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Touchscreen performance and knowledge transfer in the red-footed tortoise (*Chelonoidis carbonaria*)

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ABSTRACT

In recent years red-footed tortoises have been shown to be proficient in a number of spatial cognition tasks that involve movement of the animal through space (e.g., the radial maze). The present study investigated the ability of the tortoise to learn a spatial task in which the response required was simply to touch a stimulus presented in a given position on a touchscreen. We also investigated the relation between this task and performance in a different spatial task (an arena, in which whole-body movement was required). Four red-footed tortoises learned to operate the touchscreen apparatus, and two learned the simple spatial discrimination. The side-preference trained with the touchscreen was maintained when behaviour was tested in a physical arena. When the contingencies in the arena were then reversed, the tortoises learned the reversal but in a subsequent test did not transfer it to the touchscreen. Rather they chose the side that had been rewarded originally on the touchscreen. The results show that red-footed tortoises are able to operate a touchscreen and can successfully solve a spatial two-choice task in this apparatus. There was some indication that the preference established with the touchscreen could transfer to an arena, but with subsequent training in the arena independent patterns of choice were established that could be evoked according to the test context.

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1. Introduction

The ability to navigate through space successfully and efficiently can be considered to bestow a survival advantage as it allows for the successful passage between feeding grounds, sleeping quarters, and so on. Most research on spatial cognition has concentrated on navigation by mammals and birds (reviewed by Healy, 1998). There has been less research with reptiles, and much of what exists has been concerned with the study of seasonal, large-scale movements of sea turtles (Dutton et al., 1999) which are guided by the use of a variety of cues, including geomagnetic (e.g., Lohmann et al., 2001, 2004), visual (Avens and Lohmann, 2003), and celestial cues (DeRosa and Taylor, 1980). However, the majority of reptiles do not face the challenge of navigation on such a scale. For example, when painted turtles (*Chrysemys picta marginata*) were displaced a mile from their home pond they became disorientated and failed to find their way back (Emlen, 1969). This species can, however, navigate successfully on a smaller scale. When the turtles were released 100 m from home they were able to return quickly, and did so on a direct route. The turtles appeared to be using landmarks, such as the edge of a wood near the home pond, to guide their choices. This finding is perhaps unsurprising as this species, like the majority of reptiles, spend their lives within a small area, with which they are familiar. Research investigating small-scale navigation (for a review see Mueller et al., 2011) has shown that in this case too, reptiles are able to use a range of different strategies to find a goal. These are exemplified in a series of studies of spatial learning in the red-footed tortoise (*Chelonoidis carbonaria*; Wilkinson et al., 2007, 2009; Mueller-Paul et al., 2012a,b).

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This species is a land-dwelling chelonian, native to Central and South America. It is food motivated and is considered an omnivore, although much of its diet is fruit (Strong and Fragoso, 2006). The red-footed tortoise is a relatively active species, and is capable of travelling up to 85 m/h (Moskovits 1985, cited by Strong and Fragoso, 2006). They are highly visual, appear to have good colour vision and, whenever possible, use vision to solve a task (Wilkinson and Huber, 2012). Their liveliness and food motivation, in addition to their visual abilities (Wilkinson and Huber, 2012) makes them an ideal species for studying visual based spatial learning.

Recent research has revealed that the red-footed tortoise is able to master an eight-arm radial maze, in which it is required to remember several different spatial locations within a single trial (Mueller-Paul et al., 2012a,b; Wilkinson et al., 2007). These tortoises appear to be able to use room cues for navigation in a cognitive map-like manner, but they also exhibit stereotypic response strategies if cues are less salient (Mueller-Paul et al., 2012a,b; Wilkinson et al., 2009). Odour, too, has been identified as a possible cue, but appears to be used only when other cues are not available (Mueller-Paul et al., 2012a,b). Although red-footed tortoises are able to use different mechanisms to reach a goal they appear to prefer the first successful strategy they used, even if another might be simpler under changed circumstances (Mueller-Paul et al., 2012a,b). More flexibility was observed in a study by Wilkinson et al. (2010a). They showed that red-footed tortoises can learn the path that leads to a goal by observing a demonstrator tortoise. But the tortoises did not learn simply about the exact route followed by the demonstrator as they were able to apply the principles of the task even when the path to food was altered by introducing additional turns (Wilkinson and Huber, 2012). To this extent, red-footed tortoises have demonstrated an ability to generalize knowledge across variations of a previously learned task.

