Domestic hens succeed at serial reversal learning and perceptual concept generalisation using a new automated touchscreen device

Rachel Degrande, Fabien Cornilleau, Léa Lansade, Plotine Jardat, Violaine Colson, Ludovic Calandreau

HAL Id: hal-03753546
https://hal.inrae.fr/hal-03753546

Domestic hens succeed at serial reversal learning and perceptual concept generalisation using a new automated touchscreen device

Rachel Degrande [a,*], Fabien Cornilleau [a], Léa Lansade [a], Plotine Jardat [a], Violaine Colson [b], Ludovic Calandreau [a]

[a] CNRS, IFCE, INRAE, Université de Tours, PRC (Physiologie de la Reproduction et des Comportements), F-37380 Nouzilly, Indre-et-Loire, France
[b] INRAE, LPGP (Laboratoire de Physiologie et Génomique des Poissons), Campus de Beaulieu, F-35042 Rennes cedex, Ille-et-Vilaine, France

ARTICLE INFO

ABSTRACT

Improving the welfare of farm animals depends on our knowledge on how they perceive and interpret their environment; the latter depends on their cognitive abilities. Hence, limited knowledge of the range of cognitive abilities of farm animals is a major concern. An effective approach to explore the cognitive range of a species is to apply automated testing devices, which are still underdeveloped in farm animals. In screen-like studies, the uses of automated devices are few in domestic hens. We developed an original fully automated touchscreen device using digital computer-drawn colour pictures and independent sensible cells adapted for cognitive testing in domestic hens, enabling a wide range of test types from low to high complexity. This study aimed to test the efficiency of our device using two cognitive tests. We focused on tasks related to adaptive capacities to environmental variability, such as flexibility and generalisation capacities as this is a good start to approach more complex cognitive capacities. We implemented a serial reversal learning task, categorised as a simple cognitive test, and a delayed matching-to-sample (**dMTS**) task on an identity concept, followed by a generalisation test, categorised as more complex. In the serial reversal learning task, the hens performed equally for the two changing reward contingencies in only three reversal stages. In the dMTS task, the hens increased their performance rapidly throughout the training sessions. Moreover, to the best of our knowledge, we present the first positive result of identity concept generalisation in a dMTS task in domestic hens. Our results provide additional information on the behavioural flexibility and concept understanding of domestic hens. They also support the idea that fully automated devices would improve knowledge of farm animals' cognition.

Implications

Understanding farm animals' cognitive capacities is important for improving their welfare. However, information about the cognitive range of many farm animal species, notably poultry, is limited. This study focuses on developing an automated device relevant to farm animals with the aim of testing a larger range of cognitive capacities. We have developed an automated touchscreen device adapted for large-range cognitive testing in domestic hens. Through this device, we collected results that suggest that laying hens possess concept generalisation abilities, thus stressing the interest in applying complex cognition testing devices to farm animals.

Introduction

From a welfare perspective, improving farm animals' living conditions depends on our knowledge of how they perceive and interpret their environment, which in turn depends closely on their cognitive abilities (ANSES, 2018). The cognition of farm birds is relatively poorly studied even though they are the most abundant farmed animals in the world (FAO, Global Livestock Distribution Data). Among farm birds, the majority of cognition studies have focused on domestic hens, mainly chicks (Garnham and Løvlie, 2018; Vallortigara, 2006, 2021). A few studies have suggested that domestic hens may possess complex cognitive capacities such as retrospective metamemory (Nakamura et al., 2011) or transitive inference (Daisley et al., 2010). However, there are still many capacities to explore in this species, and the methods to study its cognitive modalities still need to be developed.

A strong relationship exists between the range of cognitive abilities of a given species and its ability to cope with environmental variability. On one hand, behavioural flexibility is the ability to adapt one's behaviour in response to environmental contingencies (Brown and Tait, 2010), which underlies a wide range of adaptive behaviours. For example, individual recognition of social conspecifics and a flexible memory of their hierarchical position are suited to group living and allow for saving energy in terms of cognitive demand and stress response (Elgar and Riehl, 2021). On the other hand, concept understanding requires the discrimination and generalisation of a rule to many stimuli for which the same behaviour can be applied (Smith et al., 2012; see Versace et al., 2017 in chicks). It enables animals to cope with novelty in their physical environment, thus reducing unpredictability and subsequent related stress. Behavioural flexibility and concept generalisation are the two main components of adaptive capacities in animals. Investigating these capacities facilitates an approach to more complex cognitive capacities. Meanwhile, it offers solid ground to suit husbandry practices to animals' behavioural needs and welfare by understanding how animals cope with environmental variability.

Automated testing devices are an effective approach to explore the cognitive range of a species (Livesey et al., 1972; Gabor and Gerken, 2012). Several automated devices have been developed to investigate or operate simple cognitive tasks in farm animals, such as discriminative learning, notably from the cognitive enrichment perspective (for example in goats: Langbein et al., 2008; in pigs: Zebunke et al., 2013). More specifically, a few screen-like devices have been developed with the aim of operating tasks that require more complex cognitive capacities in farm animals, such as relational learning or concept understanding tasks. Some of these devices have proven effective in fish (Kleiber et al., 2021), horses (Gabor and Gerken, 2010), goats (Meyer et al., 2012), and laying hens (Werner et al., 2005). Automated testing devices remain particularly underdeveloped for farm birds (for a review on farm animal cognition tests, see Bushby et al., 2018). There may be a vested interest in copying screen devices used for primate cognition, for example, because they are automated and flexible enough to easily set up many cognitive tests of increasing complexity (Rowe and Healy, 2014; Calapai et al., 2022). This would allow the exploration of farm animals' cognitive capacities, such as self-control (Beran, 2018), concept understanding (Zentall et al., 2008), and more broadly relational learning and retrieval.

In domestic hens, most cognition tests have been conducted with three-dimensional (3D) apparatus, from the arena and mazes to operant boxes, including detour task structures and location- or object-choice tests (for a review, see Garnham and Løvlie, 2018). In screen-like studies, uses of automated devices in domestic hens, mainly as part of delayed matching-to-sample procedures or stimuli discrimination procedures, are few (but see specific research based on imprinting process in chicks: Zanon et al., 2021). Ryan and Lea (1994) and Deakin et al. (2016) developed non-automated screen-pecking tasks using computer-coloured slides. Forkman and Vallortigara (1999) used an automated system with infrared beams to detect chicks' pecks at symbols displayed on a computer screen. More recently, Dudde et al. (2018) used a touch-kit automated device coupled with a simple screen, in which pecks on the monitor were detected by a mesh of infrared lights from a frame laid over the monitor screen.

