CONDITIONAL SAME/DIFFERENT CONCEPT LEARNING IN THE SHORT-BEAKED ECHIDNA (TACHYGLOSSUS ACULEATUS)

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Echidnas have evolved separately from other mammalian groups for around 200 million years and incorporate a mixture of reptilian and mammalian features. Because of these attributes, they have historically been considered "primitive" animals. However, they have successfully adapted to a wide variety of ecological niches and their neurophysiology demonstrates a number of unusual and apparently sophisticated characteristics, including a relatively large brain and cerebral cortex and a comparatively massive frontal cortex. Studies of learning in the echidna have thus far been limited to only a handful of experiments which demonstrated relatively basic abilities such as forming a position habit in a T-maze, successive habit-reversal learning, and simple visual and instrumental discrimination. This study aimed to expand on these results and test the "primitive" echidna on what are generally considered more advanced cognitive tasks—same/different and conditional same/different concept learning. The results demonstrated that echidnas are able to discriminate on the basis of a relational same/different concept, using simultaneously presented multi-element stimuli, and transfer that discrimination to novel stimuli. After further training, they were then able to repeat the performance when the correct choice was conditional on the background color of the stimulus panels.
Key words: echidna, same/different concept, conditional discrimination

Further studies of learning will undoubtedly disclose important facts about the intelligence of these remarkable animals and modify the quaint, explicitly and tacitly-held views that echidnas are little more than animated pin-cushions or, at best, glorified reptiles.– *Buchmann and Rhodes (1978, p. 144)*

There is little doubt echidnas are "remarkable animals": Covered in both sharp spines and fur with a long snout and even longer tongue, they lay eggs like a reptile, have a pouch like a marsupial, and suckle their young like all mammals. The short-beaked echidna (*Tachyglossus aculeatus*) is a member of one of three extant species of monotremes together with the long-beaked echidnas and the platypus. Fossil records and genetic studies indicate monotremes have evolved independently from all other mammals for at least 120 million years and likely more than 200 million years (Clemens, 1979; Krubitzer & Campi, 2009; Madsen, 2009; Musser, 2003; O'Brien & Graves, 1990; Phillips, Bennett, & Lee, 2009; Woodburne, Rich, & Springer, 2003).

Their evolutionary history has influenced how monotremes are viewed in the scientific community, particularly as they are generally considered to be the mammals most distantly related to humans (Krubitzer, Manger, Pettigrew, & Calford, 1995). They have historically been referred to as mammals of the "lowliest status" (Elliot Smith, 1902) and "living fossils" (Darwin, 1959), and are still viewed by many scientists as "primitive" (Ashwell, Paxinos, & Watson, 2007; Musser, 2003). This view is compounded by the fact that monotremes, in addition to their mammalian characteristics, display numerous plesiomorphic reptilian traits in their anatomy, physiology, and reproduction, such as laying keratin-covered eggs and having a single cloacal outlet (Augee, Gooden, & Musser, 2006; Griffiths, 1989).

Because of its status as a "primitive" animal, it is often assumed that the echidna would be incapable of complex cognitive tasks. This bias

stems from the outdated idea of a phyloge-
netic intelligence hierarchy, in which intelli-
gence is distributed in an ordinal progression
based on a phylogenetic scale from simplest
(least intelligent) to most complex (most intel-
ligent) (Jensen, 1980), an idea that has been
heavily criticized (Deacon, 1990; Hodos &
Campbell, 1969; Mackintosh, 1988; Salas, Bro-
glio, & Rodriguez, 2003; Tomasello & Call,
1997). The adaptive, branching nature of evo-
lution means there is no sequential increase in
complexity—phylogeny cannot be used to
organize animals into a single, hierarchical
scale, let alone according to some ill-defined
concept of general "intelligence" (Mackintosh,
1988; Shettleworth, 1993).

An alternative approach to the phylogenetic
hierarchy theory is that of mosaic evolution, in
which each ecological problem leads to the
development of a separate cognitive mechan-
ism, or module (Musser, 2003; Northcutt &
Kaas, 1995; Shettleworth, 1998). According to
this approach, each ecologically distinct group
will evolve those modules required by the
demands of its environment (Shettleworth,
1998). This would suggest that a greater vari-
ety of ecological challenges would lead to the
development of a broader range of cognitive
abilities. The short-beaked echidna inhabits an
extensive range of environments as the most
widely distributed native mammal in Australia;
it is found in every major terrestrial ecosystem
from desert to alpine; and, together with the
house mouse, it has the most widely divergent
habitats of any mammalian species (Augee
et al., 2006; Griffiths, 1968, 1978).

Mosaic evolution provides an explanation
for why highly specialized or advanced fea-
tures can occur alongside archaic features
(Musser, 2003), and the echidna's neurophysi-
ology provides a striking example. While its
brain does retain some "primitive" features,
studies have almost universally indicated that
the echidna's brain is in many respects much
more "advanced" than its evolutionary history
or physiology might suggest (Ashwell, 2013;
Divac, 1995). Echidnas have large brains rela-
tive to their weight, body size, spinal cord
mass, and basal metabolic rate (Divac, 1995;
Hassiotis, Paxinos, & Ashwell, 2003; Jerison,
1973), with a high proportion of cerebral cor-
tex (Pirlot & Nelson, 1978) and cortical sur-
face area and thickness (Hassiotis et al., 2003),
as well as a relatively complex sensory cortex

(Krubitzer et al., 1995). Their neocortex is
also markedly gyrencephalic (folded), in con-
trast to the neocortex of the platypus and
many marsupials (Griffiths, 1989; Rowe & Boh-
ringer, 1992).

The most notable aspect of the echidna's
brain is the size of the prefrontal cortex, which
takes up a remarkable 50% of the cerebral
cortex, proportionately more than any other
animal, including humans (Augee & Gooden,
1993; Lende, 1969; Rowe, 1990). Whether the
prefrontal region in the echidna can be con-
sidered comparable with that found in pri-
mates should obviously be approached with
caution. However, it is worth noting the results
of numerous comparative microcircuitry stud-
ies (e.g. Divac, Holst, Nelson, & McKenzie,
1987; Divac, Pettigrew, Holst, & McKenzie,
1987; Hassiotis et al. 2003; Krubitzer et al.,
1995; Welker & Lende, 1980) which led Has-
siotis et al. (2003) to declare that, in most
structural parameters, the echidna's cerebral
cortex is "comparable to those placental mam-
mals usually considered neurologically
advanced and behaviorally complex" (p. 848).

The echidna's seemingly advanced brain
features, together with its diverse ecological
range and unique evolutionary history, make
it a compelling subject for cognitive testing. It
is an ideal candidate to explore competing
theories of cognitive evolution by examining
whether a phylogenetically and physiologically
"primitive" species can perform what are gen-
erally considered to be "advanced" cognitive
tasks. Using an echidna as a subject also
expands on the comparatively small number
of species used for cognitive testing, and its
distinct evolutionary history means these
results provide a valuable comparison to the
cognitive development of more commonly
studied species.

However, studies of learning in the echidna
have thus far been limited to only a handful of
relatively simple experiments. These have
demonstrated that echidnas: are capable of
easily forming a position habit in a T-maze
(Saunders, Teague, Slonim, & Pridmore,
1971); show rapid improvement across a series
of successive habit-reversals (Saunders,
Chen, & Pridmore, 1971); are capable of
learning basic visual discriminations (Gates,
1973, 1978); and perform well in instrumental
(operant) discrimination tests (Buchmann &
Rhodes, 1978).

To examine whether echidnas are more cognitively capable requires testing them with more challenging tasks. Relational concept learning, in which stimuli are discriminated based on their relationship to one another irrespective of their specific attributes, is considered higher-order learning by many authors (e.g. Herrnstein, 1990; Huber, 2001; Wasserman, Hugart, & Kirkpatrick-Steger, 1995; Wright, Rivera, Katz, & Bachevalier, 2003; Zayan & Vauclair, 1998). In his hierarchy of learning abilities, Thomas (1996) placed relational categorization at level 6 on an 8-level scale of increasing complexity.