To examine further the mechanisms controlling spatial learning in this species it will be informative to test the tortoise's performance on comparable tasks in different domains. In the study to be reported here we made use of a 2-dimensional (2-D) display presented on a touchscreen and a traditional testing arena in which "real" 3-dimensional (3-D) objects could be presented. Assessing differences and similarities of behaviour in such distinct domains has the potential to tell us about the generality of spatial cognitive processes. Spontaneous transfer of knowledge from one domain to another would indicate a high level of generality of the acquired spatial knowledge. In particular, transfer from the touchscreen to a 3-D arena might be taken to indicate that a kind of mental map could be derived from the overview of the entire set-up that was provided in the touchscreen situation. A series of studies investigating transfer in pigeons has revealed strong similarities between spatial learning performance on a touchscreen and in a 3-D arena (reviewed by Cheng et al., 2006). For example, Kelly and Spetch (2004) and Kelly et al. (1998) demonstrated that pigeons were able to use feature and geometric cues to a similar extent when presented in a 2-D schematic and in a navigable 3-D environment. Further, the birds appear to use the configuration of landmark arrays to do this (Spetch et al., 1996). This suggests that similar spatial learning mechanisms govern the performance in these different domains, at least in this species.

Efficient transfer on a task of this type requires the subject to recognize that a picture represents an object, and evidence of this ability in non-human animals is scanty (for a review see Fagot, 2000). Recently, however, picture–object recognition has been investigated in the red-footed tortoise (Wilkinson et al., 2013). The findings revealed that the tortoises were able to recognie a correspondence between real objects and 2-D images of them. The animals were trained to distinguish colour-matched food and non-food items and were later able to make the same distinction between colour photographs of similar food and non-food items, the tortoises confused the real food items with the corresponding photographs, finding it difficult to differentiate between a photograph and the 3-D item that it represented, suggesting similar processing of 2-D and 3-D stimuli.

The present study made use of the 2-D-image recognition ability of red-footed tortoises in order to further investigate the mechanisms underlying tortoise spatial navigation. The first stage involved training subjects on a spatial discrimination in a touchscreen task that provided small-scale stimuli and a full overview of the situation. (The ability of this species to touch a stimulus-defined location in order to receive a reward in a different feeder location, has yet to be demonstrated; however, the proficient use of a pecking key has been shown in terrapins, *Chrysemys picta picta*; Bitterman, 1964; Powers et al., 2009.) We then went on to study performance on a comparable test in an arena that required walking through space towards one of a pair of 3-D objects. This allowed us to assess the possibility of transfer from touchscreen to the arena. To investigate the possibility of transfer in the other direction, we then trained subjects in the arena (the rewarded spatial position being reversed from that selected in the first phase of touchscreen training) prior to a test with the touchscreen.

2. Methods

2.1. Subjects

Four juvenile red-footed tortoises (*Chelonoidis carbonaria–formerly Geochelone*) with plastron lengths of 13 cm (Esme), 13 cm (Molly), 12 cm (Quinn) and 11 cm (Emily), took part in the study. The tortoises' sex was unknown, as unambiguous sexual dimorphism develops only later in the life of this species. The tortoises were housed as a group of four in a 120×70 cm arena, at 28 ± 2 °C and approximately 60% humidity, with permanent access to fresh water, shelter, UV light, and heat lamps. The tortoises were not food deprived. Small pieces (approximately 0.5×0.5 cm) of preferred fruit and vegetables, such as mushroom, strawberry, and sweet corn were provided as rewards during experimental sessions while a variety of less preferred food types, such as cucumber, grape, and apple was offered in their home enclosure after training. The same types of food rewards were used throughout the different stages of the experiment. In accordance with standard husbandry practice they experienced one day a week without food. All four animals had previous experimental experience (see Mueller et al., 2011; Wilkinson et al., 2010a,b) but they had never previously been trained with a touchscreen, pecking key, or similar apparatus.

2.2. Apparatus

2.2.1. Touchscreen apparatus

The setup was based on the Vienna comparative cognition technology (VCCT, for details see Steurer et al., 2012). A 15-inch IR "CarrollTouch" touchframe (Model D87587-001, 15 in., without filter) by Elo (Menlo Park, CA; http://www.elotouch.com) with a resolution of 1024×768 pixel and 32-bit colour depth was used. The software controlling stimulus presentation and movement of the feeder in the learning chamber was CognitionLab 1.9 (see Steurer et al., 2012).