We developed a standardised and fully automated touchscreen device for domestic hens, enabling a wide range of test types from low to high complexity under standard conditions. The aim of this study was to introduce and perform experiments with our device using two cognitive tests from existing procedures. The first test was a discrimination learning task followed by a serial reversal learning task (**SRL**), which is classified as a simple cognitive task as it demands procedural learning. The second test is a delayed matching-to-sample (**dMTS**) task followed by a generalisation test for the concept of identity, which is classified as more complex as it demands flexible working memory, a declarative report of the response, and concept understanding. Both tasks typically require the individual to use a given stimulus to conduct its behaviour on a one-trial scale and, at the same time, to use a more general understanding rule asked throughout the task. For the SRL task, we expected a decline in performance from the discrimination to the first reversal learning stage (i.e. more sessions needed to reach the criterion in the first reversal stage) and an increase in performance through the next reversal stages (i.e. fewer sessions needed to reach the criterion in the following stages) (see for example, Brushfield et al., 2008). For the dMTS task, we expected an increase in performance during training (see for example, Cook and Wasserman, 2007). In the generalisation test, we did not have any expectations because concept generalisation through a dMTS task has not yet been described in domestic hens.

Material and methods

Animals and housing

The two experiments involved nine and six Isa Brown laying hens, respectively (1–3 years old) maintained at the Pôle d'Expérimentation Avicole de Tours where the experiment was performed (UE PEAT, INRAE, 2018. Experimental Poultry Facility, https://doi.org/10.15454/1.5572326250887292E12). The hens were maintained in a social group of 21 hens on a 6 am to 8 pm daylight cycle, with water ad libitum. Every day when the experiments were completed, food was provided at will. Hens had access to a barn (25 m²) equipped with nesting boxes, perches, and wood chip litter and to an outside enclosure (approximately 30 m²) enriched with perches. All experiments were conducted in the morning between 7 am and 10 am.

Apparatus

Subjects were tested individually in a playbox (44.5 × 65 × 52 cm) made of condensed wood without direct contact with or view of the experimenter to avoid any influence of the experimenter on its behavioural response. A grid ceiling allowed the experimenter to control the hen's behaviour when needed. A screen (25 × 25 cm) linked to a computer was located at one end of the box. This screen was surmounted by nine sensible cells (8 × 8 cm) that could be independently activated. At the bottom of the screen, a feeder (5 cm diameter × 3 cm depth) was used to automatically deliver mealworms as rewards. A lamp was placed 50 cm above the screen to illuminate the box (260 lx). The playbox was located on a table in a room that was independent and adjacent to the hens' aviary. The items on the screen were computer-coloured filled circles of 7.5 cm diameter. The apparatus, playbox, and the screen are illustrated in Fig. 1. The procedures described below was automated. At the beginning of the procedure, hens had been experienced with the apparatus, that is, they had been familiarised with the apparatus and to peck at different items on the screen for food.

Testing procedures

Discrimination and serial reversal learning

Nine individuals were tested in a four-stage procedure including a discrimination task (stage 1), followed by three reversal stages (stages 2, 3, and 4). Stage 1 consisted of discriminating between a green- and a red-filled circle presented on the screen (Fig. 2). Four hens were rewarded when they pecked at the green circle and five hens when they pecked at the red circle. The hens
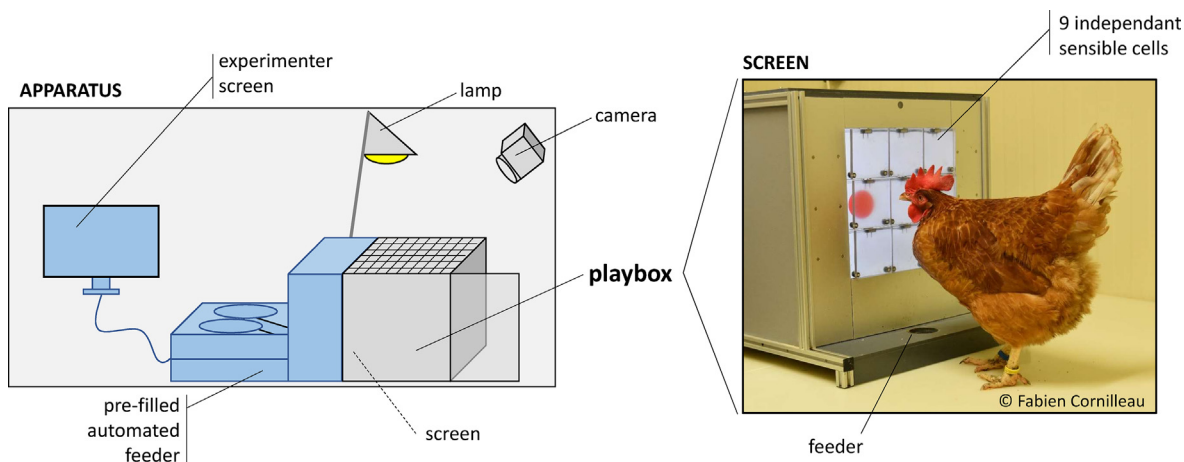
Fig. 1. Schematic view of the testing device used for the two procedures. The photograph illustrates the hen's *(Gallus gallus domesticus)* positioning when facing the screen at every trial. The apparatus system and the corresponding software were built by © Imetronic. Photograph courtesy of Fabien Cornilleau.
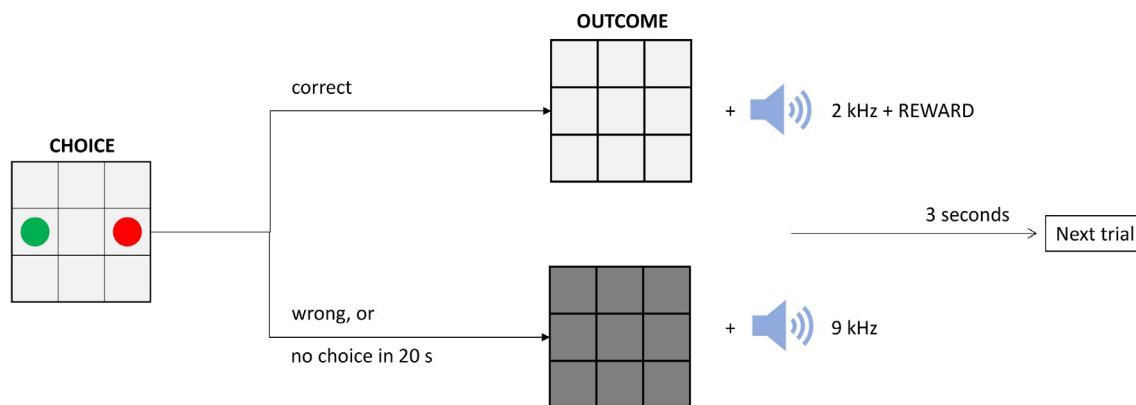