The most commonly studied relational concept is that of sameness versus difference, in which stimuli are discriminated based on whether they are all the same or all different, irrespective of the particular stimuli presented. Different procedures have been used to test for the same/different concept in animals, including matching-to-sample (MTS) and oddity-from-sample (OFS), in which subjects are required to select one of a number of stimuli that are the same as (MTS) or different from (OFS) a previously presented sample stimulus, and the same/different task, in which the subject makes a decision based on simultaneously presented stimuli. MTS and OFS, using successive presentation of stimuli, have been demonstrated in a wide variety of nonhuman species such as chimpanzees (Oden, Thompson & Premack, 1988), monkeys (D'Amato & Colombo, 1985), gorillas and orangutans (Vonk, 2003), rats (April, Bruce, & Galizio, 2011), pigeons (Zentall & Hogan, 1975), dolphins (Herman & Gordon, 1974), sea lions (Kastak & Schusterman, 1994), corvids (Wilson, Mackintosh, & Boakes, 1985), parrots (Suková, Uchytilová, & Lindová, 2013), horses (Gabor & Gerken, 2012), budgerigars (Manabe, Kawashima, & Staddon, 1995), goldfish (Goldman & Shapiro, 1979), and honeybees (Giurfa, Zhang, Jenett, Menzel, & Srinivasan, 2001). However, there is some debate about whether matching and oddity tasks demonstrate a relational concept rather than the subject merely responding to whether the item has been seen before (Premack, 1983).

There is more support for a conceptual explanation using the same/different simultaneous-presentation method, which is considered more difficult and has been demonstrated in fewer species (Castro, Kennedy, & Wasserman, 2010; Premack, 1983, Shettleworth, 1998). When initially only primates proved successful, including rhesus monkeys (Bhatt & Wright, 1992), capuchin monkeys (Wright et al., 2003), baboons (Bovet & Vauclair, 2001), and chimpanzees (Premack, 1971), it was suggested to be unlikely that any nonprimate would be capable of mastering the simultaneous same/different task (Premack, 1983). However, the introduction of different experimental procedures, such as increased sample size and the use of multi-element displays, led to success with other species such as coatis (Chausseil, 1991) and pigeons (Wasserman et al., 1995). The list has since expanded to include more species such as harbor seals (Scholtyssek, Kelber, Hanke, & Dehnhardt, 2013), corvids (Magnotti, Katz, Wright, & Kelly, 2015), and colonies of bees (Brown & Sayde, 2013).

Because it was more likely to provide evidence of conceptual learning, it was decided to use a simultaneous same/different task in this study. If the subject was successful, then a more complex task could be tested by adding a conditional parameter to the same/different task (level 7 of Thomas', 1996, learning-intelligence hierarchy), in which a second layer of stimuli would be used to inform the subject which stimulus was correct on any given trial. While there have been a number of conditional matching studies, conditional same/different concept learning has so far been demonstrated in only a few species including monkeys (Burdyn & Thomas, 1984; Flemming, 2011; Flemming, Beran, & Washburn, 2007) and pigeons (Castro et al, 2010; Castro & Wasserman, 2010).

General Method

Subject

The subject of all the experiments in this study was a 13-year-old female short-beaked echidna (subspecies *Tachyglossus aculeatus aculeatus*) kept at Taronga Zoo in Sydney, Australia. The subject, named Pitpa (ARKS number 870143, Fig. 1), was born in captivity and was parent-reared. Pitpa was weighed monthly throughout the course of the study and maintained an average weight of around 4.5-5 kg. She experienced no major health problems during the experiments.

Pitpa was an experimentally naïve subject who had previously only experienced normal husbandry activities with zoo staff, but was used to regular handling as part of animal education talks. The subject was housed off-exhibit in a 10 m x 10 m open enclosure containing the experimental apparatus together with another echidna who did not participate in the study.

It was originally planned that this experiment would be conducted using more than one subject. However, one of the problems with conducting experimental studies with echidnas is the difficulty in obtaining and maintaining subjects. As a protected species, it is hard to get permission to take echidnas from the wild (Gates, 1973; Nicol, 2003), and wild-caught echidnas can also be difficult to keep healthy in captivity (Gates, 1973). In this case, the zoo's other captive echidnas were either unavailable or unused to being handled. Echidnas are difficult to habituate to handling (Gates, 1973), and while attempts to habituate two other echidnas were made for several weeks, due to time constraints and ethical considerations, it was decided not to continue.

Although the use of one subject is not optimal, the objective of this type of study is to determine what members of a species *can* do. Abilities demonstrated by an individual show those abilities are within the capacity of that species (Hanggi, 1999; Pepperberg & Brezinsky, 1991). This type of testing with a single subject has an established history, including a number of well-known experimental series such as Irene Pepperberg's cognitive experiments with Alex the African Grey parrot (e.g. Pepperberg, 1983, 1987; Pepperberg & Brezinsky, 1991), Kastak and Schusterman's equivalence studies using a single California sea lion, Rio (Schusterman & Kastak, 1998), and a number of long-term primate language studies (Gardner & Gardner, 1969; Savage-Rumbaugh & Lewin, 1994). Single-subject studies have also been conducted with a dolphin (Roitblat, Penner, & Nachtigall, 1990), a chimpanzee (Gillan, Premack, & Woodruff, 1981; Tanaka, 1996), and a harbor seal (Hanggi & Schusterman, 1995).

Apparatus

The apparatus was a custom-built plywood y-maze variant, with dimensions as shown in Figure 2, with the third maze arm blocked off for these experiments. The front wall of the start box contained two hinged swinging doors on which laminated stimulus panels were fixed with Velcro, which the subject pushed through to enter one of the two maze arms (see Fig. 3). The design using stimulus panels attached to push-through doors is similar to that used by Gates (1978) in his study of visual discrimination in the echidna and also in
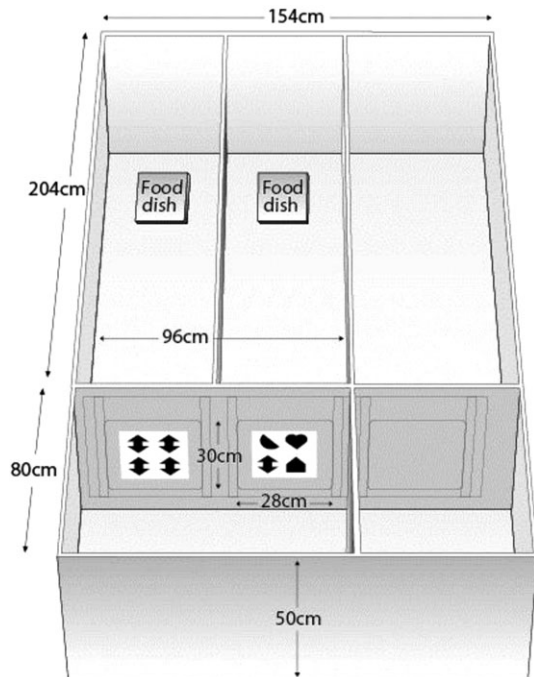

Fig. 1. Pitpa in the Taronga Zoo enclosure.

Fig. 2. Three-dimensional diagram of the apparatus showing stimulus panels and covered food dishes.

Fig. 3. Pitpa pushing through a swing door.

Sappington and Goldman's (1994) examination of concept formation in horses.

Located in each maze arm was a round metal food dish. To control for olfactory cueing, the food dishes were located at the end of the approximately 2-m long maze arms and each dish was covered with a 20 cm x 20 cm x 2 cm wooden lid. Earlier experiments conducted at Taronga Zoo (Burke, Cieplucha, Cass, Russell, & Fry, 2002; Quince, 1998) had demonstrated that the wooden lids prevented echidnas from locating food in the covered dishes on the basis of olfactory cues.

Stimuli

Each stimulus consisted of a 21 cm x 21 cm black-and-white laminated panel containing pictures of solid geometric and irregular shapes. The echidna's visual capacity was taken into account in determining the nature of the stimulus items. The echidna's visual anatomy is an unusual mix of mammalian and reptilian characteristics and was historically considered to be very limited (Augee et al., 2006; Gates, 1978). Echidnas do rely more on their other senses to forage (Gates 1978; Griffiths 1968); however, experiments by Gates (1973, 1978) showed they have visual acuity equal to that of a rat and can discriminate stimuli on the basis of black/white and geometric shapes. Shapes were also selected as stimulus items as they have proved a popular choice for categorization experiments with a number of other less visually capable species, for example, coatis (Chausseil, 1991) and horses (Hanggi, 1999).