The touchscreen was placed in a rectangular (30×50 cm) Skinner box (Fig. 1) having white plastic walls (21 cm high) and a floor covered with grey, grip-ensuring, rubber lining. A feeder hole was positioned in the centre of the floor 2 cm from the touchscreen. The feeder mechanism was located directly below the floor of the Skinner box and was driven by a 24-V motor. It consisted of a round polyoxymethylene plate (diameter 47 cm) and 16 small indented

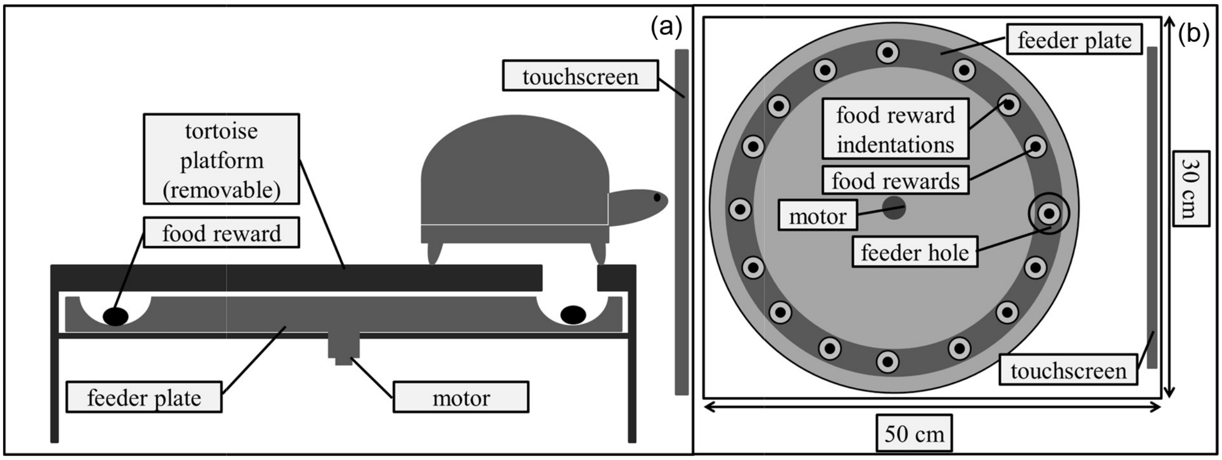

Fig. 1. *Tortoise touchscreen apparatus:* (a) side view of the Skinner box, (b) top view of the feeder plate (illustrations not drawn to scale).

place-holders indicating the reward positions around the outer edge. A correct response resulted in the feeder plate turning by one reward position, which resulted in a reward being presented below the feeder hole, making it accessible to the tortoise. An important concern in the construction of the feeder was the safety of the subjects. For this reason the indentations in the feeder plate were very shallow and without sharp edges, and the rotation speed was slow, so that a tortoise stepping into the feeder hole would not result in injury. The touchscreen apparatus stood in the centre of a 2.24 m × 2.24 m room that was lit with two 25 W fluorescent tube lights; the walls displayed a variety of posters.

2.2.2. *Arena apparatus*

The arena was a rectangle of 100 × 80 cm, with walls 40 cm high. The lower 20 cm of the side walls were covered with white paper, the upper 20 cm being of transparent glass. The floor was covered in wood shavings. This apparatus was positioned in a different room (2.28 m × 2.24 m) from that used for the touchscreen apparatus and at a different spatial orientation, to control for the possible use of geomagnetic cues. The room was lit by two 25 W fluorescent tube lights. Furnishings, wall decorations, and positions of light sources of the room differed from those of the room containing the touchscreen apparatus. A separate 40 × 32 × 20 cm light-grey plastic box containing a blue bowl was available for use as a reward box.

2.2.3. *Stimuli*

The digital stimuli presented on the touchscreen were: a red equilateral triangle with sides of 2.5 cm presented centred and with its lower edge level with the tortoise platform; two 2.5-cm diameter blue circles, presented 10 cm apart, and were positioned on either side of, and 6 cm above, the level of the tortoise platform. All tortoises were able to reach these targets without moving from a central location directly in front of the screen.