Fig. 2. Schematic view of the successive screens during the serial reversal learning task (SRL). The two filled circles are presented in the middle left and right sensible cells of the screen. The hen stood in front of the screen and pecked at a filled circle on the screen. A peck at the correct colour induced a reward delivery accompanied by a 2 kHz sound and a white screen. A peck at the wrong colour induced no reward delivery and a black screen accompanied by the 9 kHz sound.

then underwent three successive reversal learning stages: pecking at the non-rewarded colour during the previous stage was now rewarded (e.g. pecking at the red circle if they had to peck at the green circle at the previous stage). Individuals had to meet the criterion of 80% of success in two consecutive sessions to move on to the following stage, with a maximum of 49 sessions for the overall procedure.

Each hen was individually subjected to one session of 30 trials per day, with an inter-trial interval of 3 s. A correct response was always accompanied by a reward of two mealworms, a 2-second 2 kHz sound (62 dB), and a white screen. An incorrect answer was always accompanied by a 2-second 9 kHz sound (51 dB), dark screen, and no reward. A cut-off was set when the hen did not peck at the correct item within 20 s, and the trial was recorded as failed. Item presentations were pseudo-randomised and presented equally on the left and right sides for each session, with the rewarded stimulus presented no more than two consecutive times on the same side. Both the percentage of success at the first session for each stage (**PCT**) and the number of sessions per stage required to reach the criterion (**STC**) were scored.

Delayed matching-to-sample and generalisation task

Six hens were tested in a delayed matching-to-sample task (**dMTS**). This included two hens from the SRL task, namely *Samba* and *Yuna* (among the hens that participated in the SRL task, four

hens deceased before the dMTS task was implemented, and three hens did not respond to the matching rule from the start). Before the testing procedure, individuals were gradually trained to give a five-key pecking at a black circle and then at a coloured circle on the screen to obtain the reward, including the colours used in the dMTS procedure. Overall, six colours were used in the different stages of training and testing: green, red, yellow, blue, brown, and purple.

General procedure. For the dMTS task, a trial typically consisted of presenting a coloured filled circle at the centre of the screen (i.e. the sample). A five-key pecking within a maximum of 45 s was required for the hen to move to the choice phase. For the choice, a second screen presented two coloured filled circles as comparison stimuli: one of the filled circles was of the same colour as the sample and the second one was of another colour. The hens were rewarded only if they pecked at the comparison stimulus corresponding to the previous sample (Fig. 3). A correct response was always accompanied by a reward of two mealworms, a 2-second 2 kHz sound (62 dB), and a white screen, and an incorrect answer was always accompanied by a 2-second 9 kHz sound (51 dB) and a dark screen. A cut-off was set when the hen did not achieve the five-key pecks at the sample within 45 s or when the hen did not choose a comparison stimulus within 10 s, and the trial was recorded as incorrect. Three consecutive cut-offs were considered
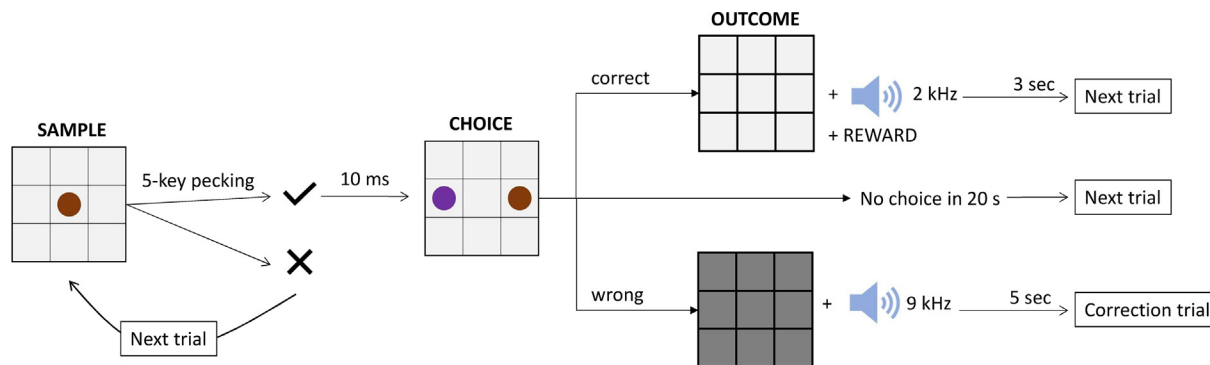
Fig. 3. Schematic view of the successive screens during the delayed matching-to-sample task. The sample is presented in the middle cell. The two choices are then presented in the middle left and right cells of the screen. The hen stands in front of the screen and pecks at the colour corresponding to the sample to obtain a reward.

as a lack of motivation and lead to the end of the session. The hen was then taken back again later in the morning. After an incorrect response, correction trials were proposed to rectify the eventual side or colour biases. The correction trials consisted of presenting the exact same trial once again after the presentation of the dark screen and 9 kHz sound, with a maximum of five corrections per trial. One session included 120 trials, not counting the correction trials. The inter-trial interval was fixed at 2 s after a correct response and 5 s after a wrong answer to increase the negative outcome. Three pairs of colours were used progressively: green and red (**GR**), yellow and blue (**YB**), and purple and brown (**PBr**). Item presentations were pseudo-randomised for the left and right sides for each session. A given trial configuration (sample identity and side of the correct comparison stimulus) was presented no more than two consecutive times.