The same/different stimulus items in the experimental phase of this study were presented in multi-element arrays on panels made up of either all the same or all different elements in a design similar to Wasserman et al. (1995). Each stimulus panel contained four elements, each approximately 6–10 cm wide. One consideration in selecting the number of shapes on each panel was the suggestion that the Wasserman et al. (1995) same/different study may have been solved on the basis of a generalizable order–disorder rule due to the fact that the 16-element *same* arrays had a greater linear orderliness of rows and columns than the *different* arrays (Young & Wasserman, 1997). While later experiments indicated that pigeons were able to successfully perform the task using nonlinear, disorderly arrays (Young & Wasserman, 1997), the use of four rather than 16 items in the arrays for this experiment reduced the chance of this effect confounding the results. With only two items in any direction it was unlikely that perceptual grouping principles would organize the display into rows or columns (Palmer & Rock, 1994). Fewer items also reduced the likelihood of an entropy-based explanation for the subject's performance, as fewer items yield a smaller difference in variability between the *same* and *different* arrays than arises with higher-item arrays (Young & Wasserman, 1997) (see discussion below).

The shapes used on the stimulus panels were selected to include both regular and irregular shapes of different surface areas and orientations in order to deter the subject from using perceptual cues such as uniformity, regularity, or relative brightness, a criticism that has been levelled at other same/different experiments (Delius, 1994).

As with Wasserman et al.'s (1995) study, the same shapes were used in both the *same* and *different* panels to control for item-specific cueing from individual shapes. For similar reasons, the six shapes used in the *same* panels for the same/different experiments were each used the same number of times (four) in the six *different* panels. Each shape also appeared in different positions on the panel as far as was possible—three of the shapes appeared in all four positions, while the other three shapes appeared in three different positions and appeared in one of the positions twice.

For the conditional phases of this study, the stimuli were designed to contain both the shape elements and conditional cues in the form of the background color of the panels. This combined-stimulus method has also been used to study conditional same/different categorization in pigeons (Castro et al., 2010) and monkeys (Flemming, 2011; Flemming et al., 2007).

Procedure

Because of the echidna's tendency to sleep for some of the day or enter torpor for short periods even in warmer weather (Grigg, Beard, & Augee, 1989), it was decided to begin testing only when the subject was awake and motivated. The session was initiated when the subject indicated a willingness to proceed by displaying behaviors such as approaching and interacting with the experimenter and the apparatus. Lack of motivation was considered indicated when the subject stayed buried in the enclosure after the experimenter entered, even when tempted with food.

In order to minimize stress on the subject and reduce the chance of her losing interest, it was decided in conjunction with zoo staff to limit the amount of time Pitpa spent being tested. One session of trials was conducted per day. The session was concluded when 10 correct choices were made, although there was no upper limit set on the number of trials it took the subject to reach that criterion. A reward of 10 ml of food was given per correct trial and the echidna's regular daily food allotment of 100 ml was consumed during the session. The echidna's zoo-supplied food mix consisted of minced beef, wheatbran, eggs, and olive oil, as well as vitamin, mineral, and glucose supplements (Glucodin, Equine E, Calcium carbonate, and Soluvet). Food limitation was not used during the study and no additional food was given other than insects caught by the animal in the enclosure.

A trial consisted of the simultaneous presentation of one pair of stimuli. One correct (S+) and one incorrect (S-) stimulus panel were attached to the two swinging doors in the apparatus. Food dishes with lids were placed at the ends of the maze arms, with the dish behind the S+ stimulus containing food, the other empty. For each day's session, only one of the dishes was used to contain the food

reward, the other remained empty so there was no possibility of even a small reward for an incorrect choice. The dishes were swapped between the maze arms so the dish containing food was always located behind the correct stimulus.

At the start of each trial, the subject was held at the back and centre of the start box at eye-level to the stimulus panels for approximately 3–5 s of viewing time, then placed straight down on the ground. The viewing period was introduced to counteract the subject's initial tendency to rush the doors without looking and also to increase the sample exposure time in line with sample identification theories which suggest it provides increased sample encoding and choice confidence (Roitblat & Harley, 1988; Roitblat et al., 1990), effects demonstrated in other same/different studies (e.g., Bailey & Thomas, 1998). A choice was considered to have been made when the subject pushed through one of the doors. In common with Gates' (1973) procedure, an error was not recorded if the subject approached, but did not push the incorrect door.

After Pitpa either ate the food at the end of the maze arm or lifted the lid to discover an empty food dish, she was placed into a holding bin during the intertrial period of approximately 2 min while the food dishes and stimuli were changed. The echidna could not see out of the bin to observe into which maze arm the food was placed.

Measures were taken to control for auditory cues, both from the noise of the Velcro on the stimulus panels and from the sounds of the experimenter and the dishes. Regardless of whether the panels had to be changed or not, both panels were removed and replaced for each trial. The experimenter stood in the same maze arm each time the food dish was replenished irrespective of which maze arm the food dish was located. In addition, both dishes and both lids were picked up and put down whether or not the dish containing food had to be swapped into the other maze arm.

To control for position habit, the S+ and S- stimulus panels were randomly placed on the left and right doors according to a schedule generated at www.randomizer.org. The S+ and S- stimulus panel sets were each shuffled between trials to randomize the stimuli.

To determine whether Pitpa had learned the task and not just memorized the training stimuli, transfer trials using novel stimuli were conducted. During the transfer trials, novel pairs of stimuli were randomly introduced throughout each session (using the randomization schedule) to ensure the subject did not become confused about the task, leading to an overall deterioration in performance (Thompson, 1995).

The differential reinforcement (rewarding only correct responses) that was used in the training phase of each experiment was also used in the transfer trials to enhance detection of the rate of learning the novel stimuli (Flemming et al., 2007; Zentall & Hogan, 1975). The novel stimuli contained all new shapes, so there would be no confounding influence from previously seen items (Wasserman et al., 1995).

Analysis of Results

To obtain a more reliable estimate of performance than is reflected in individual sessions, the data for each experiment were pooled into blocks of sessions for statistical analysis. The criterion for the training phase of each experiment was two consecutive blocks significantly different from chance. For the transfer trials, the criterion was one block significantly different from chance and no significant difference between the training and transfer blocks.

Due to the time constraints on the availability of the subject, both in terms of how long the zoo would allow the subject to be off-exhibit and the fact that echidnas periodically enter torpor and sometimes true hibernation during colder weather (Augee & Gooden, 1993), it was decided to limit each experiment to a maximum of 20 sessions.

Discrimination Training

Following an initial period familiarizing the subject with the experimental apparatus and procedures, the first phase of the study consisted of training the subject on basic color, shape, and conditional discriminations. Pitpa learned to discriminate between a black and a white stimulus panel, as well as between stimulus panels containing a black circle and a black triangle on white backgrounds,

confirming the findings of Gates (1973, 1978) that echidnas are capable of performing black/white and shape discriminations. Pitpa was then successfully taught to perform a simple conditional discrimination in which she had to choose the circle shape when the stimulus panels featured black shapes on a white background and the triangle shape when the panels featured white shapes on a black background. (The circle and triangle shapes were not used again during the rest of the study).

Experiment 1

Prior discrimination training showed the subject was capable of performing discriminations based on color and shape; however, these stimuli are defined by simple physical characteristics. This experiment attempted to determine whether an echidna could discriminate between stimuli that have more abstract properties emerging out of the relationship between stimuli rather than the stimuli themselves. Experiment 1 tested the same/different relational concept, with the S+ stimulus being *same*. To ensure the subject was not merely memorizing all of the stimuli, transfer trials were conducted using novel stimuli.

Stimuli

For this experiment, the stimuli all had black backgrounds, each containing four white shapes. There were six distinct *same* panels containing four identical shapes and six distinct *different* panels containing four nonidentical shapes made up of combinations of the shapes used for the *same* panels. The six shapes were each used the same number of times in the six *different* panels and, as far as possible, in different positions (see Fig. 4).

For the transfer trials, six new *same* panels and six new *different* panels were introduced using six novel shapes (see Fig. 5).

