. The question of such anticipation can be addressed with the self-control paradigm.

Self-control can be broadly defined as the ability to resist immediate gratification for a later benefit and may be associated with the development of self-awareness (Genty et al. 2004). In children a high degree of self-control is correlated with cognitive competence in later life and adaptive long-term developmental outcomes (Metcalfe & Mischel 1999). Impulsive behaviour (the opposite of self-control) is generally regarded as undesirable. Humans sometimes choose the short-term immediate benefit, for example gambling, alcoholism or overeating, despite potentially negative longer-term consequences, for example losing money or ill health. The self-control paradigm has been used to investigate choice behaviour and timing, and to model the occurrence and control of impulsive behaviour, in several species, primarily pigeons, *Columba livia* (e.g. Grosch & Neuringer 1981; Logue et al. 1985; Mazur 2000), rats, *Rattus norvegicus* (e.g. Chelonis & Logue 1997; Chelonis et al. 1998; Evenden & Ryan 1999) and humans (e.g. Logue 1988; Logue et al. 1990; Tobin & Logue 1994), but also nonhuman primates (e.g. Tobin et al. 1996; Beren et al. 1999) and honeybees, *Apis mellifera* (Cheng et al. 2002). In the laboratory, self-control can be defined more specifically as choosing a large reinforcer available after a 'long' delay over a small reinforcer available immediately or after a 'short' delay (Logue et al. 1988; Chelonis & Logue 1996). This is a prospective timing task (Killeen et al. 1997) that requires prediction of the outcome, based on experience, learning and restraint. Both types of reinforcer are offered with the same frequency, so that the subject choosing to wait for the larger reward shows 'self-control' and maximizes gain, whereas the subject choosing the smaller, proximate reward shows 'impulsiveness' and gains far less. Assuming an adaptive animal chooses to maximize fitness (Collier 1982), self-control behaviour indicates an awareness of the near future consequences of current choice.

To investigate the predisposition of hens for self-control or impulsive behaviour, we used mature laying hens with a standard (temporal presentation) operant key-pecking method (e.g. Logue et al. 1985, 1988) and food reinforcement. We assessed the responses of these hens in parallel with a novel two-choice return maze (TCRM) method (spatiotemporal presentation) to examine the influence of the task. While the keypeck response used in the majority of pigeon studies on self-control does not itself appear to predispose to impulsivity compared with a nonautoshaped response (treadle pressing; Chelonis & Logue 1996), behaviour of pigeons in this paradigm can be influenced by various factors (e.g. the presence of neutral cues or the opportunity to make a response during the delay;

Grosch & Neuringer 1981; Logue & Peña-Correal 1984; Peña-Correal & Logue 1984), suggesting that the way in which choices are presented is important. In addition, Timberlake (1988) suggested that impulsivity should be decreased in pigeons making a response associated with a 'general search' behaviour mode, such as locomotion to a location (TCRM), where subjects are physically, as well as temporally, distant from the reward, compared with a 'focal search' mode, such as key pecking, that is more related to actual location and capture of food (as opposed to increasing its likelihood). In two further experiments we examined reasons why hens might show impulsive behaviour in an operant task. Specifically, we tested whether, in practice, longer access times provided proportionately more valuable rewards and whether hens might be cognitively constrained by an inability to combine both time predictions (delay to feed availability) and outcome predictions (duration of feed access time or absolute reward value).

GENERAL APPARATUS

Operant Apparatus

The operant apparatus consisted of a white wooden chamber (0.5×0.5 m and 0.75 m high) with a black rubber floor and a cup drinker fixed to the back wall. A small door in the back wall allowed access into the box. The front panel (Fig. 1) consisted of two 3.0-cm-diameter Perspex response keys symmetrically placed (to prevent bias) 10 cm from the chamber sides and a food trough (internal dimensions $6.5 \times 5.5 \times 5.0$ cm) positioned 6 cm below and centrally between the keys. The keys required a maximum of 1.6 N $\pm$ 10% to operate, and could be transilluminated by 5.2-V halogen light sources to produce red, green or white light (using coloured gel filters) at intensities corrected for perceived brightness according to the spectral sensitivity of domestic fowl (Prescott & Wathes 1999). Food (approximately 6.1 g per operation) was delivered to the food trough from a holding funnel via an electronically controlled pneumatic system which could be operated manually or controlled by computer software. After the scheduled feed
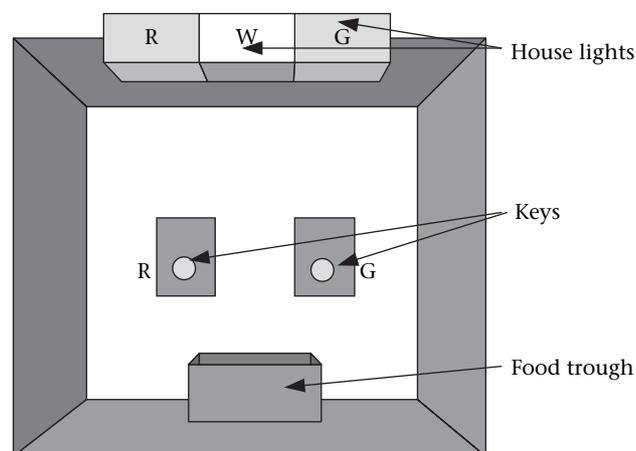