Training and generalisation test. First, hens were trained to match the sample to the corresponding choice between the two colours presented: GR. All achieved at least 90% of success for this pair. Following this, hens were trained in a dMTS task with a second pair (YB) until they achieved at least a mean of 70% of success during five consecutive sessions containing at least three sessions with a minimum performance of 75% of success. These two training stages were part of a common pretesting procedure which was not recorded from the start. The hens were then trained with mixed sessions containing equal GR and YB trials until they reached 80% of success for three consecutive sessions before moving to the test. Test sessions included a third unknown pair, PBr. The test lasted for 11 sessions of 120 trials each: 40 test trials with the new pair (PBr) and 80 trials with the training pairs (40 YB trials and 40 GR trials). The test trials were differentially reinforced as the baseline trials. The variable of interest was the mean percentage of success in each session of the test pair.

Statistical analysis

Less than 10 individuals were tested; therefore, we chose a non-parametric approach for model fitting and detailed analyses. The results are presented as the mean performance and standard deviation. To analyse the effect of fixed variables on performance, results were analysed using generalised linear models with individuals as repeated measures (Supplementary Material S1). The fixed variables tested were (1) for the SRL task: the stage of learning (1–4) and the group (i.e. if hens started to learn to peck independently at the red or green circle); (2) for the dMTS task: the colour pairs and the stage (training or testing sessions). Independently, we controlled for side or colour bias for the dMTS task. With regard to the fixed variables described above, we compared the likelihood of interaction versus additive models with the

Akaike information criterion (all parameters were otherwise equal), and only the results with the best fits are reported, which are additive models for each analysis. Further analysis was performed using Wilcoxon tests to assess the statistical significance of the performance above chance at the group level and at the individual level, as well as to compare group performance between conditions. At the individual level, binomial tests were conducted to assess the statistical significance of performance above chance within one session. All tests and figures were performed using RStudio (version 1.4.1106). P-values below 0.05 were considered statistically significant for all statistical analyses. Chance level was at 50%.

Results

Serial reversal learning task

The results of the model analysis for the two response variables showed the same tendency and are presented respectively, that is, the number of sessions to reach the criterion (STC) for each stage (1–4) and the percentage of success at the very first session (PCT) for each stage. Five individuals did not meet the criterion for the fourth reversal stage in the time allowed and were considered not to have passed it (NA). We found no effect of the group (i.e. depending on the first colour learned) on performance throughout stages (for STC: $F = 0.08$, df = 1, $P = 0.79$ and for PCT: $F = 1.89$, df = 1, $P = 0.18$). Moreover, no effect of the group was observed on performance within each stage, indicating that the first colour learned, red or green, had no impact on the performance within and between the stages ($P > 0.05$).

We found an effect of stage on performance (STC: $F = 4.63$, df = 3, $P = 0.01$; PCT: $F = 3.98$, df = 3, $P = 0.02$). As expected, the first reversal stage (stage 2) significantly affected the performance of hens: individuals took 14.44 ± 3.57 sessions to reach the criterion, that is, on average, four sessions more than the discrimination stage (paired Wilcoxon test, $P = 0.03$; Fig. 4). PCT at stage 1 was significantly higher than that at stages 2 and 3 (paired Wilcoxon tests, $P = 0.04$ and $P = 0.04$, respectively; Fig. 5). Performance increased across the three reversal learning stages: PCT at stage 4 was almost significantly higher than that at stage 2 (Wilcoxon test, $P = 0.051$; Fig. 5). Accordingly, the mean STC decreased from the reversal stage 2 to the reversal stage 4.

Delayed matching-to-sample task

Performance for the training pairs (green and red and yellow and blue)

The six individuals took 17 to 22 sessions to reach the learning criterion of 80% of success in mixed sessions containing equal GR and YB trials (last training phase). The mean percentage of correct
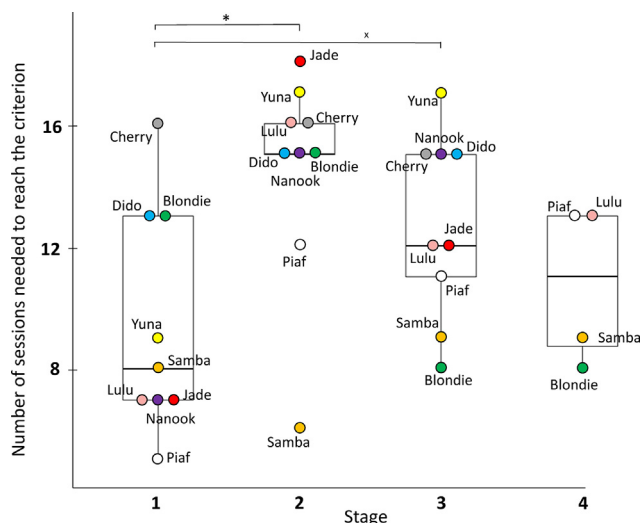
Fig. 4. Number of sessions required to reach the criterion for the discrimination learning task (stage 1) and for the reversal learning task (stages 2–4). Individual's performances are represented with one colour per individual. *P-value < 0.05; x P-value < 0.1.
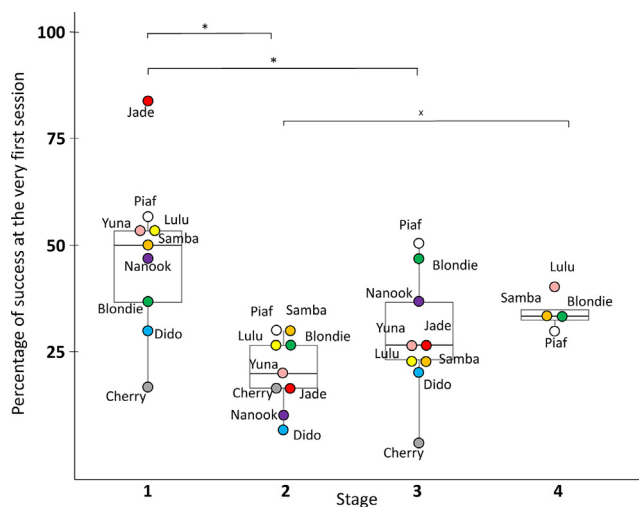

Fig. 5. Percentage of success of all hens for the very first session of each learning stage. Individual's performances are represented with one colour per individual. *P-value < 0.05; x P-value < 0.1.

responses for the two stimulus pairs was not significantly different in the three last sessions before testing (paired Wilcoxon test, GR: 87.5 ± 7.00% and YB: 88.3 ± 6.9, P = 0.91). Consistently, the percentage of correct responses was not different between the two training pairs during testing (paired Wilcoxon test, GR: 86.3 ± 9.1% and YB: 83.7 ± 11.1%, P = 0.13); these pairs were therefore analysed as one. At the group level, we found a colour bias among the known pairs for blue over yellow before the testing sessions and for green over red during the testing sessions (paired Wilcoxon tests, P < 0.01). A side bias was found for the right over left, either before or during the testing sessions (paired Wilcoxon test, P < 0.01).