Results

The learning phase results were pooled into two blocks of six sessions, with the transfer trials a separate block of six sessions, and the results analyzed using a two-tailed binomial test. The results were graphed (see Fig. 6) and analyzed using two measures of performance:
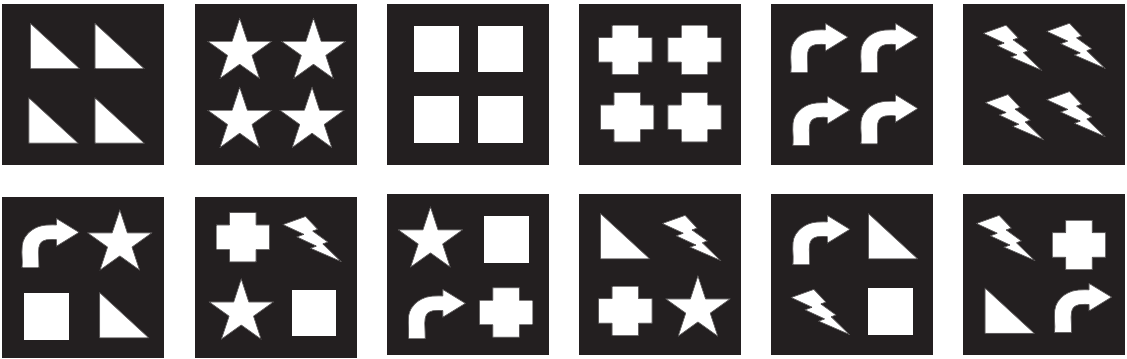
Fig. 4. Stimulus panels for Experiment 1 – same/different discrimination, S + = *same*.
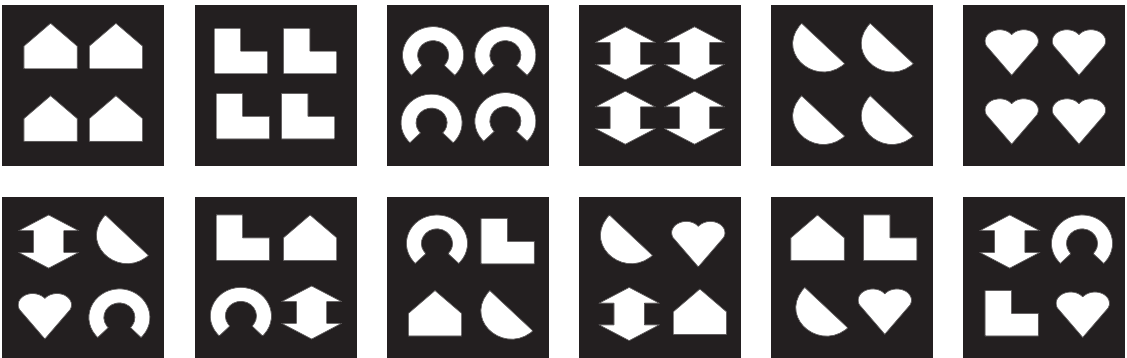

Fig. 5. Novel stimulus panels for Experiment 1 – transfer of same/different discrimination, S + = *same*.
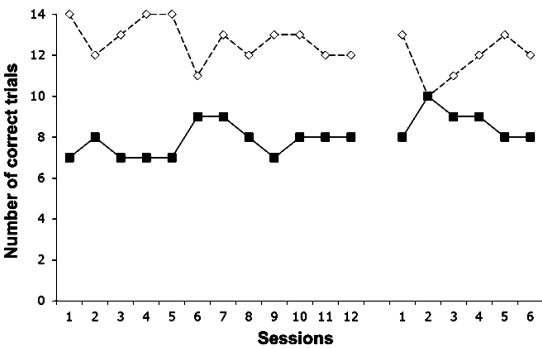

Fig. 6. Number of correct responses to same/different task, S + = *same*. The first 12 sessions show the learning phase, the subsequent six sessions show the transfer trials. ◇ = the number of trials until 10 correct responses were made, ■ = the number of correct responses in the first 10 trials.

y/10 (y = the number of correct responses in the first 10 trials) and 10/x (x = the number of trials until 10 correct).

Training trials. In the learning phase, performance was significantly different from chance in the first block (y/10: correct responses = 45/60, $z = 3.87$, $p < .001$; 10/x: correct responses = 60/78, $z = 4.76$, $p < .001$) and the second block (y/10: correct responses = 48/60, $z = 4.65$, $p < .001$; 10/x: correct responses = 60/75, $z = 5.20$, $p < .001$).

Transfer trials. Performance in the transfer phase was also significantly different from chance (y/10: correct responses = 52/60, $z = 5.68$, $p < .001$; 10/x: correct responses = 60/71, $z = 5.82$, $p < .001$) and was not significantly different from performance in the second block of the training phase using a chi-squared test on 10/x data ($x^2 = 0.51$, $p = 0.48$). On Day 1 of the transfer trials, performance on the novel stimuli was greater than chance and even slightly higher than that for the repeated training stimuli—83% correct (novel stimuli) versus 71% correct (training stimuli).
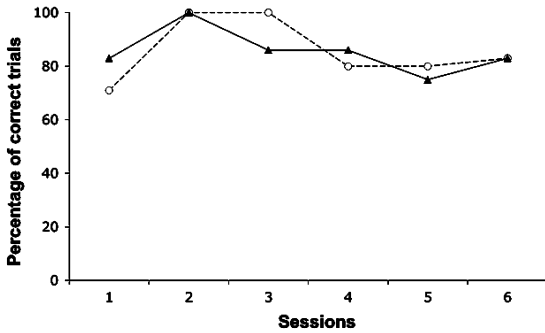
Fig. 7. Percentage of correct responses to training and novel stimuli during same/different transfer trials. S + = *same* (using 10/x data, x = the number of trials until 10 correct). ○ = percentage of correct responses to training stimuli, ▲ = percentage of correct responses to novel stimuli.

Using the 10/x data, the results were analyzed to compare the subject's performance on the novel stimuli to that of the training stimuli used in the transfer trials (training stimuli = 28/33 correct, novel stimuli = 32/38 correct). A chi-squared test found no significant difference between performance on the training and the novel stimuli ($x^2 = 0.01$, $p = 0.94$). The results were then converted into percentages in order to graphically compare the varying proportions of each stimulus type in each session caused by the randomization procedure (see Fig. 7).

Discussion

This experiment showed that an echidna was able to categorize stimuli on the basis of the same/different concept, the first time this ability (or any form of categorization) has been demonstrated in a monotreme. The fact that the results in the transfer trials were not significantly different from those of the second block of the learning phase, and that there was no significant difference in performance between the training and novel stimuli in the transfer trials, indicates she was not merely memorizing the stimuli, but had learned to apply a generalized same/different rule. The parity of Pitpa's performance between the training and test stimuli in the transfer trials is in contrast to that found in a perceptual categorization task with pigeons using a similar testing procedure with interspersed novel and repeating stimuli (Bhatt, Wasserman, Reynolds, & Knauss, 1988). While the pigeons

in that study were able to categorize the novel stimuli at levels exceeding chance, they performed better on the repeated stimuli suggesting that, unlike Pitpa, memorization may have facilitated their performance.

This ability to transfer performance to novel stimuli is the generally accepted criterion for same/different concept learning (Thompson, 1995; Wasserman et al., 1995); however some authors have created more rigorous criteria. One such criterion is that transfer be equivalent to baseline with both performances above 80% to ensure that the subject is utilizing relational information in both the transfer and training trials (Wright & Katz, 2006). Pitpa was able to satisfy this requirement, with an average of 80% correct in the final block of the training trials and an average of 87% in the transfer block.

Another criterion is that the demonstration of "conceptual" behavior must be based on first-trial transfer data (Chausseil, 1991; Herman, Pack, & Wood, 1994; Macphail, 1982; Pearce, 1997; Thomas, 1996). Although this requirement is by no means universally accepted due to its limited statistical power (Wright & Katz, 2006), it is worth noting that Pitpa's Day 1 transfer performance was substantially better than chance. This rapid acquisition was no doubt facilitated by the fact that Pitpa had already undertaken training trials in basic discriminations (see above) during which her performance started at chance and was strongly influenced by positional bias (e.g. "choose left") then rapidly improved as she became used to the experimental procedure and learned to make choices based on stimulus information.