The physical stimuli presented in the arena were two blue bowls (diameter 8 cm, height 2.5 cm), positioned at one end of the arena at a distance of 50 cm from the starting position, and placed 50 cm apart. They contained one piece of food each. The food in one bowl was covered by a perforated, odour-permeable, transparent plastic cover. The food rewards and cover were arranged so that they only became visible to the tortoise when it had approached close to the bowl and thus made a choice. A black cardboard barrier (43 cm long and 30 cm high) showing a red triangle (10 × 9.5 cm) could be positioned in the centre of the arena. The colours of the physical and the digital stimuli were not matched for wavelength.

2.3. *Procedure*

The experiment was run over a period of 33 weeks between December 2010 and August 2011. The animals were tested five days a week between 9 am and 5 pm. All training and test sessions were recorded on video.

2.3.1. *Habituation*

Prior to the discrimination phases, the animals were habituated to the apparatus. The tortoises were placed individually in the touchscreen box and the test arena for 30 min. Habituation was considered complete when the animals had eaten the available food for three consecutive trials. In the touchscreen box food items were freely available in the feeder hole; in the arena food was provided in one blue feeding bowl in the centre of the arena. All four tortoises habituated to both the touchscreen and the arena apparatus within three 30-min periods. Additionally, to ensure that the tortoises were habituated to the sound and vibrations caused by the feeder, further trials were given in the touchscreen box with the display consisting of an unchanging white screen while the feeder was operated, presenting food at 30-s intervals. Habituation to the feeder took four periods for Esme and Quinn, 10 for Molly and 18 for Emily.

2.3.2. *Touchscreen pre-training*

Pre-training began with an autoshaping phase during which the tortoises were presented with a photograph of a strawberry. This stimulus appeared at regular intervals in combination with a food reward. It remained on the screen for 10 s, after which the screen went blank. The stimulus was presented again after a 30-s inter-trial interval. Next the tortoises were manually shaped using a successive approximation procedure in which the experimenter triggered the feeder in response to the tortoise showing ever-closer approximations to the desired behaviour of touching the stimulus on the screen. Once able to touch the stimulus and initiate the release of a reward by themselves, the tortoises were put through a sequence of pre-training phases, requiring first one touch on each stimulus, then two touches, and then the selection of different stimuli (see Table 1). The tortoises were transferred to the next phase when they had performed reliably for at least three sessions in a row, or after the minimum number of sessions shown in Table 1.

2.3.3. *Touchscreen training*

For the subjects that successfully completed *pre-training* (Section 2.3.2), touchscreen training took place between 4 April and 6 May 2011. Each trial started with the presentation of the red

Table 1
Number of training sessions received by the tortoises for successful acquisition of the various phases of the touchscreen pretraining.

Type of training	Response required	Min. no. of sessions	Esme	Quinn	Molly	Emily
Auto-shaping	Take food from feeder	3	3	10	3	12
Manual shaping	Move towards screen and start touching	2	2	2	3	3
Shaping 1	1 touch on strawberry stimulus	10	10	10	11	10
Shaping 2	2 touches on strawberry stimulus	10	10	10	10	10
Shaping 3	2 touches on circle stimulus	10	10	10	10	14
Sequence 1	Triangle and circle displayed, 1 touch on triangle, then 1 touch on correct circle	10	(20[a])	–	–	–
Sequence 2	1 touch on triangle, circle appears, 1 touch on correct circle	10	10	10	33[b]	24[b]

[a] As Esme, the first to reach this phase of sequence-training, was unable to learn the correct response to this stimulus arrangement, the training procedure was altered and the other tortoises did not engage in this phase of the training.
[b] Tortoise training was discontinued at this stage.

triangle. Once the triangle was touched it disappeared and the two blue circles appeared, the circle position (either left or right) was designated as positive. The spatial position of the positive stimulus was counterbalanced across individuals. If the circle on the correct side was chosen, both stimuli disappeared and a reward was provided via the automatic feeder. If the circle on the incorrect side was chosen the tortoise was given a 3-s time out during which the screen remained empty; then the trial was repeated. Each correction trial started with the red triangle. The tortoise received correction trials until the correct choice was made. Repeated trials did not count in analysis of correct choices. The criterion for this phase of training required a minimum of 10 completed 20-trial blocks, with performance on the last three blocks being above chance.