Performance for the generalisation test pair (purple and brown)

At the group level, the mean percentage of correct responses for PBr trials (11 sessions) was 62.4 ± 10.5% of success, which is lower than that for the two training pairs (paired Wilcoxon test, P < 0.001) but still significantly above the chance level (Wilcoxon test, P < 0.001; Fig. 6). Confirming this, at the individual level, the
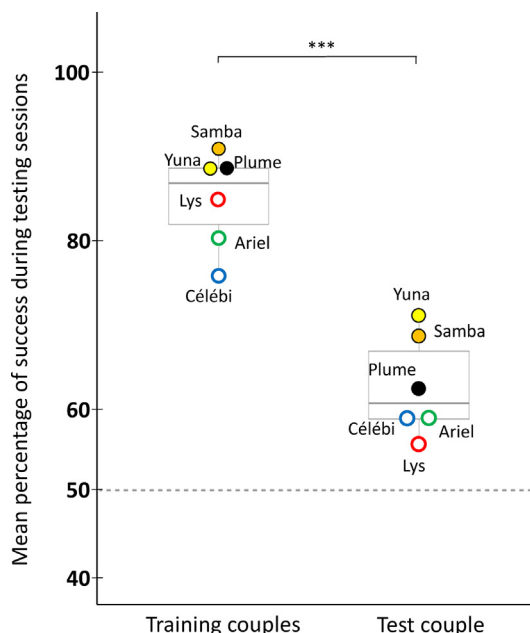

Fig. 6. Mean percentage of success for training pairs during test sessions (GR and YB) and for the test pair (PBr). Each point represents the mean percentage of success for a hen individual over the 11 sessions for the training pairs (GR-YB) and for the test pair (PBr). ***P-value < 0.001.

mean percentage of correct responses for the PBr pair was significantly greater than chance for each hen, except for *Lys* (binomial test, P = 0.11).

Fig. 7 shows individual performances for PBr trials through the sessions. In the first session, group performance achieved 52.92% of success with three hens (*Yuna*, *Celebi* and *Ariel*) performing better than 50%, even if not significant (binomial tests, P > 0.05). *Samba* significantly performed above chance from the third session, that is, within 120 test trials. Similarly, *Casquette* and *Yuna* performed significantly above chance from the fourth session, that is, within 160 test trials. Moreover, *Samba* and *Yuna* consistently and significantly performed above chance until the end of the test (binomial tests for each session for each individual, P < 0.05). In addition, even if it was not consistent throughout the next sessions, *Plume* significantly performed above chance at the fourth session, *Ariel* at the seventh session, and *Lys* and *Célébi* at the eighth session (Fig. 7). Overall, group performance significantly increased from session 1 to session 11 (paired Wilcoxon test for group performance between sessions 1 and 11, P = 0.02). Upon PBr trials, a side bias for right over left (paired Wilcoxon test, P = 0.004) was confirmed for four out of six individuals (binomial tests, P < 0.05), and a colour bias for purple over brown (paired Wilcoxon test, P < 0.001) was confirmed for three out of six individuals (binomial tests, P < 0.05). Only *Ariel* had no colour or side bias.

Discussion

Our automated screen device allowed us to effectively test one simple and one more complex cognitive task in domestic hens. In the SRL task, hens reached a similar performance for the two changing reward contingencies in only three reversal stages, which refines the existing data on their behavioural flexibility in this task. In the dMTS task, our results suggest that at least two hens (*Samba* and *Yuna*) may have generalised the identity concept as their performance for the novel colours fits in what is mentioned in the literature. Both tasks are discussed below.
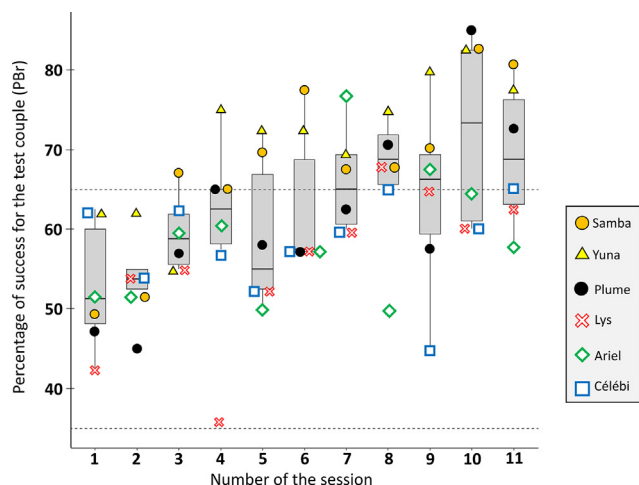
Fig. 7. Percentage of success in PBr trials for each hen at each session. Horizontal dashed lines at 65% and 35% of success represent the percentage for which the individual performance is greater than chance and worse than chance, respectively. Abbreviation: PBr = test pair purple-brown.

