Behavioural and physiological expression of arousal during decision-making in laying hens

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HIGHLIGHTS

• Anticipatory arousal was detectable around the time of decision-making in chickens.
• Increased heart-rate and head movements were measured prior to preferred goal access.
• More head movements were measured when two preferred goals were available.
• Fewer head movements were measured preceding decisions not to access a goal.
• Provides an important foundation for exploring arousal during animal decision-making.

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ABSTRACT

Human studies suggest that prior emotional responses are stored within the brain as associations called somatic markers and are recalled to inform rapid decision-making. Consequently, behavioural and physiological indicators of arousal are detectable in humans when making decisions, and influence decision outcomes. Here we provide the first evidence of anticipatory arousal around the time of decision-making in non-human animals. Chickens were subjected to five experimental conditions, which varied in the number (one versus two), type (mealworms or empty bowl) and choice (same or different) of T-maze goals. As indicators of arousal, heart-rate and head movements were measured when goals were visible but not accessible; latency to reach the goal indicated motivation. We found a greater increase in heart-rate from baseline to the goal-viewing period, more head movements and shorter latencies in all conditions including mealworms compared to those with empty bowls. More head movements when two mealworm bowls were available compared to just one, and prior to occasions when hens accessed an empty bowl rather than declining to move, showed that arousal preceded and influenced decision-making. Our results provide an important foundation for investigating arousal during animal decision-making and suggest that the somatic-marker hypothesis might not only apply to humans.
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1. Introduction

The theory of optimal decision-making assumes that animals have perfect knowledge of their external environment and their own internal state at any one time. In reality, it is extremely unlikely that animals have such perfect knowledge or that they are perfect processors of such knowledge. Indeed, animals frequently seem to behave in a sub-optimal manner, by making decisions that violate the principles of rationality [1–4]. However, a closer examination reveals that across a range of species, mistakes are systematic and not random [5]. Under conditions where the information available is incomplete (or overwhelming), it is not surprising that "fast-but-inaccurate" strategies are sometimes employed [6,7].

One potentially "fast-but-inaccurate" decision-making strategy, of growing interest in the human literature, concerns the role of emotion [8]. It has been suggested that when humans are faced with uncertain, complex or difficult choices, their reliance upon rational and conscious thought processes declines, and that information is channelled via short subcortical pathways, resulting in emotional reactions playing a larger role in choice behaviour [9]. Crucially, it is proposed that prior affective physiological reactions to choice options are stored within the brain as associations called somatic markers [8]. During decision-making, the somatic markers created by the relevant stimuli are summed to produce a net state that enables a rapid decision. This

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intriguing idea suggests that when making decisions, humans, and indeed other animals, will experience evoked emotions consciously or unconsciously associated with their past experience of each option. Behavioural and physiological signals, particularly those indicative of arousal, should therefore be detectable at around the time of decision-making and should influence the decision made.

Researchers have begun to investigate how arousal measured by skin conductance or heart-rate is associated with decision-making in humans [9–11]. Humans with deficits in emotional, but not cognitive, processing have a diminished anticipatory arousal response and make poorer decisions in gambling tasks [12]. Moreover, people who perform best during such tasks show higher anticipatory arousal preceding risky decisions that result in a net loss [10]. Behavioural and physiological expression of anticipatory arousal has also been investigated to some extent in non-human mammals and birds [13–20], although not to our knowledge during decision-making. Previously, we found that some long-term physiological reactions (e.g. blood glucose or corticosterone concentrations) to different choice options were associated with future decisions made by chickens [21,22]. However, in that work we did not assess their physiological responses at the time that decisions were made. Thus, it is not clear whether any prior emotional state influenced the arousal level of the chickens at the time of their decision.

As a first step in examining how arousal is associated with decision-making in non-human animals, we here manipulated reward outcome for chickens in a simple T-maze choice apparatus. We measured both heart-rate (HR), using a non-invasive methodology [23,24], and head movements [18] as indicators of arousal. Whilst chickens were in the T-maze start-box, we measured their baseline HR prior to any presentation of the goals. We then measured both HR and the number of head movements during a period when goals were visible but could not yet be accessed.

