



Subproblem learning and reversal of a multidimensional visual cue in a lizard: evidence for behavioural flexibility?

Birgit Szabo^{a,*}, Daniel W. A. Noble^b, Richard W. Byrne^c, David S. Tait^d,
Martin J. Whiting^a

^a Department of Biological Sciences, Macquarie University, Sydney, Australia

^b University of New South Wales, School of Biological, Earth and Environmental Sciences, Ecology & Evolution Research Centre, Sydney, Australia

^c University of St Andrews, School of Psychology and Neuroscience, Centre for Social Learning & Cognitive Evolution, St Andrews, U.K.

^d University of St Andrews, School of Psychology and Neuroscience, St Andrews, U.K.

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Behavioural flexibility, the ability to adjust behaviour to environmental change by adapting existing skills to novel situations, is key to coping with, for example, complex social interactions, seasonal changes in food availability or detecting predators. We tested the tree skink, *Egernia striolata*, a family-living skink from eastern Australia, in a set-shifting paradigm of eight colour/shape discriminations including reversals, an intradimensional acquisition of a new colour/shape and extradimensional shift from colour to shape (and vice versa). Skinks could learn to discriminate between colour/shape pairs and reverse this initial stimulus–reward association; however, they showed no significant decrease in the probability of making a correct choice in the extradimensional shift suggesting that they did not form an attentional set. Subjects appear to have learnt each stage as a new problem instead of generalizing stimuli into specific dimensions (set formation). In conclusion, tree skinks solved a discrimination reversal by focusing their attention towards visual stimuli and flexibly adjusting their choice behaviour accordingly. These lizards learned to use multidimensional visual stimuli to find a food reward but did not generalize stimuli into dimensions. Furthermore, this study is the first to test for set shifting in a lizard species and thereby allows us to extend set-shifting theory to a new taxon for comparison with primates, rodents, a bird and a turtle.

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Social living has many benefits but can also be a demanding environment in which interactions between individuals shape their social structure (Hinde, 1987). The resulting selective pressure is thought to have led to the evolution of extensive abilities in attention, memory and learning (Byrne & Whiten, 1988; Byrne, 1994, 1998), forming the foundation of the ‘social intelligence hypothesis’ (Humphrey, 1976). Complex cognition has been frequently investigated through behavioural flexibility: the ability to adjust behaviour to changes in the environment (Brown & Tait, 2015) by directing attention to essential stimuli (Dias, Robbins, & Roberts, 1996; Welsh & Pennington, 1988) and adjusting existing skills to a new problem (Manrique & Call, 2015). Behavioural flexibility can be a valuable tool in the social domain. To react flexibly to a change in the social environment (addition or removal of group members) and to selectively pay attention to interactions between individuals

can be useful for tracking relationships within a social group (social monitoring; McNelis & Boatright-Horowitz, 1998). The insights gained can then be used to adjust behaviour directed towards conspecifics according to the current state of their interindividual relationships (Byrne, 1998; McNelis & Boatright-Horowitz, 1998).

A common test for behavioural flexibility involves a test of attentional set shifting which investigates the ability to apply an acquired attentional bias (by forming an attentional set) to novel situations (ID: intradimensional; Brown & Tait, 2015; Mukhopadhyay et al., 2008) and then to shift attention away from this established bias when relevance changes to a previously irrelevant stimulus aspect or dimension (ED: extradimensional; Brown & Tait, 2015). It is possible to examine set formation in a series of discriminations by quantifying acquisition speed and errors during each stage (Brown & Tait, 2015; Garner, Thogerson, Wurbel, Murray, & Mench, 2006). Perseverative errors to the former relevant dimension and a performance drop during a shift indicate a subject’s level of behavioural flexibility (Brown & Tait, 2015; Garner et al., 2006).

* Correspondence: B. Szabo, Department of Biological Sciences, Macquarie University, 209 Culloden Road, Building W19A, Marsfield, NSW 2122, Australia.
E-mail address: birgit.szabo@gmx.at (B. Szabo).

A touch screen test for ID/ED attentional set shifting was first developed to compare human and nonhuman primates' attentional set-shifting ability (Dias et al., 1996; Roberts, Robbins, & Everitt, 1988). The task consists of multiple sequential visual discriminations (using shapes and lines as stimulus dimensions), designed to encourage an attentional set (through repeated exposure to consistently relevant and irrelevant information; Sutherland & Mackintosh, 1971) and then test the ability to shift away from that set. First, subjects learn a simple discrimination (SD) between stimuli of only one dimension. After reaching a predetermined learning criterion the stimulus–reward association is reversed and the other stimulus in the pair is reinforced. Next, stimuli of the irrelevant dimension are superimposed onto the SD stimuli, producing compound cues (CD), with the SD stimuli still associated with reward. After reaching criterion the reward associations are again reversed. Next, during the intradimensional acquisition (ID), new examples of shapes and lines are introduced. With dimensional relevance staying the same, subjects must maintain their attentional set and apply it to unfamiliar stimuli. After reaching criterion, the reward contingencies are again reversed. Finally, during the extradimensional shift (ED), again, unfamiliar shapes and lines are introduced. In contrast to the intradimensional acquisition, the reinforcement is now associated with the formerly irrelevant dimension. If set formation occurred during earlier stages, performance in the extradimensional shift is expected to be worse compared to the intradimensional acquisition, since the previously established attentional set no longer applies (Garner et al., 2006; Roberts et al., 1988). The extradimensional shift is again followed by a reversal.