2.3.4. *Transfer to arena test 1*

Once a tortoise had successfully completed *touchscreen training* (Section 2.3.3) it was given 20 test trials in the arena apparatus. Each subject was tested on two consecutive days directly following the last touchscreen training day. It was placed in the arena facing the black barrier showing a red triangle. The trial was started by the experimenter lifting the barrier and releasing the tortoise to walk towards one of the blue bowls. The experimenter stepped out of the tortoise's range of vision immediately after placing it in the arena. This was done to minimize any potential experimenter influence and avoid the risk of inadvertent cueing. When the tortoise approached within 5 cm of a bowl, the trial ended and the choice position was recorded. The tortoise was then placed into the reward box for 30-s where it received a food reward from a blue bowl, irrespective of the side chosen in the arena. Animals were given no more than 10 trials a day with variable inter-trial intervals. This reward procedure was designed to minimize the effects of rewarding choice of a given position while maintaining the animal's motivation to work in a novel environment. Between trials the wood shavings covering the arena floor were redistributed to avoid the development of an odour trail leading in one particular direction.

2.3.5. *Arena reversal training*

After completion of *arena transfer test 1* (Section 2.3.4), the tortoises received reversal training in the arena apparatus. The reversal training was conducted between 30 May and 11 July 2011. The side (left or right) that was rewarded during the *touchscreen training* (Section 2.3.3) was now unrewarded, and the opposite side was now rewarded. The procedure was identical to that of *arena transfer test 1* (Section 2.3.4) except that no separate reward box was used and reinforcement was contingent on choosing the correct spatial location. If the incorrect bowl was chosen the tortoise was removed from the arena and no reward was provided. The criterion of mastery was the same as was used in *touchcreen training* (Section 2.3.2); subjects received ten 20-trial blocks in this phase, with performance on the last three blocks being above chance.

2.3.6. *Transfer to touchscreen test*

After successful completion of *arena reversal training* (Section 2.3.5) the tortoises' side choice on the touchscreen was tested. They were given 20 test trials with variable ITIs spread over two consecutive days directly following the last day of arena training. The procedure was identical to that of *touchscreen training* (Section 2.3.3) except that once one of the blue circles had been selected the stimuli disappeared and the tortoise was subjected to a delay of between 5 and 10-s before receiving a food reward from the feeder, which was given irrespective of which stimulus was chosen. The interval between the choice and the reward was varied to simulate the procedure used in the arena test where slight differences in the time to reward presentation were inevitable due to the manual transfer of the subjects from the arena to the reward box. To make the measures comparable with those used in the *arena test* (Section 2.3.4) the first approach to within 0.5 cm of one of the stimuli (as recorded on video) was analysed, rather than the actual touch of the stimulus. This measure was chosen because in the arena test the first approach to a bowl was recorded and analysed.

2.3.7. *Transfer to arena test 2*

After the *touchscreen test* (Section 2.3.6), the tortoises were given a second test in the arena using the same procedure as in the first arena test.

3. Results

3.1. *Habituation*

3.1.1. *Acquisition of touchscreen operation*

All four tortoises learned to operate the touchscreen and to collect rewards from the feeder. Table 1 shows the number of sessions required by each individual to reach the criterion in each pretraining phase.

3.1.2. *Touchscreen training*

Emily and Molly did not progress to this stage as they stopped working during the sequence 2 stage of pretraining. The reason for this is unknown, as up to this stage they had performed reliably and with levels of success comparable to those of Esme and Quinn. Esme and Quinn, however, successfully met the criterion of three above-chance blocks in a row and progressed to the next stage (Fig. 2a). Above-chance performance on a block was determined by a one-sided binomial test with Esme showing 18 ($p < .001$), 19 ($p < .001$) and 15 ($p = .041$) and Quinn 19 ($p < .001$), 17 ($p = .003$), and 20 ($p < .001$) correct responses out of 20 trials.

3.1.3. *Transfer to the arena test 1*

When tested in the arena, both subjects readily approached one of the blue bowls. Each showed a distinct side preference in accordance with the side it was trained initially on the touchscreen (see Fig. 2b), i.e., left side for Esme and right side for Quinn. Binomial