Figure 1. Front panel of the operant cage. Light colours: R: red; G: green; W: white.
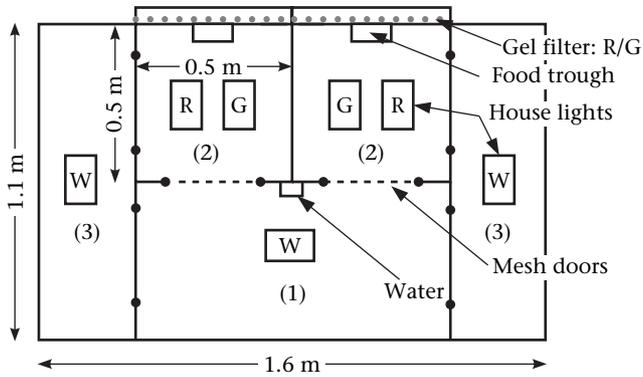
Figure 2. Plan view of the TCRM apparatus. Light colours: R: red; G: green; W: white. The maze consisted of a choice area (1), reinforcement areas (2) and return corridors (3).

access time, the food trough was emptied via a drop-away floor into a container fixed outside the chamber. Three halogen (150-W) house lights were fixed above the mesh roof of the chamber. Coloured gel filters were used to alter one light to green illumination and one to red, also corrected according to the spectral sensitivity of domestic fowl. An overhead camera linked to a VCR and monitor system allowed us to observe and record behaviour.

Two-choice Return Maze (TCRM)

The TCRM apparatus (Fig. 2) was designed as a spatial equivalent of the operant apparatus and, consistent with this, allowed the bird to return to the start without handling, avoiding interference with task performance (Mendl 1999). The TCRM was constructed from plywood painted white with a black rubber floor. It comprised several discrete areas. The choice area (1) allowed access to one of two reinforcement areas (2) via 10-mm-gauge wire-mesh doors on manually operated pulleys. It contained a cup drinker fixed to the wall between the mesh doors and was lit by an overhead white halogen house light (150 W). The mesh doors allowed birds to observe the lighting in the reinforcement areas (2). The back panel of each reinforcement area consisted of opaque pearlescent Perspex and could be alternately lit by two pairs of 150-W halogen lights according to interchangeable red or green gel filters. This allowed the lit cues to be automatically corrected for the spectral sensitivity of the hen when the gel filters were swapped. A feed trough was fixed to the floor in the centre of each back panel. Food delivery and removal systems were identical to those in the operant apparatus. Red and green (via coloured gel filters) halogen house lights (150 W), corrected for the spectral sensitivity of the hen, were also fixed over each reinforcement area. Infrared light beams, set horizontally 15 cm, into the reinforcement areas at a height of 15 cm, recorded entrance of a bird. Solid doors on pulleys allowed birds to exit the reinforcement areas into the return corridors (3) which were lit by further 150-W halogen house lights and led, via a second set of solid doors on pulleys, back to the choice area. All light sources could be controlled

manually or automatically. An overhead camera linked to a VCR and monitor system allowed us to observe and record behaviour.

EXPERIMENT 1: PREDISPOSITION FOR SELF-CONTROL

In this experiment we performed a standard self-control procedure (e.g. Logue et al. 1985, 1988), using the same birds with the operant apparatus and TCRM, to determine predisposition for self-control or impulsive behaviour.

Subjects and Housing

Sixteen naïve ISA Brown layer hens were obtained from a commercial supplier (Country Fresh Pullets Ltd) at point-of-lay and housed in two groups of eight within the same room, one with a further four companions and one with a further seven companions. These birds had been beak-tipped at a few days old as is standard commercial practice to control feather pecking. Standard pelleted layer ration was available ad libitum in 50-kg galvanized feeders modified to allow automatic removal of food at set times. The pens, with wood shavings for bedding, also accommodated automatic drinkers, grit, nestboxes, perches, and barriers to hide behind. Room temperature averaged $15 \pm 4°C$. The light cycle was 14:10 h light:dark. Light intensity was originally at 40 lx, but from 36 days into training we reduced it to 5–15 lx to control sporadic occurrence of vent pecking. Four test birds were temporarily removed from procedures, for up to a week respectively, and isolated to treat minor wounds from vent pecking.

Methods

Birds were allocated to two groups: group 1 were tested in the TCRM and then the operant chamber and group 2 were tested in the reverse order. All birds were given a choice between an impulsive option of a 2-s delay to a 3-s feed access and a self-control option of a 6-s delay to a 7-s feed access. Food obtained operantly was the same as the food provided in the home pen. The feed access times were originally selected to be 2 s and 6 s, in keeping with the delay times used in previous pigeon studies (Logue & Peña-Correal 1985; Logue et al. 1985, 1988). However, several birds were unable to obtain food during only 2-s access, possibly because they were beak-tipped, making small pellets harder to grasp, so we increased both feed access times. The experimental design balanced (operant) key/compartment (TCRM) colour, key/compartment position and the associated delay and feed access contingencies across birds. These conditions remained the same for each bird within and between methods.

Training

Food was removed 6–8 h before every training session. From the start of training the keys and compartments were lit red or green for each individual as they would be during testing and birds were trained to the operant

apparatus and TCRM in the order in which they would be tested. We initially placed hens in the operant chamber or TCRM in pairs for 15 min to accustom them to the apparatus and social isolation. Subsequent training proceeded with individuals. Over a series of training sessions we increased the session length from 10 to a total of 24 free-choice trials randomly interspersed with three forced-choice trials for each option. At the end of any training session, the bird was returned to her home pen where she received ad libitum food not less than 45 min and not more than 120 min post training.