Serial reversal learning task

As expected, learning performance decreased at the first reversal learning stage (PCT stage 2) in comparison with the discrimination stage (PCT stage 1). This tendency has already been observed with spatial or 3D object discrimination procedures in many species (Tello-Ramos et al., 2019), including laying hens (among others: Bona et al., 2018). In our study, the performances of the hens at the discrimination stage (STC stage 1) were similar to those observed by Werner et al. (2005), in which hens also had to interact with a screen-like apparatus. Research investigating reversal learning abilities in hens with a 3D procedure seems to yield better performance results than when hens are assessed for the same cognitive task on a board. This observation is at least true for the discrimination and the first reversal learning stage (Sorato et al., 2018; among others: Loconsole et al., 2021), based on the results of Werner et al. (2005) and the present study, which were designed with screen-like boards (referring to performance as STC). Such a difference between a 3D procedural and a screen reversal task has been observed in keas (O'Hara et al., 2015). This contradicts with the argument of Loconsole et al. (2021) who supports that spatial SRL tasks *might not be optimal to allow* the study of behavioural flexibility in view of their strong brain *hemispheric specialisation*. We hypothesised that a larger physical involvement could have an intrinsically deeper reinforcement effect by being more biologically relevant to hens. In line with this view, learning efficiency can be improved by the spatial location of the reward in accordance with comparison stimuli (Williams et al., 1990), the many possible distinctive attributes, and the longer inter-trial intervals at stake in 3D tasks (Pearce, 1997).

Hens performed two more reversal learning stages corresponding to a serial reversal learning task (for a review, see Tello-Ramos et al., 2019). Despite the normal decrease in performance in comparison to the first stage due to the changing reward contingency, the performance increased through successive reversal learning stages (stages 2–4). At the group level, some difficulties must be emphasised because five out of nine hens did not manage to reach the criterion for the third reversal task (stage 4) in the time allowed. These individuals' performance at stages 2 and 3 was the most affected by the change in reward contingency. Variations in individual performance could be explained by several parameters, including personality, hierarchical position, physiological state, and emotional state of the individual (for a review, see Bushby et al., 2018).

When considering the four successful hens, they performed statistically equal to the discrimination stage (stage 1) at the third reversal stage (stage 4), that is, they performed equally for two different rewarded contingencies only after three reversals which is rather fast, thus demonstrating that our device is appropriate for implementing such flexibility tasks. This result is in line with those of other studies which set up to 20 reversals. Following the assumptions of Loconsole et al. (2021) on chicks' performance, hens seem to pass through the novelty of inconsistent orders and to generalise the underlying reversal rule as a *win stay-loose shift* rule according to the last outcome (van Horik and Emery, 2018) within only three reversal learning stages.

Delayed matching-to-sample task

To our knowledge, this is the first report of identity concept generalisation in a dMTS task in domestic hens. For generalisation trials, the mean performance (11 sessions, i.e. 440 trials) was significantly above chance for every hen but one, and above the 50% threshold for every hen. More precisely, three individuals performed above 50% at the very first session, and two individuals performed significantly and consistently above chance from the third and fourth sessions, respectively.

Transfer studies in animals are not congruent when performance can be referred to as concept generalisation performance. The claim that generalisation must occur at the very first test trial contradicts the fact that chance can be accountable on a one-trial scale, so that more trials are needed. In most studies, concept generalisation is assumed when the performance is above chance at the very first session, either within less than 10 trials (for example: Giurfa et al., 2001 in bees) or within more trials (for example: Wright and Katz, 2006; Truppa et al., 2010 in capuchin monkeys; Obozova et al., 2015 in parrots) with generally approximately 90–120 test trials. Two out of six hens consistently performed above chance from 120 and 160 test trials, respectively, which corresponds to a performance level recognised for validating concept generalisation in other species. Since the test trials were differentially reinforced, it is not possible to exclude fast learning occurring for the novel stimuli. However, the fast increase in performance (from sessions 1–3) only concerned the two hens whose performance was still above chance in all subsequent sessions. This fast acquisition with novel stimuli indicates that the hens were able to transfer what they had previously learned in a new situation. This finding supports the application of the concept through the dMTS task to new stimuli presented. Regarding this purpose, together with the neophobic tendencies of hens (Perez et al., 2016) and the intrinsic difficulty of the dMTS task, we may consider that domestic hens are able to transfer a learned concept by generalising it to novel and unknown stimuli. This result is in line with the generalisation abilities of perceptual information shown in chicks (see Versace et al. 2017; Rosa-Salva et al. 2018 through imprinting process; see Santolin et al. 2016 through a two-choice task).

At the individual level, apart from *Samba* and *Yuna*, individuals who performed above chance at one session did not show any consistency throughout the sessions, even if their mean performance was still above chance. This intra- and inter-individual inconsistency could be explained by a lack of attention depending on individual personalities. This lack of attention may have caused a sharp decrease in performance, despite better performance in previous sessions. This observation highlights the need to consider more than one session to further evaluate concept generalisation in animals.

Another explanation is that not all hens may have solved the dMTS task in the same approach, and some may have used alternative learning strategies to respond to it. In line with this idea,

Lormant et al. (2018) showed that, to solve the same spatial task, quails with a higher emotionality trait rely on spatial memory which is an explicit form of memory, whereas less emotional quails adopt preferentially cue-based memory, which is an implicit form of memory. Hens who did not effectively acquire the identity concept may have resolved the generalisation test with a cognitive process that does not imply explicit concept learning of the identity rule but procedural learning. This strategy, based on a simple stimulus response, could have allowed hens to rapidly increase their performance over time (Gabor and Gerken, 2010).

When presented with the testing stimuli, that is, PBr, individuals showed a significant bias towards purple over brown. Interestingly, blue was preferred over yellow in the training stage (mixed sessions containing equal GR and YB trials). Jones et al. (2001) showed that chicks who learned to choose two colours (e.g. red and yellow) among many colours, spontaneously generalised their behaviour to an intermediate colour (e.g. orange). Whether the learning parameters for a particular colour affect the behaviour of hens facing colours in a wavelength range remains to be addressed. We also found a side bias for the right over the left side at the group level. Recent studies in chicks have shown that using the right eye is crucial to attend to object-specific cues (Regolin et al., 2005), which could explain the right-side bias observed in our experiment.

Conclusion

We introduced an original fully automated touchscreen device using digital computer-drawn colour pictures and independent sensible cells adapted for cognitive testing in domestic hens. Our device allowed us to confront individuals both to a simple and a more complex cognitive task, to which they responded positively. We demonstrated that this approach is appropriate for questioning a large range of cognitive capacities in domestic hens, and more generally, for questioning farm animals' cognition.