This study utilized multi-element stimulus arrays similar to those used by Wasserman et al. (1995), but containing fewer elements than many similar studies. This was done to help compensate for the echidna's relatively limited visual acuity, but also served to reduce the potential for perceptual cues contained in multi-element arrays that have raised questions about the results of other studies.

One such cue is uniformity, in which the *same* arrays appear to have a greater linear orderliness of rows and columns (Young & Wasserman, 1997). The likelihood of uniformity playing a role in stimulus selection in this study was reduced by the use of only four items per stimulus panel, as well as the

selection of shapes of different surface area, regularity, and orientation.

Another cue is entropy, a measure of variability that some authors believe might be behind the success of experiments using multi-element displays (Young & Wasserman, 1997). The higher the number of items in the multi-element arrays, the greater the entropy of the *different* displays and the greater the difference between them and the (zero entropy) *same* displays. It has been suggested that the only way to eliminate entropy as a factor and ensure relational information is utilized is to use only two items (Blaisdell & Cook, 2005; Premack, 1983).

This study used four items—a lower number than that used in most multi-element displays, but still higher than the two-item "gold standard". However, it could be argued that the entropy difference between a two- and four-item display is still fairly negligible. Although the 16-item *different* multi-element arrays often used by Wasserman and colleagues (e.g., Wasserman et al., 1995; Young & Wasserman, 1997) have an entropy value of 4.00, the entropy value of a four-item *different* display is 2.00, much closer to that of a two-item display with an entropy value of 1.00. In addition, experiments with a number of species have indicated that the point at which entropy differences become manifest is around eight items (a *different* stimulus entropy value of 3.00) (Castro et al., 2010; Flemming et al., 2007; Wasserman, Young, & Fagot, 2001; Young, Wasserman, & Garner, 1997). For example, Castro et al. demonstrated that pigeons could perform a conditional same/different discrimination using 24-, 20-, 12- and 8-icon arrays, but found accuracy declined with 4- and 2-icon arrays.

Another interesting aspect of this experiment is the fact that Pitpa was able to correctly transfer to novel stimuli after training with a relatively small training set of just six *same* and six *different* stimulus panels. There is some debate about whether a small training set size is more or less likely to lead to stimulus generalization rather than true concept transfer (Wright & Katz, 2007), however it has also been suggested that training set size may represent a quantitative difference in performance in same/different categorization, with smaller set sizes usually associated with primates (Wright et al., 2003).

In addition to learning with a small set of training stimuli, Pitpa was able to successfully transfer performance to novel stimuli after just 153 training trials (including both correct and incorrect responses). Although this is relatively high compared to some primate studies (D'Amato, Salmon, & Colombo, 1985; Oden et al., 1988), it is considerably less than is typical for pigeons, which can require thousands of trials to reach criterion even when utilizing multi-element displays (Wasserman et al., 1995). One possible reason for Pitpa's relatively rapid acquisition using low-entropy stimuli and a small training set is the fact that this study incorporated a number of procedural elements that have previously been associated with improved same/different relational learning–multi-element stimuli, simultaneous presentation of stimuli, direct stimulus contact and relatively simple stimulus items (Blaisdell & Cook, 2005; Castro et al., 2010; Chausseil, 1991; Flemming, 2011; Wasserman et al., 1995).

Experiment 2

In Experiment 1, the subject successfully learned to discriminate on the basis of the same/different concept and in discrimination training at the start of the study was able to perform a conditional discrimination based on shape. This experiment attempted to combine these two abilities and determine if the subject could perform a conditional discrimination based on the same/different concept. This time the S+ for each trial was conditional on the background color of the stimulus panels.

Stimuli

For this experiment, there were two sets of multi-element stimuli. The first set was the transfer stimulus panels used in Experiment 1 (Fig. 5) in which each panel contained four white shapes on a black background. There were six distinct *same* panels containing four of the same shapes and six distinct *different* panels containing four different shapes made up of combinations of the shapes used for the *same* panels. The six shapes were each used the same number of times in the six *different* panels and, as far as possible, in different
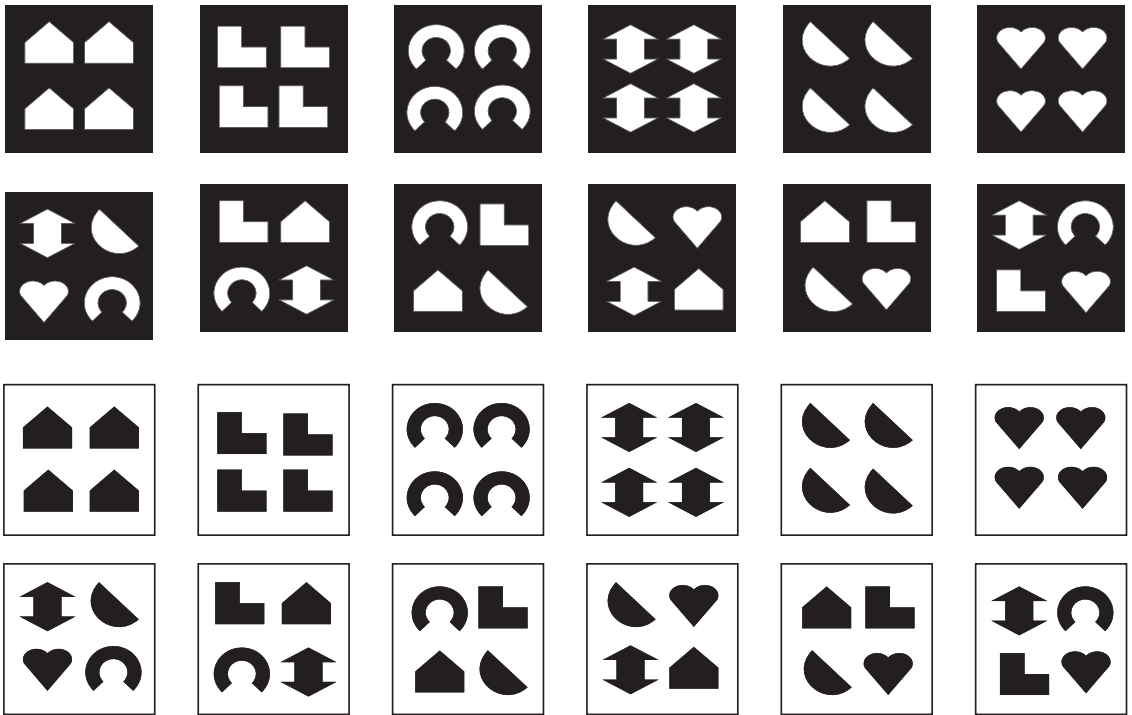
Fig. 8. Stimulus panels for Experiment 2 – conditional discrimination. S + = *same* (white-on-black panels), *different* (black-on-white panels). The *same* panels are the transfer panels used in Experiment 1 (Fig. 5).

positions. The other set of stimuli were identical to the first, except they contained black shapes on a white background (see Fig. 8).

For each trial, the subject was shown a pair of stimuli from either the white-on-black or the black-on-white set which each contained a *same* and a *different* panel. She had previously been rewarded for choosing *same* when using the white-on-black panels in Experiment 1 and that condition was also reinforced here. However, in this experiment, when the subject was presented with a pair of black-on-white panels she was reinforced for selecting *different*. The randomization schedule described earlier was used to determine whether a stimulus pair from the white-on-black or the black-on-white set was used in each trial.

Results

The trials were grouped into four blocks of five sessions. The results (shown in Fig. 9) were analyzed with a two-tailed binomial test using two measures of performance—y/10 (y = the number of correct responses in the
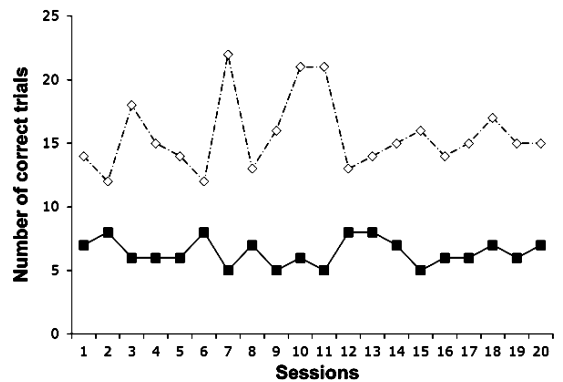

Fig. 9. Number of correct responses to same/different conditional discrimination task. S + = *same* (white-on-black panels), *different* (black-on-white panels). ◊ = the number of trials until 10 correct responses were made, ■ = the number of correct responses in the first 10 trials.

first 10 trials) and 10/x (x = the number of trials until 10 correct).