Hens were taught to peck the two lit Perspex keys equally on a fixed ratio = 1 (FR1) food reinforcement schedule with no scheduled delays and 5-s feed access available from both keys. Initially keys were individually lit in a random order with equal numbers of presentations. Response to an unlit key was never rewarded. Next, birds were given a series of free-choice trials, where both keys were available, randomly interspersed with forced-choice trials where only one key was available (the other remaining unlit). The forced-choice trials ensured that the subjects were exposed to the contingencies for each key, regardless of preference. If a side bias became obvious, the next session included extra forced-choice trials for the avoided side. When a bird was reliably pecking both lit keys equally, the delay and feed access times associated with the impulsive and self-control options were introduced. The intertrial interval (ITI), i.e. the time between the start of one trial and the start of the next, was increased over a series of sessions from 0 to 60 s. The ITI duration was dictated by performance in the TCRM (see below), which took longer than the operant task, to maintain comparability. Figure 3 illustrates the procedure for a free-choice trial. In this example, green is associated with the impulsive option and red with the self-control option but other combinations were used. The overhead house lights were used to indicate trial stages. The coloured lighting did not appear to affect intake during access times, so no other illumination was used. Forced-choice trials commenced with only one key lit, leading to the same events as it did in a free-choice trial; the other key remained unlit and pecks on it had no consequences. If a bird did not peck a key within 5 min of the trial start, we aborted the session and returned the hen to the home pen.

Training in the TCRM paralleled training in the operant chamber. Over a series of sessions, individual hens were taught to enter equally the two reinforcement areas on a FR1 food reinforcement schedule (5-s feed access), during which time the areas were lit for each individual as they would be during testing. When a bird was reliably entering both reinforcement areas, the training sessions were structured into a series of free- and forced-choice trials and the associated delay and feed access times were introduced to the reinforcement areas, along with an ITI of 60 s. A free-choice TCRM trial commenced with the individual bird in the white-illuminated choice area with all doors closed. The start of the trial was indicated by the illumination of one reinforcement area back panel with green and one with red light. The reinforcement areas could be seen through the mesh doors. After 3 s, both of
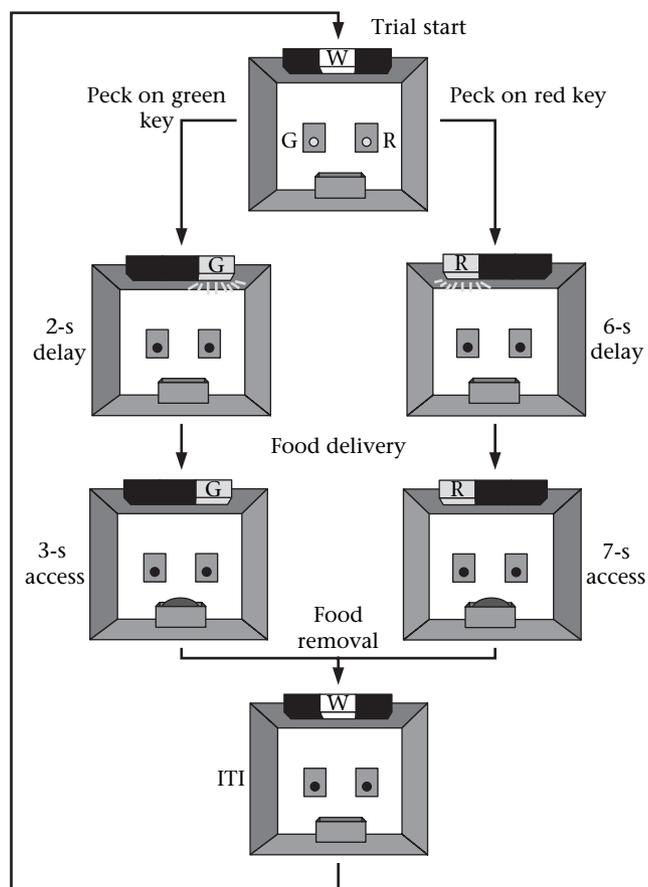

Figure 3. Flow diagram of the procedure for a single operant free-choice trial (total duration 60 s). Light colours: R: red; G: green; W: white. In this example, the green key is associated with impulsivity and the red with self-control. The operant keys are represented by pale grey circles when lit and black circles when unlit. Trial start was indicated by illumination of the red and green keys under the white house light. A peck on the green key darkened the white house light and both keys and initiated flashing of the green house light (1 Hz) for the duration of the delay e.g. 2 s. A peck on the red key darkened both keys and all but the red house light which flashed for a different duration e.g. 6 s. Next, food was delivered and the coloured house light corresponding to the previously pecked key remained constantly illuminated during the associated feed access period (e.g. 3 s for green, 7 s for red). Finally food was removed, the coloured house lights darkened and the white house light illuminated for the remainder of the intertrial interval (ITI).

the mesh doors were raised allowing the bird to enter either area. A registered entry resulted in the mesh door closing behind the bird, the choice area darkening and the coloured house light flashing for the duration of the delay, then remaining constant for the feed access time. If a bird did not make a choice within 5 min, the mesh doors were lowered again and another trial was initiated. If the bird did not enter a choice within a second 5 min, we aborted the session and returned the hen to her home pen. After reinforcement, the coloured house lights were darkened, and the doors to the return corridors and choice area, now illuminated white, were opened. The bird was trained to return to the choice area for the start of the next trial. The doors were shut, and lights darkened behind her as she

progressed. If she did not return within 5 min the operator gently pushed her into the next area.