We investigated whether a differential arousal response occurred to conditioned stimuli indicating goals of greater (i.e. mealworms: [25]) or lesser value (i.e. an empty bowl) by examining the chickens' response to presentation of one option at a time. To check that the birds were more motivated to approach mealworms than the empty bowl, we assessed their latency to approach the reward [26]. To assess any effects of goal quantity, we provided experimental conditions where two identical options (two mealworm bowls or two empty bowls), one on each side of the T-maze, were available. The remaining test condition provided the chickens with a choice between the mealworms and the empty bowl to allow us to assess whether making a decision between goals of unequal value was associated with changes in arousal.

2. Materials and methods

2.1. Animals, housing and husbandry

Sixteen Lohmann Brown laying hens were obtained at approximately 35 weeks of age and leg-tagged for identification. They were housed on day 1 in groups of four, in four out of eight available pens (0.96 × 1.2 m, 2 m high) in the same room (home room). The home room was arranged so that opposite pens could be joined by a Perspex tunnel (1.79 × 0.24 m, 0.47 m high). Between days 1 and 20, hens were allowed to settle, being handled minimally.

Ad libitum feed (Farmgate Layers Mash, BOCM Pauls, Ipswich, Suffolk, UK) was provided via two feed troughs external to each pen. Water was available from a hanging drinker in the back corner of each pen. A nest box (0.39 × 0.38 × 0.47 m) and a round perch (0.96 m, 0.25 m high) were also provided. Wood shavings were used as bedding at a depth of 5–10 cm. During weekly cleaning, each group of four birds was switched to the opposite pen within the home room to avoid a side-housing bias. The room temperature was kept at 19–22 °C and the lighting schedule was 12 L:12 D (with lights on at 07:00).

All work was conducted under UK Home Office licence (30/2332). The hens were re-homed to small free-range holdings after the study.

2.2. Experimental room

The experimental room contained two pens (one on each side of the room), which were identical to those in the home room and could similarly be joined by a Perspex tunnel. The exceptions were that the feed trough openings were blocked using wooden panels and the pens did not contain nest boxes and perches. The experimental room was separated from the home room by solid wooden doors and a corridor, providing an area where hens could be tested away from the noise of conspecifics. Within the experimental room, a CCTV camera was attached to the ceiling above the test apparatus, which was connected to a computer on one side of the room. Another computer for HR monitoring was set-up on the other side of the room.

2.3. Habituation and training phase

Habituation (to the HR monitor and the T-maze procedure) and training (to establish an association between feed bowl and reward identity) began on day 20. Training and habituation continued until day 40.

2.3.1. Harness and HR monitor

HR was monitored using a non-invasive remote telemetric unit [23]. Harnesses containing a HR monitor were made using elastane from a template designed to fit the hen without restricting movement and were fastened using press studs. The harness contained a padded integrated pocket to provide protection for the ECG cables and monitor without providing discomfort to the hen. The pocket containing the monitor was positioned over the hen's back and the ECG cables were threaded through the harness and attached to the monitor. Self-adhesive electrode sensors (Ambu Blue sensor M-00-S) were attached to pre-cleansed skin either side of the keel bone at the start of each test day.

Twelve of the 16 hens had previously experienced wearing the HR monitor and harness for an unrelated study. Additional habituation was given to the hens that had no such prior experience. Specific criteria (that hens were able to walk and behave normally in their home environment, without moving backwards or stopping excessively) had to be satisfied before individuals progressed to each next stage of HR habituation. Initially, the length of time wearing the harness alone was increased from 1 to 3 h in 30 minute increments. The ECG cables were then added to the harness and finally the monitor (weighing approx. 100 g) was added. The final few sessions of HR habituation were carried out whilst hens were trained in the experimental room, to ensure that they were able to perform the test wearing the monitor and harness. It took between 2 and 5 min to fit the hen with the heart-rate monitor and harness at the start of each session. In total, each individual wore the harness for approximately 18 h during habituation.

2.3.2. Feed bowls

Hens were trained to discriminate between two different feed bowls: one, a black-and-white spotty bowl (internal diameter: 118 mm, 37 mm deep) (containing mealworms); the other, an empty beige bowl (internal diameter: 114 mm, 46 mm deep) (containing no reward). To reduce initial fear of novel stimuli, bowls were first presented to whole groups for a 1-hour period of familiarisation. After approximately three such sessions, all birds approached the bowls without signs of fearful behaviour (i.e. they approached the bowl quickly without stopping or hesitating). Training individuals to discriminate between the bowls continued during T-maze habituation. Birds were deemed able to discriminate when they consistently