The assumption that the number of trials to reach criterion during extradimensional shifting is higher than during the intradimensional acquisition (as a measure of attentional set shifting) does not rely on absolute values. It is therefore possible to compare shift performance in different species (Table 1). For example, marmosets, *Callithrix jacchus*, can form an attentional set and shift to a previously irrelevant second dimension (Dias et al., 1996; Roberts et al., 1988) and similar results have been obtained in rhesus monkeys, *Macaca mulatta* (Baxter & Gaffan, 2007; Weed, Bryant, & Perry, 2008). Rodents, such as rats, *Rattus norvegicus* (e.g. Birrell & Brown, 2000; Hecht, Will, Schachtman, Welby, & Beversdorf, 2014; Kim, Choi, Jeon, & Han, 2016; McAlonan &

Brown, 2003; McGaughy et al., 2014) and mice, *Mus musculus* (e.g. Bissonette, Lande, Martins, & Powell, 2012; Colacicco, Welzl, Lipp, & Wuerbel, 2002; Garner et al., 2006; Janitzky et al., 2015) also show the ability to form and shift attentional sets. Comparable findings in other taxa such as birds, fishes and reptiles are scarce (Table 1). One study in great tits, *Parus major*, showed their ability to form an attentional set and shift to a new dimension (Titulaer, van Oers, & Naguib, 2012). Painted turtles, *Chrysemys picta*, show an improved performance during successive compound discrimination reversals, perhaps indicative of set formation. However, without comparison between intradimensional and extradimensional stages, this improvement could equally be evidence of learning set formation (training effect) instead of attentional set formation (Cranney & Powers, 1983).

Most studies in lizards lack the details needed for a comprehensive comparison of attentional set shifting because most focus on reversal performance only. For example, *Anolis evermanni* (Leal & Powell, 2012) were presented with two food wells covered by lids which animals had to dislodge to access a reward. Lizards learnt to open the food dishes using multiple methods and to discriminate between the two wells based on colour (blue and yellow); furthermore, two of four individuals could reverse this learnt association showing flexibility in their use of visual information. A similar study investigated discrimination learning and reversal in hatchling three-lined skinks, *Bassiana duperreyi*. Almost all lizards (13/14) that learnt to displace lids could associate lid colour with reinforcement and eight showed flexibility by reversing this learnt association (Clark, Amiel, Shine, Noble, & Whiting, 2014).

We tested tree skinks, *Egernia striolata*, which are viviparous, diurnal, family-living lizards found in arboreal and rocky habitats throughout eastern Australia (Wilson & Swan, 2008). Tree skinks show complex sociality in which lizards frequently live in family groups consisting of a socially monogamous parental unit and at least one generation of offspring (Chapple, 2003; Duckett, Morgan, & Stow, 2012; Whiting & While, 2017). They are visual foragers that eat plant material (including fruits) as well as insects such as cockroaches and grasshoppers (Chapple, 2003). As a diurnal, visual forager, *E. striolata* is a good model to investigate learning in a visual discrimination task. Furthermore, flexibly adjusting behaviour to changing conditions is beneficial for survival (Manrique & Call, 2015). Finally, complex sociality can select for enhanced cognitive

Table 1
Literature comparison between studies incorporating the described methodology

Species	Age	Methodology	Dimensions	ED>ID	Study
Primates					
Common marmoset	Subadult	CANTAB ID/ED	Visual	Yes	Dias et al., 1996
Common marmoset	Subadult	CANTAB ID/ED	Visual	Yes	Roberts et al., 1988
Rhesus monkey	Juvenile	CANTAB ID/ED	Visual	Yes	Weed et al., 2008
Rhesus monkey	Adult	CANTAB ID/ED	Visual	Yes	
Rhesus monkey	Adult	CANTAB ID/ED	Visual	Partly validated	Baxter & Gaffan, 2007
Rodents					
Wistar rats	Adult	ID/ED	Olfactory/touch	Yes	Kim et al., 2016
Sprague–Dawley rats	Adult	ID/ED	Olfactory/touch	Yes	Hecht et al., 2014
Long-Evans hooded rats	Adult	ID/ED	Olfactory/touch	Yes	McGaughy et al., 2014
Lister hooded rats	Adult	ID/ED	Olfactory/touch	Yes	McAlonan & Brown, 2003
Lister hooded rats	Adult	ID/ED	Olfactory/touch	Yes	Birrell & Brown, 2000
Mice (B6.Cg-Tg(Th-cre)1Tmd/J)	Adult	ID/ED	Olfactory/touch	No	Janitzky et al., 2015
Mice (C57BL/6)	Adult	ID/ED	Olfactory/touch	Yes	Bissonette et al., 2012
Mice (C57BL/6)	Adult	ID/ED	Olfactory/touch	Yes	Garner et al., 2006
Mice (C57BL/6j)	Adult	ID/ED	Olfactory/touch	Yes	Colacicco et al., 2002
Birds					
Great tits	Adult	Reversals and shift	Visual/spatial	Yes	Titulaer et al., 2012
Reptiles					
Painted turtle	Adult	Series of ED and REV	Visual	No direct comparison	Cranney & Powers, 1983

Column ED > ID indicates whether set formation impaired performance during the extradimensional shift (yes/no). ID: intradimensional acquisition; ED: extradimensional shift; REV: reversal; CANTAB ID/ED: Cambridge neuropsychological automated test battery ID/ED attentional set-shifting test.

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