Testing

Once birds had completed a session of 24 trials in both apparatus sets, they were considered trained. Food was removed 6–8 h before any test session. Daily experimental sessions were conducted in the same way as the final training session and consisted of 24 free-choice trials randomly interspersed with three forced-choice trials for each option with a 60-s ITI. Each bird was tested at the same time each day. The fixed ITI meant that the total access time to food could be increased only by increasing choices for the self-control condition. If a preceding trial took more than 60 s, the next trial commenced immediately. The session terminated after 30 trials or according to the 'abort' criterion used in training and food was returned as in training. The experimental phase for each method was terminated when the hen had completed 10 sessions of 30 trials. A minimum criterion of 20/24 completed free-choice trials was set as the definition of a 'completed session'. The 10 completed sessions required for each method per bird were not always consecutive. A single 'reminder' training session was given in the second experimental phase before to testing with the next task.

Ethical note

This work was regulated under the Animals (Scientific procedures) Act 1986 because of the food deprivation involved in standardizing motivation to perform the self-control tasks. However, when experimenting, food was removed only temporally, not absolutely, and was available ad libitum when access was allowed, i.e. for a minimum of 6 h continuously during the light part of the cycle and unlimited access over weekends. We monitored body weight daily for experimental animals and weekly for companion animals. A minimum variation of 10% body weight within the group at any one time was expected, together with changes in individual body weights over the laying cycle. Removal of birds from procedures was a predetermined intervention in the event of body weight dropping on any two of the following criteria: (1) to 20% below the mean weight of experimental birds undergoing the same procedure; (2) to 20% below the mean weight of nonexperimental birds at the same stage in the laying cycle; (3) to 20% below the individual bird's body weight before the experimental procedures. These criteria were set in consultation with the Named Veterinary Surgeon, the Named Animal Care and Welfare Officer and the Home Office Inspector. No birds required removal from the experiment under these criteria.

Data analysis

We calculated the proportions of free self-control choices made in each completed session for each bird for each task. We used Genstat 5, release 4.1 (4th edition) for Windows (1998 Lawes Agricultural Trust IACR, Rothamsted, U.K.) to analyse these data on the natural scale with an analysis of variance (ANOVA) after the approach taken by studies of similar design (Logue & Peña-Correal

1985; Chelonis et al. 1998). Diagnostic plots of the residuals confirmed that no transformation of the data was necessary. Trials not completed ($\leq 4/24$ per session) were treated as missing data. The blocking structure of the ANOVA was a split-plot design as follows, with each factor nested within its preceding factor to describe the data: 'set' (two) of replicate birds within a group, 'group' (two) according to which method the bird was tested with first, 'bird' (eight) within a group, 'task' describing from which task the data were derived and 'session' (10 per task). The treatment structure examined the effects of order of testing, task, session and interactions as well as considering a first-order polynomial contrast for session (i.e. a simple linear regression for a change in response with respect to time). The factors in the treatment structure were arranged using Genstat notation as follows: order*method*pol(session;1), where 'pol' is short for polynomial contrast. A proportion of 0.5 self-control would be expected of subjects choosing randomly. We calculated significant differences from chance (King & Logue 1990) by subtracting the estimated means (from the analysis) from the expected value of 0.5 and dividing the result by the standard error of the estimated mean. These values were compared to the t distribution values (two tailed) for the associated degrees of freedom.

Results

The number of training sessions before qualifying for experimental testing (reinforcement received on 24 trials) varied between individuals, but an average of seven sessions was required for the operant task and six sessions for the TCRM. Of the 16 birds tested, one bird completed only nine of the 10 TCRM sessions and one completed only one of the 10 operant sessions. No within-session trends in choice were observed for either task. The analysis indicated no effect of order of method testing on the proportion of self-control shown by birds (ANOVA: $F_{1,1} = 2.67$, $P = 0.35$). The overall mean $\pm$ SD proportions of self-control shown by birds in the two tasks were 0.45 $\pm$ 0.20 for the TCRM and 0.29 $\pm$ 0.26 for the operant chamber. Figure 4 illustrates the interaction (ANOVA: $F_{9,242(10)} = 3.14$, $P = 0.001$) between task and successive sessions (standard error of differences between the means, SED = 0.08, $df = 62$, except comparing within the same task, where SED = 0.06, $df = 242$). The first-order polynomial regression indicated that this effect could be attributed to linear trends across the 10 sessions which differed for the two methods (ANOVA: $F_{1,242(10)} = 25.37$, $P < 0.001$). The proportion of choices for self-control stayed consistent in the TCRM, but progressively declined over sessions in the operant cage. The mean proportions of self-control choices in the operant task were significantly lower than 0.5 for sessions 3 ($P < 0.05$), 4, 6 ($P < 0.01$), 5 and 7–10 ($P < 0.001$). However, choices in the TCRM did not differ significantly from random.