Knowing the range of cognitive capacities of farm animals is crucial for understanding their perceptions and psychological needs. Husbandry practices can be improved by fundamental cognition research, which can answer common welfare issues of rearing systems by understanding the animal point of view (for a review on chickens, see Ferreira et al., 2021). This issue is even more current considering that the impact of the current development of new farm management technologies on animal welfare depends on the cognitive capacities of animals.

Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.animal.2022.100607.

Ethics approval

The experimental protocol was approved by the Val de Loire Ethics Committee (Approval No.: CE19-2021-0712-1, CEEA VdL, France). Animal care and experimental treatments complied with the French and European guidelines for the housing and care of animals used for scientific purposes (European Union Directive 2010/63/EU).

Data and model availability statement

The data that support the study findings are deposited in an official repository and are available from the authors upon request at https://doi.org/10.15454/QHEW7B.

Author ORCIDs

Rachel Degrande: https://orcid.org/0000-0003-4976-1073
Léa Lansade: https://orcid.org/0000-0002-4185-9714
Plotine Jardat: https://orcid.org/0000-0003-0374-5588
Violaine Colson: https://orcid.org/0000-0003-0934-7935
Ludovic Calandreau: https://orcid.org/0000-0002-7535-5733

Author contributions

Fabien Cornilleau, Ludovic Calandreau, Léa Lansade and **Violaine Colson** conceived the study. **Fabien Cornilleau** carried out the experiments. **Rachel Degrande** analysed the data and drafted the manuscript. **Ludovic Calandreau** supervised the research. All authors read, reviewed and approved the final manuscript.

Declaration of interest

None.

References

Agence Nationale de Sécurité sanitaire de l'alimentation, de l'Environnement et du travail (ANSES), 2018. Avis de l'Agence nationale de sécurité sanitaire de l'alimentation, de l'environnement et du travail relatif au 'Bien-être animal : contexte, définition et évaluation' Saisine n° 2016-SA-0288. ANSES, Maisons-Alfort Cedex, France.

Beran, M.J., 2018. Self-control in Animals and People. Academic Press, Cambridge, MA, USA.

Bona, L., van Staaveren, N., Pokharel, B.B., van Krimpen, M., Harlander-Matauschek, A., 2018. The Effect of Low Protein Energy-Rich Diets on Plasma Hepatic Markers, Hepatic Damage, and Discrimination Reversal Learning in Young Female Chicks. Frontiers in Veterinary Science 5, 107.

Brown, V.J., Tait, D.S., 2010. Behavioral Flexibility: Attentional Shifting, Rule Switching, and Response Reversal. In: Stolerman, I.P., Price, L.H. (Eds.), Encyclopedia of Psychopharmacology. Springer Berlin Heidelberg, Berlin, Heidelberg, Germany, pp. 1–7.

Brushfield, A.M., Luu, T.T., Callahan, B.D., Gilbert, P.E., 2008. A comparison of discrimination and reversal learning for olfactory and visual stimuli in aged rats. Behavioral Neuroscience 122, 54–62.

Bushby, E.V., Friel, M., Goold, C., Gray, H., Smith, L., Collins, L.M., 2018. Factors Influencing Individual Variation in Farm Animal Cognition and How to Account for These Statistically. Frontiers in Veterinary Science 5, 193.

Calapai, A., Cabrera-Moreno, J., Moser, T., Jeschke, M., 2022. Flexible auditory training, psychophysics, and enrichment of common marmosets with an automated, touchscreen-based system. Nature Communications 13, 1648.

Cook, R.G., Wasserman, E.A., 2007. Learning and transfer of relational matching-to-sample by pigeons. Psychonomic Bulletin & Review 14, 1107–1114.

Daisley, J.N., Vallortigara, G., Regolin, L., 2010. Logic in an asymmetrical (social) brain: Transitive inference in the young domestic chick. Social Neuroscience 5, 309–319.

Deakin, A., Browne, W.J., Hodge, J.J.L., Paul, E.S., Mendl, M., 2016. A Screen-Peck Task for Investigating Cognitive Bias in Laying Hens. PLoS ONE 11, e0158222.

Dudde, A., Krause, E.T., Matthews, L.R., Schrader, L., 2018. More Than Eggs – Relationship Between Productivity and Learning in Laying Hens. Frontiers in Psychology 9, 2000.

Elgar, M.A., Riehl, C., 2021. Editorial: Mechanisms of Communication and Recognition in Social Evolution. Frontiers in Ecology and Evolution 8, 625–831.

Ferreira, V.H.B., Guesdon, V., Calandreau, L., 2021. How can the research on chicken cognition improve chicken welfare: a perspective review. World's Poultry Science Journal 77, 1–20.

Food and Agriculture Organization of the united Nations (FAO), 2010. Livestock Systems/Global distributions/Chickens. Retrieved on 29 June 2022 from https://www.fao.org/livestock-systems/global-distributions/chickens/en/.

Forkman, B., Vallortigara, G., 1999. Minimization of modal contours: an essential cross-species strategy in disambiguating relative depth. Animal Cognition 2, 181–185.

Gabor, V., Gerken, M., 2010. Horses use procedural learning rather than conceptual learning to solve matching to sample. Applied Animal Behaviour Science 126, 119–124.

Gabor, V., Gerken, M., 2012. Cognitive testing in horses using a computer based apparatus. Applied Animal Behaviour Science 139, 242–250.

Garnham, L., Løvlie, H., 2018. Sophisticated Fowl: The Complex Behaviour and Cognitive Skills of Chickens and Red Junglefowl. Behavioral Sciences 8, 13.

Giurfa, M., Zhang, S., Jenett, A., Menzel, R., Srinivasan, M.V., 2001. The concepts of 'sameness' and 'difference' in an insect. Nature 410, 930–933.

Jones, C.D., Osorio, D., Baddeley, R.J., 2001. Colour categorization by domestic chicks. Proceedings of the Royal Society of London. Series B: Biological Sciences 268, 2077–2084.

Kleiber, A., Valotaire, C., Patinote, A., Sudan, P.-L., Gourmelen, G., Duret, C., Borel, F., Legoff, L., Peyrafort, M., Guesdon, V., Lansade, L., Calandreau, L., Colson, V., 2021. Rainbow trout discriminate 2-D photographs of conspecifics from distracting stimuli using an innovative operant conditioning device. Learning & Behavior 49, 292–306.