Performance in Block 1 was significantly different from chance (y/10: correct responses =

33/50, $z = 2.26$, $p < .05$; 10/x: correct responses = 50/73, $z = 3.16$, $p < .01$), Block 2 was not significantly different from chance (y/10: correct responses = 31/50, $z = 1.70$, $p > .05$; 10/x: correct responses = 50/84, $z = 1.75$, $p > .05$). In Block 3, the results were significantly different from chance (y/10: correct responses = 33/50, $z = 2.26$, $p < .05$; 10/x: correct responses = 50/79, $z = 2.36$, $p < .05$). In Block 4, the results were significantly different from chance (y/10: correct responses = 32/50, $z = 1.98$, $p < .05$; 10/x: correct responses = 50/76, $z = 2.75$, $p < .01$). Visual examination of Figure 9 suggests more consistent performance in the last two blocks.

A further analysis was conducted to examine whether the results in this experiment were influenced by the subject selecting *same*, the correct response in the previous experiment, regardless of the color condition. The results for each condition (white-on-black and black-on-white) were calculated separately (using the 10/x data) (white-on-black = 95/152, black-on-white = 105/160). A chi-squared test found no significant difference between performance on the *same* versus the *different* trials ($x^2 = 0.33$, $p = 0.57$).

Discussion

Despite the fact that the subject seemed to be showing some improvement in the final blocks of sessions, she found this task much more difficult than the previous experiment. While she technically reached the training criterion (two consecutive blocks significantly different from chance), it was by such a small margin, particularly the y/10 figure for Block 4, that it was decided the result was insufficiently robust to claim she had mastered this task.

A chi-squared test comparing the number of correct responses to the *same* stimuli, on which she was trained to a high standard in Experiment 1, to correct responses to the *different* stimuli, which she had not previously encountered, revealed no evidence the poor results were due to the subject favoring *same*. In fact, it appeared the subject started to perform better on the *different* panels at the expense of the *same* panels toward the end of the experiment, perhaps indicating she was learning the *different* condition. However, in general the results suggest the introduction of the conditional discrimination led to confusion and an overall deterioration in performance.

Due to the increased task difficulty, it was possible that the subject simply required more training to learn the task. Considering the subject did show some signs of learning, and to ensure she had every chance to perform successfully in this experiment, it was decided to train the *different* condition separately, then retest the conditional same/different experiment and see if previous training in both conditions would facilitate learning.

Experiment 3

Following the lack of success with the same/different conditional discrimination tests conducted in Experiment 2, this experiment aimed to enable the subject to learn the *different* condition separately in the same manner as the *same* condition was learned in Experiment 1. Due to the fact that the same/different discrimination had already been successfully demonstrated in Experiment 1, and that this experiment was designed primarily to train the *different* condition before repeating the conditional same/different experiment, transfer trials were not conducted. In addition, the opportunity was taken to conduct blind trials at the end of the experiment to demonstrate there was no unintentional cueing from the handler during these experiments.

Stimuli

The stimuli used for this experiment were the black-on-white, S + = *different* panels used in Experiment 2 (see Fig. 8), with the same stimuli being used for the blind trials. In this experiment the *different* panels were reinforced.

Blind trials

During the blind trials, a 42 cm x 103 cm plywood board was placed on top of the start box directly above the swing doors. At the beginning of each trial, the handler lowered the subject underneath the blind board to view the stimuli and make her selection. The board blocked the view of the stimulus panels on the doors, preventing the handler from knowing on which side the correct stimulus was located. Another person was enlisted to

change the stimulus panels and food dishes between trials while the handler was located in a position where they could not see the apparatus.

Results

The results were analyzed using a two-tailed binomial test in two blocks—the seven initial training sessions and the five blind trial sessions. The results were analyzed using two measures of performance—y/10 (y = the number of correct responses in the first 10 trials) and 10/x (x = the number of trials until 10 correct).

Training trials. Performance in the block of training sessions was significantly different from chance (y/10: correct responses = 50/70, $z = 3.59$, $p < .001$; 10/x: correct responses = 70/94, $z = 4.74$, $p < .001$).

Blind trials. Performance in the block of blind sessions was also significantly different from chance (y/10: correct responses: 38/50, $z = 3.68$, $p < .001$; 10/x: correct responses = 50/70, $z = 3.59$, $p < .001$). A chi-squared test using the 10/x data showed there was no significant difference between the training and blind trial results ($x^2 = 0.19$, $p = 0.66$).

Discussion

Despite the lack of transfer trials, the results of this experiment training the *different* condition provided some confirmation of the Experiment 1 results showing the subject was able to learn an abstract discrimination on the basis of the same/different concept. The results of this experiment are comparable to those of the *same* discrimination in Experiment 1, with both showing results significantly different from chance. The results are also much improved on those in Experiment 2, indicating the subject's poor performance in that experiment was most likely due to the test itself and not some other factor.

Blind trials. The results for the training trials and the blind trials were both significantly different from chance, and a chi-squared test confirmed that there was no significant difference between them, indicating the introduction of the blind board did not lead to deterioration in performance. This result suggests that inadvertent handler cueing

did not contribute to the subject's performance in these experiments.

Additional support for this view can also be found in the fact that Pitpa performed poorly in the previous experiment. The inability of a subject to perform a particular task while succeeding on others trained in the same manner suggests that the subject is unlikely to be making use of inadvertent experimental cues or more basic associative processes relating to stimulus reinforcement (Huber, 2001).

Experiment 4

In previous experiments, the subject was successfully trained on both the *same* and the *different* discriminations. Having been trained in both conditions, this experiment repeated the conditional same/different discrimination tested in Experiment 2 to determine whether the additional training on the *different* discrimination would improve her performance on this task. One possible reason for an improved performance could be that the subject had merely now memorized all of the stimuli. To assess this possibility, transfer trials with new stimuli were given at the end of the experiment. To ensure that transfer in this experiment was truly above chance, it was decided to conduct an additional block of five sessions after transfer criterion (one block significantly different from chance and no significant difference between the training and transfer blocks) had been reached.

Stimuli

The stimuli for the first part of the experiment were the same as those used in Experiment 2 (see Fig. 8). The stimuli for the transfer trials were created using six novel shapes arranged in the same fashion into six *same* and six *different* black-on-white panels and six *same* and six *different* white-on-black panels (see Fig. 10).