Discussion

With the time conditions tested, birds behaved impulsively in the operant apparatus but showed no
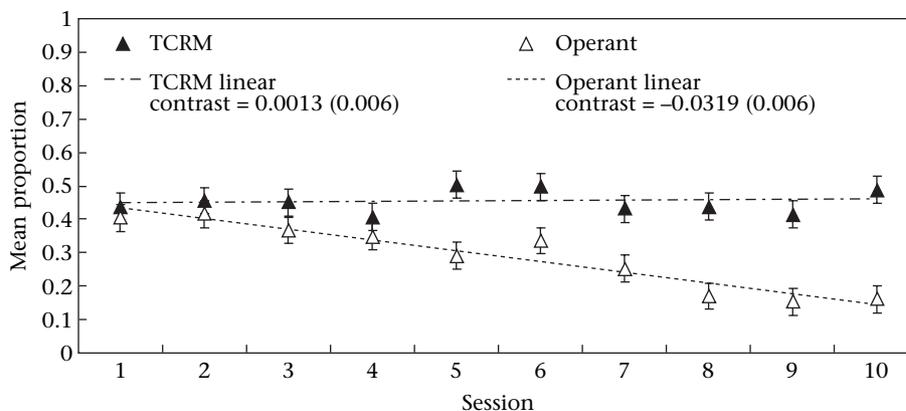
Figure 4. Experiment 1. Mean ± SE proportion of choices made for the self-control (6-s delay to 7-s feed access) option over 10 sessions in each of the TCRM and operant tasks and associated linear contrasts. Numbers in parentheses are standard errors for the linear contrasts.

predisposition for self-control or impulsivity in the TCRM. Without further work it is not possible to ascertain whether choices in the TCRM were active or whether hens chose randomly as a result of not learning the compartment contingencies, but the latter is suggested by the consistency between sessions. The decrease in self-control over operant sessions might be explained by either (1) progressive learning, as birds were not tested until their responses were stable, or (2) progressive frustration, resulting from the intertrial interval, promoting impulsive behaviour. Grosch & Neuringer (1981) showed that provision of an independent distraction task to perform during waiting intervals promoted self-control. The operant task findings suggest that self-control behaviour of hens is low compared with pigeons performing the same task (Logue & Peña-Correal 1985; four subjects, mean proportions of choices for self-control ranging from 0.50 to 0.80).

There are a number of possible reasons for the lack of self-control of hens in our first experiment, which we explored in further studies. First, it was possible that our assumption, based on previous work (Logue & Peña-Correal 1985; Logue et al. 1985, 1988), that 7-s access to food was proportionately more valuable to a hen than 3-s feed access was flawed. If so, it would make no sense for hens to choose to wait. We examined this in experiment 2. Second, certain methodological aspects may have interfered with discrimination and learning, in particular presentation of the same amount of food for both options and the potentially aversive periods of darkness corresponding to the flashing house lights. Third, there may be a cognitive constraint on the hens' abilities to process future outcomes. The fact that hens did choose the impulsive option with a 2-s delay indicates that they can predict differences in short time intervals, but perhaps they may be unable to combine predictions of both time (delay) and value (access) to reach the self-control decision. Fourth, hens may have discounted the value of the temporally distant reward. Impulsive behaviour has been explained using temporal discount functions that mathematically describe how the perceived value of a reward is depreciated because of the uncertainty (cumulative probability of loss) associated with its delay (Rachlin 2000). Thus, depending on the absolute values of both rewards,

the perceived value of the reward further removed in time may be depreciated enough to render it less desirable than the proximate reward. In experiment 3 we addressed these possibilities by incorporating some methodological modifications, increasing the self-control access times and setting a self-control condition which would allow us to distinguish between an absolute cognitive constraint and temporal discounting.

EXPERIMENT 2: VALUE OF FEED ACCESS TIMES

We used eight new operant-trained Hyline Brown adult layer hens to investigate whether increasing access times allowed a proportionate increase in the amount of food consumed. These beaked-tipped birds were obtained from Deans Food Group Ltd at point-of-lay along with 22 additional birds. We used Hylines in experiments 2 and 3 because of the previous vent-pecking problems with the ISA Browns. In this experiment, possible strain differences were not expected to affect the amount of food obtained during short feed access periods. Housing and food regime were the same as for experiment 1 except that the lights remained undimmed. Recorded amounts of standard pelleted layer ration were immediately delivered to individual birds on pecking of the lit operant keys (Fig. 1) in dummy trials scheduled at 60-s intervals. Feed access times of 2–30 s were randomly allocated to trial number. We weighed food remaining after each access period. Data were collected in two replicates per bird. Figure 5 shows the results. There was a clear linear relation between access time and food consumed, indicating that an estimated 0.37 g was obtained during 3-s feed access and 0.85 g was obtained during 7-s feed access (2.3 times as much food). Therefore, the original assumption that an increase in feed access time allowed birds to obtain a proportionately greater amount of food was supported.

EXPERIMENT 3: SELF-CONTROL UNDER STANDARD AND 'JACKPOT' CONDITIONS

The premise of this experiment was that if hens discount the value of the more temporally distant reward and we
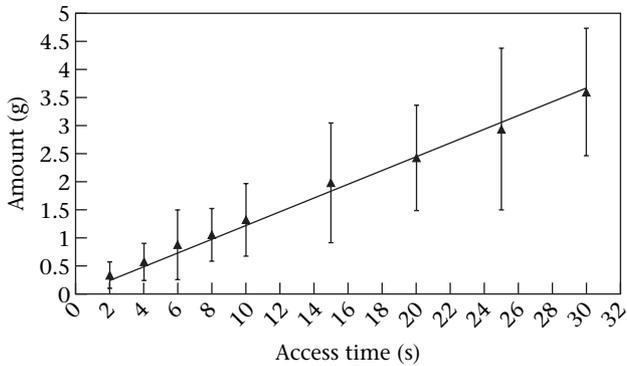
Figure 5. Relation between food access time and amount of food ($\overline{X} \pm$ SD) that hens consumed.