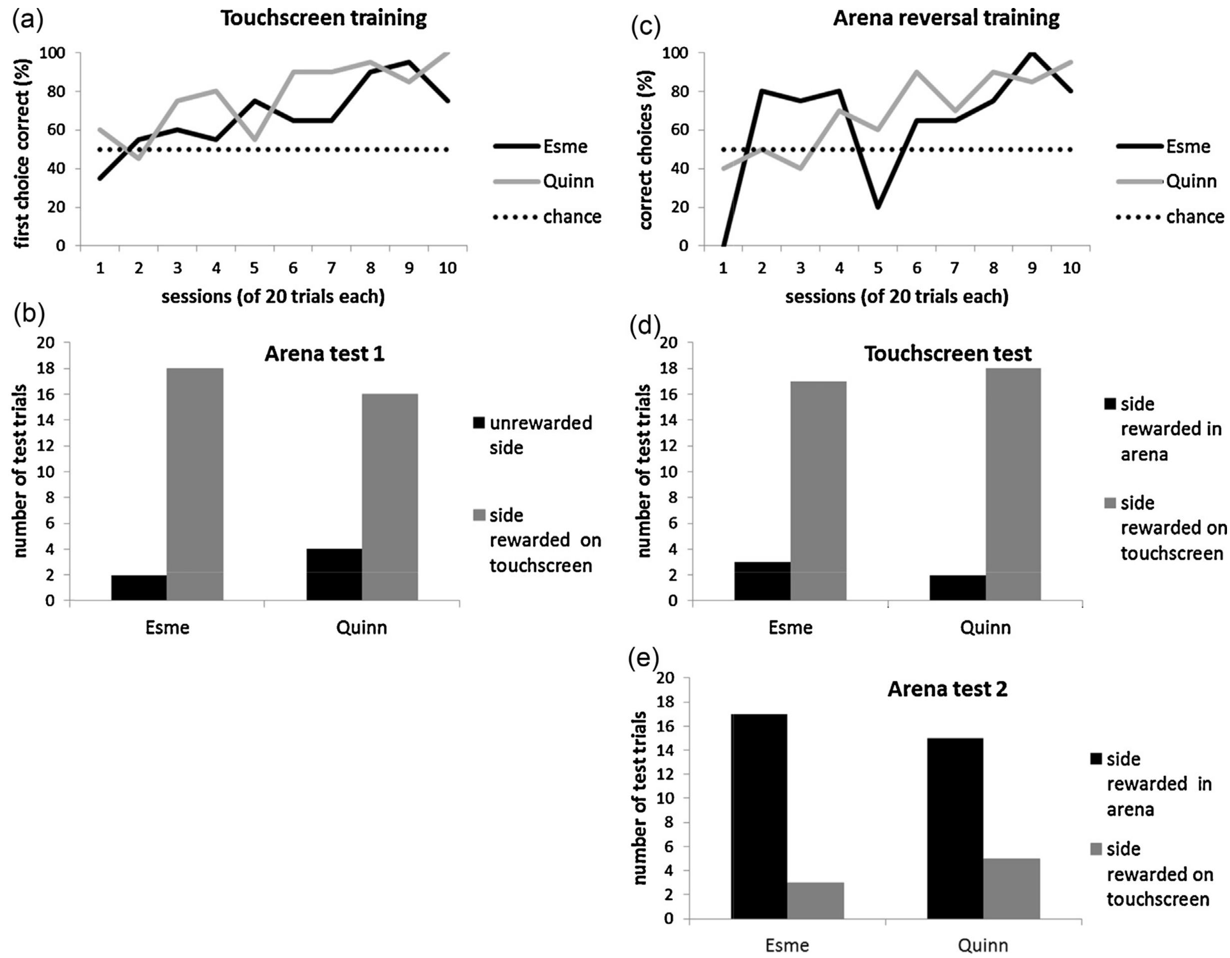

Fig. 2. *Learning curves* for touchscreen and arena training, and test results in both setups for Esme and Quinn.

tests showed that both Esme ($p < .001$) and Quinn ($p = .012$) chose the arena side that was rewarded during touchscreen training significantly more often than would be expected by chance.

3.1.4. Arena reversal training

Esme and Quinn reached the criterion of three blocks with above-chance performance within the minimum number of 200 trials (Fig. 2c). Above-chance performance of a block was determined by a binomial test with Esme showing 15 ($p = .041$), 20 ($p < .001$) and 15 ($p = .041$) and Quinn 18 ($p < .001$), 17 ($p = .003$), and 18 ($p < .001$) correct responses out of 20 trials.

3.1.5. Transfer to the touchscreen test

Upon return to the touchscreen apparatus, each subject tended to choose the side on which it had been trained initially in this apparatus (Fig. 2d). Binomial tests showed that both Esme ($p = .003$) and Quinn ($p < .001$) chose this side significantly more often than would be expected by chance.