Langbein, J., Siebert, K., Nuernberg, G., 2008. Concurrent recall of serially learned visual discrimination problems in dwarf goats (Capra hircus). Behavioural Processes 79, 156–164.

Livesey, P.J., Han, M.F., Lowe, H., Feakes, R., 1972. Automated apparatus for the study of learning in monkey and rat. Australian Journal of Psychology 24, 211–218.

Loconsole, M., Perovic, S., Regolin, L., 2021. A leftward bias negatively correlated with performance is selectively displayed by domestic chicks during rule reversal (not acquisition). Laterality 26, 1–18.

Lormant, F., Cornilleau, F., Constantin, P., Meurisse, M., Lansade, L., Leterrier, C., Lévy, F., Calandreau, L., 2018. A trait for a high emotionality favors spatial memory to the detriment of cue-based memory in Japanese quail. Behavioural Processes 157, 256–262.

Meyer, S., Nürnberg, G., Puppe, B., Langbein, J., 2012. The cognitive capabilities of farm animals: categorisation learning in dwarf goats (Capra hircus). Animal Cognition 15, 567–576.

Nakamura, N., Watanabe, S., Betsuyaku, T., Fujita, K., 2011. Do birds (pigeons and bantams) know how confident they are of their perceptual decisions? Animal Cognition 14, 83–93.

O'Hara, M., Huber, L., Gajdon, G.K., 2015. The advantage of objects over images in discrimination and reversal learning by kea, Nestor notabilis. Animal Behaviour 101, 51–60.

Obozova, T., Smirnova, A., Zorina, Z., Wasserman, E., 2015. Analogical reasoning in amazons. Animal Cognition 18, 1363–1371.

Pearce, J., 1997. Animal learning and cognition: An introduction. Psychology Press, Hove, East Sussex, UK.

Perez, E., Georgelin, M., Consantin, P., Cornilleau, F., Meurisse, M., Bertin, A., Calandreau, L., 2016. What the brain tells us about food neophobia in the young chicken Gallus gallus domesticus. Poster presented at the 8th European Conference of Behavioural Biology, 12–15 July 2016, Vienna, Austria.

Regolin, L., Garzotto, B., Rugani, R., Pagni, P., Vallortigara, G., 2005. Working memory in the chick: parallel and lateralized mechanisms for encoding of object- and position-specific information. Behavioural Brain Research 157, 1–9.

Rosa-Salva, O., Fiser, J., Versace, E., Dolci, C., Chehaimi, S., Santolin, C., Vallortigara, G., 2018. Spontaneous Learning of Visual Structures in Domestic Chicks. Animals 8, 135.

Rowe, C., Healy, S.D., 2014. Measuring variation in cognition. Behavioral Ecology 25, 1287–1292.

Ryan, C.M.E., Lea, S.E.G., 1994. Images of conspecifics as categories to be discriminated by pigeons and chickens: Slides, video tapes, stuffed birds and live birds. Behavioural Processes 33, 155–175.

Santolin, C., Rosa-Salva, O., Vallortigara, G., Regolin, L., 2016. Unsupervised statistical learning in newly hatched chicks. Current Biology 26, R1218–R1220.

Smith, J.D., Berg, M.E., Cook, R.G., Murphy, M.S., Crossley, M.J., Boomer, J., Spiering, B., Beran, M.J., Church, B.A., Ashby, F.G., Grace, R.C., 2012. Implicit and explicit categorization: A tale of four species. Neuroscience & Biobehavioral Reviews 36, 2355–2369.

Sorato, E., Zidar, J., Garnham, L., Wilson, A., Løvlie, H., 2018. Heritabilities and co-variation among cognitive traits in red junglefowl. Philosophical Transactions of the Royal Society B: Biological Sciences 373, 20170285.

Tello-Ramos, M.C., Branch, C.L., Kozlovsky, D.Y., Pitera, A.M., Pravosudov, V.V., 2019. Spatial memory and cognitive flexibility tradeoffs: Tob e or not to be flexible, that is the qustion. Animal Behaviour 147, 129–136.

Truppa, V., Garofoli, D., Castorina, G., Piano Mortari, E., Natale, F., Visalberghi, E., 2010. Identity concept learning in matching-to-sample tasks by tufted capuchin monkeys (Cebus apella). Animal Cognition 13, 835–848.

Vallortigara, G., 2006. In: The Cognitive Chicken: Visual and Spatial Cognition in a Non-Mammalian Brain. Oxford University Press, Oxford, UK, pp. 41–58.

Vallortigara, G., 2021. Born Knowing. Imprinting and the Origins of Knowledge. MIT Press, Cambridge, MA, USA.

van Horik, J.O., Emery, N.J., 2018. Serial reversal learning and cognitive flexibility in two species of Neotropical parrots (Diopsittaca nobilis and Pionites melanocephala). Behavioural Processes 157, 664–672.

Versace, E., Spierings, M.J., Caffini, M., ten Cate, C., Vallortigara, G., 2017. Spontaneous generalization of abstract multimodal patterns in young domestic chicks. Animal Cognition 20, 521–529.

Werner, C.W., Tiemann, I., Cnotka, J., Rehkämper, G., 2005. Do chickens (Gallus gallus f. domestica) decompose visual figures? Animal Cognition 8, 129–140.

Williams, D.A., Butler, M.M., Overmier, J.B., 1990. Expectancies of reinforcer location and quality as cues for a conditional discrimination in pigeons. Journal of Experimental Psychology: Animal Behavior Processes 16, 3–13.

Wright, A.A., Katz, J.S., 2006. Mechanisms of same/different concept learning in primates and avians. Behavioural Processes 72, 234–254.

Zanon, M., Lemaire, B.S., Vallortigara, G., 2021. Steps towards a computational ethology: an automatized, interactive setup to investigate filial imprinting and biological predispositions. Biological Cybernetics 115, 575–584.

Zebunke, M., Puppe, B., Langbein, J., 2013. Effects of cognitive enrichment on behavioural and physiological reactions of pigs. Physiology & Behavior 118, 70–79.

Zentall, T.R., Wasserman, E.A., Lazareva, O.F., Thompson, R.K.R., Rattermann, M.J., 2008. Concept Learning in Animals. Comparative Cognition & Behavior Reviews 3, 13–45.