disproportionately boost its actual value to take into account any perceived depreciation, it should represent a jackpot win to the hen and she should show self-control. If, however, she is constrained in her cognitive ability to process reward value and delay to obtain a combined outcome, she should remain impulsive. To test this, we introduced a jackpot condition to the previous self-control procedure, where eight naïve birds were given the choice between the impulsive condition from experiment 1 (a 2-s delay to a 3-s feed access) and a 6-s delay to a 22-s feed access (jackpot). A second group of eight birds was maintained as a control and tested with a 'standard' condition: choosing on a similar ratio regime to experiment 1, between a 2-s delay to a 3-s feed access (impulsive) and a 22-s delay to a 22-s feed access. A mean estimated food intake of 0.37 g could be obtained during a 3-s access and 2.69 g during a 22-s access (Fig. 5). Four birds from each group had been used in experiment 2.

Methods

For this experiment, we modified the operant apparatus. The rubber floor was replaced with 1.5-cm-gauge wire mesh allowing substrate to drop through and not distract the subject. To aid discrimination, we replaced the pneumatic feeder with a motorized conveyor feeder, which allowed separate specification of the amounts of food made available for each option, i.e. means of 6.1 g for 3-s feed access and 20.8 g for 22-s feed access. To investigate whether a distraction task would promote self-control, we attached a small foraging trough (38×15 cm and 10 cm deep) filled to a depth of 1 cm with shavings from the home pen to the back wall of the operant cage under the drinker. Half of each group of birds (jackpot and standard) were further assigned to this second treatment to produce a 2×2 factorial design. Thus, there were four treatment groups: jackpot + foraging trough (JF), jackpot + no foraging trough (JN), standard + foraging trough (SF) and standard + no foraging trough (SN). Birds were familiarized with the trough before the experiment.

The experiment was run as previously except for the addition of the foraging trough for those birds allocated to the distraction task and maintenance of the white house light throughout the session to avoid dark periods during the flashing signals. In this experiment, sessions were restricted by the larger reinforcements to 16 free-choice trials, randomly interspersed with two forced choices for each option (the ratio of forced to free choices therefore remaining the same as for experiment 1). To account for the possibility of a learning curve, we continued testing birds until they met the following stability criterion after a minimum of 10 complete sessions: within the last five complete sessions the total number of choices for self-control (per session) differed only by a range of two choices across the five sessions and each consecutive session differed by no more than one choice. For example, a bird could choose self-control (out of 16 free choices) on consecutive sessions 15, 15, 14, 15, 16, but could not choose 15, 15, 14, 16, 15. This criterion ensured that responses were within an expected standard deviation for the five observations. Previous studies (e.g. Logue et al. 1985; Chelonis et al. 1998) were not followed because consistency of responding was not sufficiently determined by the criterion used: a bird commencing with a large range in response could stabilize more quickly and within a greater variability of stabilized values than a bird commencing with a narrow range.

We calculated the proportions of free self-control choices made in each of the final five stable responding sessions for each bird (Logue & Peña-Correal 1985; Logue et al. 1985, 1988; Chelonis et al. 1998) and again used Genstat 5 to analyse these data statistically on the natural scale with an ANOVA, as diagnostic plots of the residuals confirmed that no transformation was necessary. The blocking structure of the ANOVA was set/bird/session where set described the replicates (two) per group, bird described subjects within a subgroup (four) and session described the five stable sessions for each bird. The treatment structure examined the effects of the two self-control conditions, provision of the foraging trough as a distraction task and the interaction.

Results

It took 6–22 training sessions for individual birds to meet the criterion for testing. Within a 12-week limit on testing, seven of eight birds in the jackpot group and all eight in the standard group met the test stability criterion. The number of completed test sessions to achieve this varied considerably from 10 to 42, but was generally greater for standard birds. The overall mean proportions of self-control shown by jackpot and standard test groups were significantly different (0.93 versus 0.22, respectively; ANOVA: $F_{1,10(1)} = 42.33$, $P < 0.001$) and also differed significantly from random choice (0.50) by $P < 0.001$ and $P < 0.01$, respectively. Figure 6 shows the mean stable responding values for individuals. We calculated the mean proportions of self-control choices at which we could confidently say an individual bird was showing self-control or impulsive behaviour at a level significantly different ($P < 0.05$) from random choice, using a conservatively estimated standard error based on five stable sessions comprising 8/16 choices for self-control. These values, 0.66 choices and above for self-control and 0.34
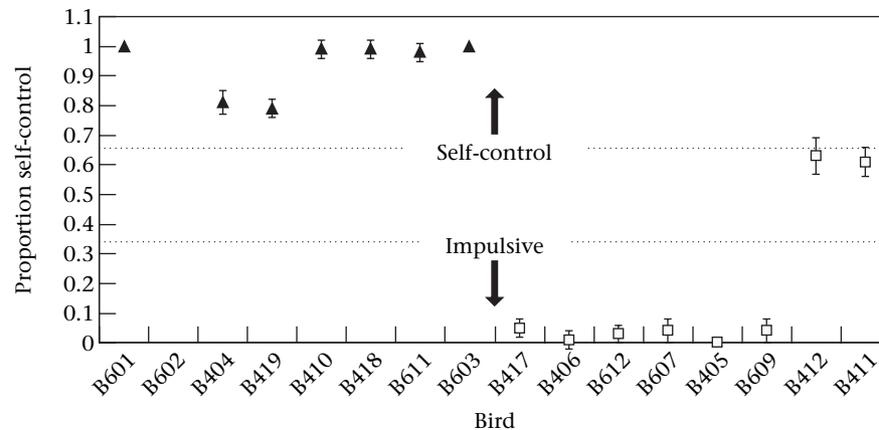
Figure 6. Experiment 3. Mean ± SD stable responding (over five final sessions) proportions of choices for the self-control option for each of the 16 birds. ▲: Jackpot group (self-control; a 6-s delay to a 22-s feed access); □: standard group (self-control: a 22-s delay to a 22-s feed access).