Results

The learning phase trials were grouped into two blocks of five sessions and the transfer trials grouped into two blocks of five sessions and the results analyzed using a two-tailed binomial test. The results were graphed (see Fig. 11) and analyzed using two measures of
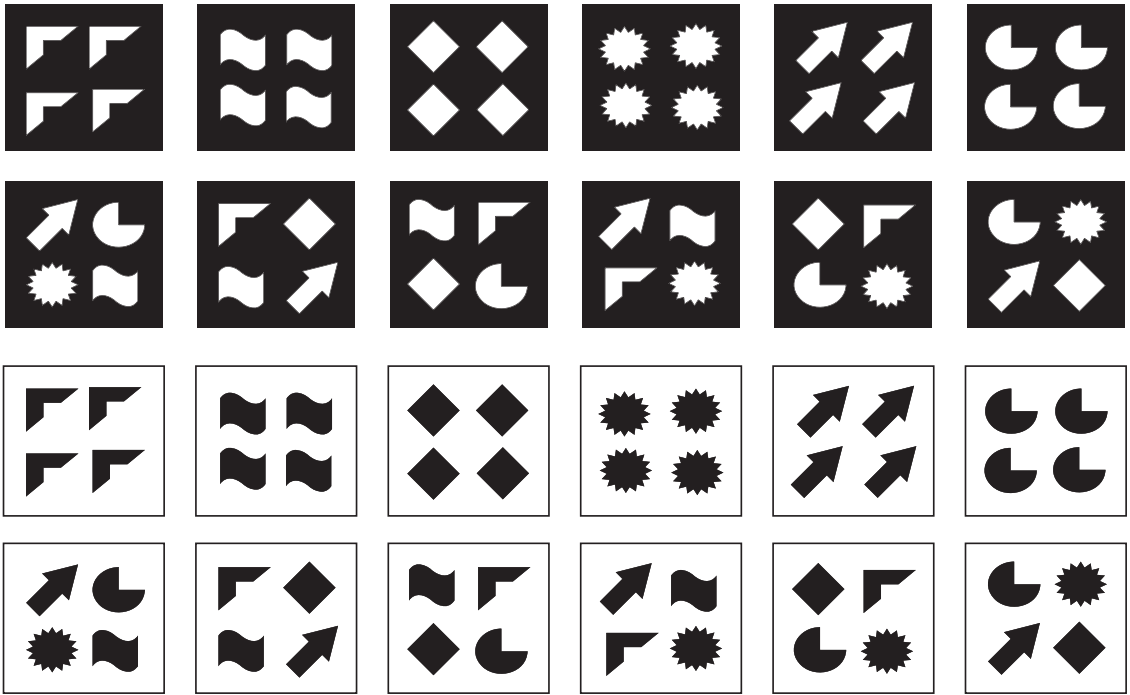
Fig. 10.   Novel stimulus panels for Experiment 4 – transfer of same/different conditional discrimination, S + = *same* (white-on-black panels), *different* (black-on-white panels).
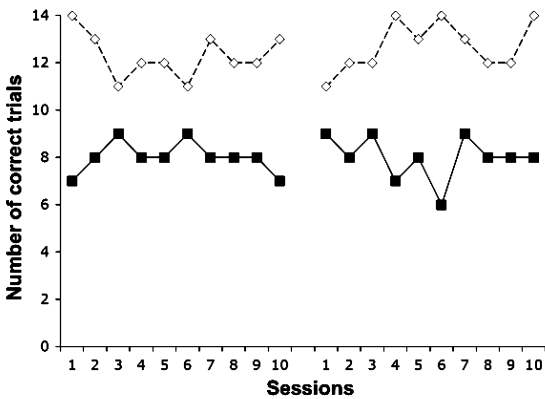

Fig. 11.   Number of correct responses to same/different conditional discrimination task. S + = *same* (white-on-black panels), *different* (black-on-white panels). The first 10 sessions show the learning phase, the second 10 sessions show the transfer trials. $\Diamond$ = the number of trials until 10 correct responses were made, ■ = the number of correct responses in the first 10 trials.

performance—y/10 (y = the number of correct responses in the first 10 trials) and 10/x (x = the number of trials until 10 correct).

Training trials. Performance in Block 1 of the training phase was significantly different from chance (y/10: correct responses = 40/50, $z = 4.24$, $p < .001$; 10/x: correct responses = 50/62, $z = 4.83$, $p < .001$) as was performance in Block 2 (y/10: correct responses = 40/50, $z = 4.24$, $p < .001$; 10/x: correct responses = 50/61, $z = 4.99$, $p < .001$), meeting the training criterion.

Transfer trials. Performance in Block 1 of the transfer phase was also significantly different from chance (y/10: correct responses = 41/50, $z = 4.53$, $p < .001$; 10/x: correct responses = 50/62, $z = 4.83$, $p < .001$) as was performance in Block 2 (y/10: correct responses = 39/50, $z = 3.96$, $p < .001$; 10/x: correct responses = 50/65, $z = 4.34$, $p < .001$). The subject met the transfer criterion, as performance in the first block of the transfer trials was not significantly different from performance in the second block of the learning phase using a chi-squared test ($x^2 = 0.04$, $p = 0.85$).

Using the 10/x data, the results were then analyzed to compare the subject's
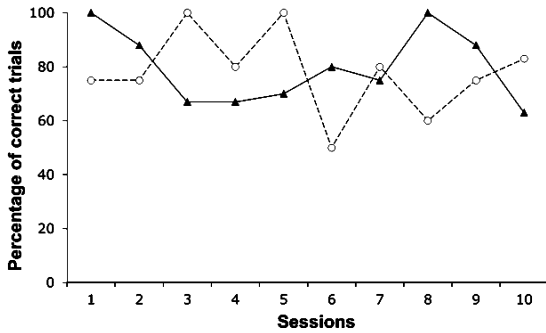
Fig. 12. Percentage of correct responses to training and novel stimuli during same/different conditional discrimination transfer trials. S + = *same* (white-on-black panels), *different* (black-on-white panels) (using 10/x data, x = the number of trials until 10 correct). ○ = percentage of correct responses to training stimuli, ▲ = percentage of correct responses to novel stimuli.

performance on the novel stimuli to that on the training stimuli (Block 1: novel stimuli = 31/40 correct, training stimuli = 19/22 correct; Block 2: novel stimuli = 33/41 correct, training stimuli = 17/24 correct). A chi-squared test found no significant difference between performance on the training and the novel stimuli in either Block 1 ($x^2 = 0.71$, $p = 0.40$) or Block 2 ($x^2 = 0.79$, $p = 0.37$) of the transfer trials. The results were then converted into percentages in order to graphically compare the varying proportions of each stimulus type in each session caused by the randomization procedure (see Fig. 12*)*.

The results also show that Pitpa's performance on the novel stimuli on Day 1 of the transfer trials was 100% correct and even better than that for the repeated training stimuli presented during the same session (75% correct).

Discussion

The fact that the results in the first block of the transfer trials were not significantly different from those of the second block of the learning phase and that there was no significant difference in performance between the training and novel stimuli in the transfer trials indicates that transfer did take place. This result is further strengthened by the fact that the significant transfer performance was repeated in a second block of transfer trials. This demonstrates that the subject was able to perform a conditional discrimination based on

simultaneously presented same/different relations—a task that had previously been demonstrated in only a few species, including monkeys (Burdyn & Thomas, 1984; Flemming, 2011; Flemming et al., 2007) and pigeons (Castro et al., 2010).

Furthermore, as with Experiment 1, the condition required by some authors, of successful performance on the first appearance of novel stimuli, was fulfilled as Pitpa scored 100% on the first presentation of the novel stimuli on Day 1 of the transfer trials. According to Thomas and Kerr (1976), this precludes the possibility of pattern learning and permits a conceptual interpretation of the results.

One issue that must be addressed is the differing results of Experiments 2 and 4. The fact that the subject was now able to succeed in the same task she had previously struggled with may be the result of the subject receiving training in both sets of conditions (*same* and *different*) before this experiment instead of just *same*. This theory gains support from the fact that some other conditional same/different researchers have also separately trained their subjects to criterion in each conditional rewarded relation (S + = *same* and S + = *different*) before testing with a randomly alternating conditional procedure (Flemming et al, 2007; Burdyn & Thomas, 1984; but not Castro et al., 2010). Alternatively, Pitpa's eventual success may have been facilitated merely by having been given more training on the conditional testing paradigm.

The fact that the subject took much longer and required more training to learn this task compared to the standard same/different categorizations in Experiments 1 and 3 suggests that she found the conditional task more difficult. This finding supports Thomas' (1996) learning-hierarchy model that places same/different conditional categorization ("relational concepts I") as a "level 7" task above the standard same/different categorization ("relative class concepts") on "level 6" and seems logical considering each selection is based on two separate discriminations instead of just one.

However, it is interesting to note that in Flemming et al.'s (2007) rhesus monkey study, the addition of discriminative cues actually seemed to facilitate learning of same/different discrimination reversals. Similarly, Castro et al. (2010) found pigeons learned the conditional same/different task faster than the

regular same/different task in other experiments (Young & Wasserman, 1997), although there were a number of experimental differences between the studies.

Further experiments would be needed to determine exactly how Pitpa solved this task. For example, as Thomas, Cook, and Terrones (1990) have pointed out, there is no way of knowing whether the putative hierarchical design of this type of conditional experiment—in this case background color as the superordinate (conditional) cue modulating the selection of the subordinate (discriminative) cue of same/different shapes—was the way in which Pitpa actually solved the discrimination. In fact, some experiments have suggested that rather than an "if–then" hierarchical strategy, simultaneous presentation of stimuli leads animals to learn "what goes with what" (e.g., Thomas & Schmidt, 1989).