3.1.6. Transfer to the arena test 2

Binomial test showed that both Emily ($p = .003$) and Quinn ($p = .041$) tended to choose the stimulus on the side that was rewarded during the previous phase of training (reversal training) in the arena (Fig. 2e).

4. Discussion

The results of the present experiment show that red-footed tortoises are capable of learning to operate a touchscreen Skinner box. This was true of all animals and is the first demonstration of such behaviour in this species, but it is in line with evidence from Bitterman (1964) and Powers et al. (2009), showing that terrapins could learn to use a pecking key. This suggests that tasks involving this sort of response are within the behavioural repertoire of chelonia generally and opens up the possibility for further investigation into the cognitive abilities of these animals.

The two subjects that maintained responding readily learned a simple, two-alternative spatial discrimination. Further, there was some indication of an ability to transfer learning from the touchscreen to a 3-D test arena in that, for the two subjects tested, both showed the same side preference in the arena as that trained on the touchscreen. No firm conclusion can be drawn from observations on only two subjects but this outcome is consistent with the possibility that these animals were able to transfer knowledge from one domain to another. Support for this possibility is provided by the fact that the ability to learn a general rule has been demonstrated for this species by Wilkinson et al. (2010a,b) and Wilkinson and Huber (2012) who found that the tortoises learned the principles of a task when observing a conspecific rather than following the exact path. Clearly, however, it will require further work, with a larger sample of subjects, to establish that tortoises have the ability to generalize across situations in way that is comparable to what has been claimed for some bird species (Kelly and Spetch, 2004; Kelly et al., 1998; Cheng et al., 2006).

Interestingly, the results of the Transfer to touchscreen test are suggestive of a context-specificity of learning, with the appropriate pattern of behaviour being effectively "turned on" by the contextual cues. This is consistent with evidence from rats indicating that the external environment at the time of learning can provide retrieval cues (Bouton and Moody, 2004) that selectively promote the occurrence of behaviour acquired in their presence. In this experiment, tortoises tested on the touchscreen after acquiring a (different) side-preference in the arena, did not select the side that had been rewarded in the arena but reverted immediately to the side that had been rewarded in original training in the touchscreen setup. When, after this, they were given a further test in the arena they immediately switched to showing the side preference that had been trained in that apparatus. Thus, the results indicate that the tortoises were able to distinguish between the two apparatuses and the requirements associated with the two different setups; further, the context appears to be more effective in controlling choice behaviour than the training provided immediately before the test.

In addition to showing that tortoises have the ability to switch between different choice behaviours according to context, the results indicate that they can maintain long-term memory for spatial stimuli. At the time of the touchscreen test the tortoises had not been exposed to the touchscreen setup for over two months during which they were involved in the reversal training in the arena. Despite this break and the potential interference from the reversal training, the tortoises performed significantly above chance in the touchscreen test. This is in line with the findings of Davis and Burghardt (2011) who showed that turtles were able to retain learned information for long periods of time.

In conclusion, red-footed tortoises proved able to operate a touchscreen to learn a simple spatial task. The results of the initial transfer test were consistent with the possibility that knowledge acquired in the touchscreen setup can be transferred to a different domain, an arena. In other tests, however, the context appeared to be able to evoke appropriate behaviour, without evidence of interference from what had been learned in a different context.