choices and below for impulsivity, are represented by dotted lines in Fig. 6. Using these criteria, we can say that all seven birds reaching stability in the jackpot group showed significant self-control and six of the eight birds reaching stability in the standard group were significantly impulsive. No significant within-session trends were observed in the standard group, but there was a tendency for jackpot group birds to choose more impulsively towards the end of test sessions, probably as they became satiated on the large rewards. There was a tendency for birds that reached stable responding soonest also to respond most extremely, i.e. towards self-control proportions of 0 or 1. There was no main effect of provision of the foraging trough on mean proportion of self-control choices (present: 0.49; absent: 0.65; ANOVA: $F_{1,10(1)} = 2.16$, $P = 0.172$) or interaction (JF: 0.87; JN: 0.99; SF: 0.12; SN: 0.32; ANOVA: $F_{1,10(1)} = 0.15$, $P = 0.707$).

Discussion

The high degree of self-control demonstrated by the jackpot group rules out the possibility that hens were impulsive in experiment 1 because they were unable to process time and quantity information to obtain outcome predictions. Instead, since standard birds were impulsive overall, this ability may be ruled by incentive, temporal discounting and availability of discrimination learning aids. The two indifferent standard birds might have been unable to discriminate between options or they might have been extremely slow at obtaining food and thus disposed to choose the longer access more often. In our experiment, there appeared to be no role for distraction in promoting self-control. This apparently contradicts previous findings (Grosch & Neuringer 1981; Metcalfe & Mischel 1999), but only if it is assumed that the foraging trough drew attention away from the reinforcers. In fact, hens given the trough did not consistently direct foraging behaviour towards it and it is possible that birds motivated to perform the self-control task did not find such foraging sufficiently like the reinforced response. A more appropriate response, such as an independent key like

that used by Grosch & Neuringer (1981), may have worked better. However, although not recorded, it is possible that birds were using other behaviour, such as pecking on the unlit keys or circling before the keys, as a self-distraction or timing mechanism (Killeen & Fetterman 1988). If so, the success of such individual strategies may partially explain individual differences in self-control behaviour.

GENERAL DISCUSSION

This study used the self-control paradigm as a tool to investigate the cognitive ability of domestic hens to anticipate future outcomes. Successful performance required hens to discriminate time delays and reward magnitudes based on previous learning, combine this information into predicted outcomes and then show self-restraint in choosing to wait an unnatural period of 'dead time' for the greatest payoff. Our findings have demonstrated first, that hens can discriminate between short time periods; second, that there is no absolute cognitive deficit preventing the hen from comprehending later consequences of food choices; and third, that there does appear to be some reduction in the perceived value of a food reward as a function of its delay.

To our knowledge, the self-control paradigm has not previously been used to investigate cognition per se. Rather, it has been used to model choice between delay and outcome trade-offs. The difference is subtle, but has meant that previous studies finding failure to show self-control have not examined why in the systematic way we adopted, that is, assuming inappropriate test procedures as opposed to cognitive failure in the first instance. Collier (1982) has pointed out that analyses of choice and cognitive capacities have been jeopardized by failure to construct test environments that yield the appropriate consequences to animal behaviour, i.e. those they are designed to predict. This has been a criticism of the self-control paradigm, especially as results from the operant laboratory are often inconsistent with behaviour predicted by optimal foraging theory (Stephens & Anderson 2001). Although animals are assumed to have evolved to maximize

gain from environmental resources at minimum cost (energy, time, etc), they may be using short-term or simple proximate rules to make decisions (Stephens & McLinn 2003). The outcomes of these rules may closely correlate with long-term gains in the natural environment, but may no longer work to maximize gains in an artificial environment, far removed from those in which progenitor species evolved. Careful examination of test environments that allow the subject to predict consequences of choices and those that do not could begin to reveal the nature of rules governing an animal's decision-making process and perhaps allow us to fine tune harmony between livestock and husbandry environments.

Stephens et al. (Stephens & Anderson 2001; Stephens & McLinn 2003) have begun this comparison by investigating responses of blue jays, *Cyanocitta cristata*, in patch-foraging and self-control paradigms. They discussed how discounting functions fitted to self-control data typically show a loss of 10–50% of the absolute reward value with the first second of delay (Mazur 2000), which seems excessive, and how a short-term decision rule may account for the contradictory behaviour seen in both paradigms. Unfortunately, it is difficult to compare their self-control context with our study because their intertrial interval was a fixed period at the beginning of the trial, rather than one spanning the beginning of one trial to the next. A small proximate reward was therefore more frequent than a larger distal one, so choosing the latter did not always lead to maximization in the long term. We deliberately avoided any ambiguity so that maximization was always associated with self-control. It is worth noting that contradictory findings between the self-control and foraging paradigms may also be explained by their different choice decision points (M. Bateson, personal communication), because learning occurs by retrospective assignment of value to the cue, at the time when food is encountered (Kacelnik & Bateson 1996). This is consistent with findings that, for the self-control paradigm, the delay-to-reward immediately following choice has almost exclusive weight in the decision process (Logue et al. 1985), whereas in the foraging paradigm subjects appear to base decisions on a period equating to the postchoice ITI and delay-to-reward combined (Stephens & McLinn 2003). Clearly care must be taken in comparing paradigms.