Whether or not a hierarchical relationship exists, it is combinations of stimuli, rather than single stimulus elements that signal reinforcement contingencies in conditional discrimination tasks (Thomas et al., 1990). In the case of this experiment, it can only be said with any certainty that the value of one cue modulated responding to the cue with which it was paired.

General Discussion

This study set out to determine whether an evolutionarily "primitive" animal like the echidna could perform a high-level cognitive task like conditional same/different discrimination; the results indicated that it could. However, what is less certain is what mental abilities were being utilized by the subject to master the complex tasks that were given—whether she used relatively prosaic perceptual mechanisms or relied on the relationship between the stimuli or even an identity "concept".

A number of criteria have been proposed to demonstrate the use of relational information, rather than more basic perceptual mechanisms, to successfully perform same/different discriminations. This experiment fulfilled a number of these, including transfer to novel stimuli (Katz & Wright, 2006), transfer performance equivalent to baseline and above 80% correct (Wright & Katz, 2006), and the utilization of only first-trial transfer data (Pearce, 1997).

Although it is important to remain open to more prosaic explanations for Pitpa's success, this experiment attempted to control for a range of unintended cues. The stimuli were designed to prevent inadvertent cueing from brightness, perceptual grouping, entropy, uniformity, color, and individual shapes; the apparatus was designed to prevent inadvertent cueing from extraneous visual, olfactory and auditory cues; and, the introduction of blind trials was intended to rule out experimenter cueing. The simultaneous stimulus presentation procedure was also selected to provide a better chance of promoting relational learning.

While it is not possible to categorically state that Pitpa did not make use of some undetermined mechanism or cue, the measures taken in the design of this experiment to prevent cueing, and the fact that performance deteriorated with the introduction of a more complex experimental paradigm, provide a reasonable degree of confidence that the results were relationally based. The factors listed above also fulfil almost all of the requirements for conceptual learning proposed by researchers such as Allen (1999), Katz, Wright, and Bodily (2007), Premack (1983), Thomas (1996), and Wasserman et al. (1995), with the obvious exception of experimental replication. Based on those criteria, it seems entirely reasonable to claim Pitpa did in fact demonstrate conceptual learning.

The term 'concept' is used here based on the convention for this type of study; however, fulfilling the prerequisites for concept learning does not mean an animal possesses the full range of a human's ability to conceptualize (Chittka & Jensen, 2011). Pitpa proved capable of concept learning based on Lea's (1984) first level of conceptualization—categorization of stimuli grouped according to human-defined concepts, in this case *sameness* and *difference*. However, even with all of the efforts taken to eliminate perceptual mechanisms, it is still difficult to definitively determine if an animal can satisfy Lea's second level—conceptualization based on human-like conceptual mechanisms. Yet, it may not be an either/or proposition. It has been argued that, even in humans, the distinction between perceptual and conceptual processes is artificial and, instead, that particular tasks lie along a perceptual–conceptual continuum

(Goldstone & Barsalou, 1998; Wasserman, Frank, & Young, 2002).

According to some authors, the echidna's ability to perform a "high-level" task like same/different concept learning would be suggestive of a relatively high level of "intelligence" (D'Amato et al., 1985; Herman, Hovancik, Gory, & Bradshaw, 1989; Herrnstein, 1990; Huber, 2001; Suková et al., 2013; Wright & Katz, 2006). The addition of the conditional component to the same/different procedure is considered to make the task even more difficult (Thompson & Oden, 1996). Using Thomas' (1996) intelligence hierarchy, an animal's learning ability is determined by how many of the eight fundamental processes it can use. The subject of this experiment was able to demonstrate abilities at level 6 (the same/different class concept) and level 7 [a class concept (same/different) in a conditional relationship (if white-on-black then *same*, if black-on-white then *different*)]. If Thomas' (1996) and others' claims are accepted, then it would suggest the echidna, far from being cognitively primitive, ranks fairly highly in terms of overall intelligence. In fact, other researchers have used Thomas' hierarchy to assess the learning ability or intelligence of their subjects (Hanggi, 2003; Sappington & Goldman, 1994).

Nevertheless, making strong claims about a species' general intelligence (however that is defined) based on the ability to perform a single task is fraught with pitfalls (Hodos, 1986). As discussed earlier, mosaic evolution suggests animals can develop a relatively sophisticated cognitive skill in one area, while continuing to use more basic cognitive mechanisms in others (Cheney & Seyfarth, 1990; Wright & Katz, 2006). The abilities demonstrated by Pitpa in this experiment may be indicative of a more generalized cognitive capacity or an isolated cognitive "module". In either case, it is not unreasonable to assert that the idea of echidnas being cognitively primitive due to their evolutionary history must be challenged. They have demonstrated the ability to perform what are generally considered to be cognitively demanding tasks.

Cognitive abilities do not evolve without some ecological selection pressure and so, while this is not an especially ecologically grounded task, it is still worth asking what in the echidnas' ecology might select for cognitive sophistication and on what neural structures these abilities might be based. A physiologically based explanation as to why an echidna might be able to perform a purportedly difficult cognitive task is found in the relative complexity of some aspects of its neurophysiology (discussed earlier). The relatively large prefrontal cortex of the echidna might also relate directly to relational categorization. In humans, for example, there is evidence the prefrontal cortex is important for category learning (Ashby & Waldron, 2000) and may play a critical role in abstract-concept learning such as same/different categorization (Freedman & Miller, 2008; Wright, 2010).

Much of the support for equating bigger brains with increased intelligence is based on the idea that additional brain size above that expected for body size may be selected for specialized or elaborate behaviors or demanding ecological niches (e.g. Clutton-Brock & Harvey, 1980; Herman, 2002; Jolly, 1966). Echidnas have no real predators (except man) and virtually no social structure (Griffiths, 1978; 1989), and their home range is smaller than comparably sized eutherian mammals (Nicol, Vanpé, Sprent, Morrow, & Andersen, 2011). They do have a relatively long life span (up to 50 years in captivity, Augee et al., 2006), which has been linked to large relative brain size (Harvey, Martin, & Clutton-Brock, 1987), although the mechanisms by which this factor contributes to brain development has not yet been fully explained.

Another ecological factor that might contribute to cognitive development are the challenges posed by foraging. Echidnas forage mainly on termite mounds and ant nests which represent temporarily abundant food patches. According to McLean (2001), foraging for food that has a patchy distribution presents unique challenges requiring the evolution of higher mental abilities (see also Clutton-Brock & Harvey, 1980; Foley, 1990; Krakauer & Rodriguez-Girones, 1995). In addition to food distribution, cognitive development may also be positively influenced by the use of optimal foraging strategies. The echidna has demonstrated the ability to employ optimal foraging by adjusting its foraging efforts in response to prey abundance, quality, and defence (Abensperg-Traun & De Boer, 1992; Abensperg-Traun, Dickman, & De Boer, 1991). These traits have been linked to

improved performance in conditioning experiments (Lea, 1981), specifically categorization and same/different concept tasks (Giurfa et al., 2001; Hanggi, 1999). The fact that echidnas seem to forage using a fairly simple win–shift strategy, however, raises some doubts about this as an adaptive force (Burke et al., 2002).

More promising is the echidna's distribution in a wide variety of environmental niches (discussed earlier). Brain size has been linked to behavioral flexibility (Sol, 2009) and the echidna has adapted to its divergent ecosystems by varying aspects of its behavior in areas such as hibernation and reproduction to suit different climates and resource availability (Augee & Gooden, 1993; Griffiths, 1978; Schmid, Andersen, Speakman, & Nicol, 2003). This ability to adapt to extremely variable environments has been associated with the development of flexible learning capabilities (Tomasello & Call, 1997) and more specifically to perceptual categorization skills (Huber, 1995; Shettleworth, 1998).

Conclusion

This study has added to the limited knowledge about the echidna's cognitive abilities, demonstrating for the first time that an echidna can perform same/different categorization using both unconditional and conditional discrimination procedures. These results are of great interest due to the echidna's unusual neurophysiology and unique evolutionary history, providing a valuable comparison case in animal cognition studies. It has also contributed to the literature on same/different concept learning by expanding the number of species in which this ability has been found, as well as demonstrating for the first time that it has also evolved in monotremes. The fact that such an evolutionarily distant mammalian species as the echidna has demonstrated supposedly "advanced" mental abilities lends credence to the argument that such abilities may be more widespread than previously thought.

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