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References

Avens, L., Lohmann, K.J., 2003. Use of multiple orientation cues by juvenile loggerhead sea turtles *Caretta caretta*. J. Exp. Biol. 206, 4317–4325.
Bitterman, M.E., 1964. An instrumental technique for the turtle. J. Exp. Anal. Behav. 7, 189–190.
Bouton, M.E., Moody, E.W., 2004. Memory processes in classical conditioning. Neurosci. Biobehav. Rev. 28, 663–674.
Cheng, K., Spetch, M.L., Kelly, D.M., Bingman, V.P., 2006. Small-scale spatial cognition in pigeons. Behav. Processes 72, 115–127.
Davis, K.M., Burghardt, G.M., 2011. Turtles (*Pseudemys nelsoni*) learn about visual cues indicating food from experienced turtles. J. Comp. Psychol. 125, 404–410, http://dx.doi.org/10.1037/a0024784.
DeRosa, C.T., Taylor, D.H., 1980. Homeward orientation mechanisms in three species of turtles (*Trionyx spinifer*, *Chrysemys picta*, and *Terrapene carolina*). Behav. Ecol. Sociobiol. 7, 15–23.
Dutton, P.H., Bowen, B.W., Owens, D.W., Barragan, A., Davis, S.K., 1999. Global phylogeography of the leatherback turtle (*Dermochelys coriacea*). J. Zool. 248, 397–409.
Emlen, S.T., 1969. Homing ability and orientation in the painted turtle *Chrysemys picta marginata*. Behaviour 33, 58–76.
Fagot, J., 2000. Picture perception in animals. Psychology Press, Hove, England.
Healy, S., 1998. Spatial Representation in Animals. Oxford University Press, England.
Kelly, D.M., Spetch, M.L., 2004. Reorientation in a two-dimensional environment: II, Do pigeons (*Columba livia*) encode the featural and geometric properties of a two-dimensional schematic of a room? J. Comp. Psychol. 118, 384–395.
Kelly, D.M., Spetch, M.L., Heth, C.D., 1998. Pigeons' (*Columba livia*) encoding of geometric and featural properties of a spatial environment. J. Comp. Psychol. 112, 259–269.
Lohmann, K.J., Cain, S.D., Dodge, S.A., Lohmann, C.M.F., 2001. Regional magnetic fields as navigational markers for sea turtles. Science 294, 364.
Lohmann, K.J., Lohmann, C.M.F., Ehrhart, L.M., Bagley, D.A., Swing, T., 2004. Geomagnetic map used in sea-turtle navigation. Nature 428, 909–910.
Mueller, J., Wilkinson, A., Hall, G., 2011. Spatial cognition in reptiles. In: Baker, K.J. (Ed.), Reptiles: Biology, Behavior and Conservation. Nova Science Publishers, Hauppauge, NY, pp. 81–100.
Mueller-Paul, J., Wilkinson, A., Hall, G., Huber, L., 2012a. Radial-arm-maze behavior of the red-footed tortoise (*Geochelone carbonaria*). J. Comp. Psychol. 126, 305–317, http://dx.doi.org/10.1037/a0026881.
Mueller-Paul, J., Wilkinson, A., Hall, G., Huber, L., 2012b. Response-based navigation in the jewelled lizard (*Lacerta lepida*). Herpetol. Notes 5, 243–246.
Powers, A.S., Hogue, P., Lynch, C., Gattuso, B., Lissek, S., Nayal, C., 2009. Role of acetylcholine in negative patterning in turtles (*Chrysemys picta*). Behav. Neurosci. 123, 804–809.
Spetch, M.L., MacDonald, S.E., Cheng, K., 1996. Learning the configuration of a landmark array: 1. Touch-screen studies with pigeons and humans. J. Comp. Psychol. 110, 55–68.
Steurer, M., Aust, U., Huber, L., 2012. The Vienna Comparative Cognition Technology (VCCT): an innovative operant conditioning system for various species and experimental procedures. Behav. Res. Methods 44, 909–918, http://dx.doi.org/10.3758/s13428-012-0198-9.
Strong, J.N., Fragoso, J.M.V., 2006. Seed dispersal by *Geochelone carbonaria* and *Geochelone denticulate* in Northwestern Brazil. Biotropica 38, 683–686.
Wilkinson, A., Huber, L., 2012. Cold-blooded cognition: reptilian cognitive abilities. In: Vonk, J., Shackelford, T.K. (Eds.), The Oxford Handbook of Comparative Evolutionary Psychology. Oxford University Press, New York, NY, http://dx.doi.org/10.1093/oxfordhb/9780199738182.013.0008.
Wilkinson, A., Chan, H.M., Hall, G., 2007. A study of spatial learning and memory in the tortoise (*Geochelone carbonaria*). J. Comp. Psychol. 121, 412–418.
Wilkinson, A., Coward, S., Hall, G., 2009. Visual and response-based navigation in the tortoise (*Geochelone carbonaria*). Anim. Cogn. 12, 779–787.
Wilkinson, A., Künstner, K., Mueller, J., Huber, L., 2010a. Social learning in a non-social reptile (*Geochelone carbonaria*). Biol. Lett. 6, 614–616.
Wilkinson, A., Mandl, I., Bugnyar, T., Huber, L., 2010b. Gaze following in the red-footed tortoise (*Geochelone carbonaria*). Anim. Cogn. 13, 765–769.
Wilkinson, A., Mueller-Paul, J., Huber, L., 2013. Picture-object recognition in the tortoise (Geochelone carbonaria). Anim. Cogn. 16, 99–107, http://dx.doi.org/10.1007/s10071-012-0555-1.