To date, research on temporal cognition in gallinaceous species has been extremely limited (see Izawa et al. 2003 for a neurological study). Taylor et al. (2002) investigated estimation of a learned time interval, concluding that domestic hens may be able to estimate a 6-min delay to reward when given a reliable visual cue. Prediction and control of events can reduce stress (Wiepkema & Koolhaas 1993). The capacity to estimate time allows prediction of events, but discrimination is required before different outcomes can be weighed up, facilitating an animal's control of its environment. The abilities of hens to estimate and discriminate time may differ with the order of time (seconds, minutes, hours, etc.), type of task (e.g. retrospective, current or prospective) and the type of cues involved. Sensitivity to what we perceive as short periods may be more important to some animals because of factors such as their life span, metabolic rate,

environmental variability, frequency of predation or food opportunities. Rather than a shortcoming, predictions further into the future may simply not be useful. Our findings dispute Roberts's (2002) explanation for failure of animals to show self-control: that animals are unaware of the future. Impulsive behaviour in hens can instead be explained by temporal discounting.

There is inherent uncertainty in obtaining delayed outcomes (Leonard & Fisher 1988) because of interruptions such as predator attack, competition or food spoilage. There may also be added value in early gains, because time is saved for other occupations (Kacelnik & Bateson 1996). If the probability of loss accumulates with time and other priorities demand the animal's time, then overvaluing more immediate outcomes, or undervaluing more delayed outcomes may be an adaptive response in an uncertain world (Kagel et al. 1986), allowing animals to make foraging decisions and prioritize behaviour to maximize energy and time usage, while minimizing the load on information processing. Such a mechanism is likely to be useful generically. Indeed, Devenport & Devenport (1994) proposed a similar mechanism (Temporal Weighting Rule) for prioritizing information about unstable patch resources according to recency. Discounting is also implicated in the Iterated Prisoner's Dilemma of social cooperation and reciprocation (i.e. duration before return on a cooperative act determining continued cooperative acts; Stephens 2000).

While it is unlikely that discounting and resulting impulsivity are under conscious control, inhibition of impulsiveness may require a greater degree of awareness (Gifford 2002) and attention. Pigeons generally perform impulsively in a self-control task; however, Logue et al. (1984) found that birds that experienced a 'fading procedure' (whereby the delay to the small reinforcer is gradually decreased from a value equalling the delay to the large reinforcer) could generalize this learned behaviour to show self-control under different delay and access conditions. An ability to inhibit impulsiveness allows an animal flexibility to adapt its behaviour. Barkley (1997) proposed that such inhibition facilitates higher cognition through reducing control of basic motor system responses by current environmental stimuli with emotional value and by interrupting ongoing behaviour that is proving ineffective. A link between emotion, impulsivity and self-control may render this paradigm a potential cognitive indicator of subjective state (Mendl & Paul 2004) in species that can show self-control. Metcalfe & Mischel (1999) implicated stress in reduced ability to show self-control.

There are additional welfare implications associated with our findings. First, public perception of the domestic hen may be positively influenced with this demonstration of greater cognitive capacity then normally attributed to her. The comparison with humans is perhaps inappropriate but inevitable. Human children under 5 years of age appear to struggle with a self-control problem (Logue 1988), although self-control is usually tested in a one-off trial, which is not possible with hens because they cannot be told what the options are. Second, although how far into the future hens can mentally travel has yet to be

determined, we now know that they are not completely 'stuck in time' (Roberts 2002). This finding supports continued confidence in methods of welfare assessment that assume hens can make informed choices, at least for the short term.

The ability to anticipate events may be associated with the capacities for pre-emptive anxiety and for generation and frustration of expectations. If this is the case, then cues and time preceding the occurrence of stressful events should be minimized and daily routines (e.g. feeding time) should remain temporally consistent. Using different types of task to estimate and discriminate the same time intervals may help to determine more closely where hens 'reside' in a temporal sense (i.e. how far into the past or future they can perceive; Duncan & Petherick 1991), how they perceive duration depending on context and what cues may be relevant. Depending on sensitivity to the period involved, event durations could then be signalled (Taylor et al. 2002) to enhance predictability and control of the environment and to aid decision making, for example, in the hen's allocation of time to resources. Mechanisms of reducing the perceived duration of an unpleasant event, potentially mitigating stress, are also plausible given findings that self-control in pigeons is facilitated by a task to perform during the wait (Grosch & Neuringer 1981; Metcalfe & Mischel 1999) and that it is possible to distract chickens from pain using attentional shifts (Gentle 2001).

We conclude that domestic hens are capable of rationally discriminating near future outcomes of choice in a self-control food-reinforced operant pecking task when the perceived reward value is sufficiently great. The nature and extent of this cognitive ability requires further investigation: in greater understanding lies the potential to predict and mitigate circumstances that may impair welfare and to facilitate those that may enhance it.

Acknowledgments

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