

Task-Switching in Pigeons: Associative Learning or Executive Control?

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Abstract

Human performance in task-switching paradigms is seen as a hallmark of executive-control processes: switching between tasks induces switch costs (such that performance when changing from Task A to Task B is worse than on trials where the task repeats), which is generally attributed to executive control suppressing one task-set and activating the other. However, even in cases where task-sets are not employed, as well as in computational modelling of task switching, switch costs can still be found. This observation has led to the hypothesis that associative-learning processes might be responsible for all or part of the switch cost in task-switching paradigms. To test which cognitive processes contribute to the presence of task-switch costs, pigeons performed two different tasks on the same set of stimuli in rapid alternation. The pigeons showed no sign of switch costs, even though performance on trial N was influenced by trial N-1, showing that they were sensitive to sequential effects. Using Pearce's (1987) model for stimulus generalisation, we conclude that they learned the task associatively - in particular, a form of Pavlovian-conditioned approach was involved - and that this was responsible for the lack of any detectable switch costs. Pearce's model also allows us to make inferences about the common occurrence of switch costs in the absence of task-sets in human participants and in computational models, in that they are likely due to instrumental learning and the establishment of an equivalence between cues signalling the same task.

Keywords: task-switching -- associative learning -- executive control -- pigeons

Executive control is presumed to be at the core of the human ability to switch between two or more different tasks in rapid alternation, and task-switching paradigms have been used extensively as a tool to assess executive-control mechanisms in human behaviour (Dreisbach, 2012; Kiesel, Steinhauser, Wendt et al., 2010; Monsell, 2003; Vandierendonck, Liefoghe, & Verbruggen, 2010). In the present experiment, this presumption is addressed through the use of a task-switching paradigm with a subject species, pigeons, which are widely thought not to have the capacity for executive control, but rather to rely on associative learning. Our principal aims were, first, to investigate whether task-switching was possible on the basis of associative learning, and second, to investigate which cognitive processes contribute to the presence of task-switch costs."

Commonly, task-switching paradigms involve the classification of the same set of stimuli along different stimulus dimensions, where the defining dimension switches frequently depending on the task that is currently being performed (Kiesel et al., 2010). A specific task cue indicates which task is relevant in a given trial: for example, subjects might be asked to judge a visual grating pattern by its spatial frequency when the colour yellow is presented, or to classify the same stimulus according to whether the pattern is vertically or horizontally orientated (whilst ignoring spatial frequency) when the colour red appears.

Evidence for humans' reliance on executive control in such paradigms is taken from the presence of 'switch costs' (Dreisbach, 2012; Kiesel et al., 2010; Monsell, 2003; Vandierendonck et al., 2010): humans generally take longer and make more errors during a 'task-switch' trial, in which the dimension that determines a correct response differs from the one in the previous trial (that is, participants have to switch from one task to the other) than in non-switch or 'task-repeat' trials, in which the same

task as in the previous trial is repeated and thus attention has to be paid to the same stimulus dimension as before (Dreisbach, 2012; Kiesel et al., 2010; Monsell, 2003; Vandierendonck et al., 2010). It is argued that switch costs exist because humans perform the executive control operations of identifying the current task, retrieving its specific stimulus-response rules into working memory (and deleting the rules of the previous task) and adjusting the response reaction to the new requirements, a process known as 'task-set reconfiguration' (Monsell, 2003; Monsell & Mizon, 2006). This process is necessary on switch trials but not on repeat trials, leading to a measurable difference in performance on these two types of trials.

The easy detectability and reliability of switch costs have made task-switching paradigms a popular instrument to assess human executive control in both experimental and clinical settings. However, current theories in cognitive research suggest that humans possess two distinguishable learning processes: in addition to the explicit, rule-based category learning aided by executive control, which extracts information from a single dimension of a (multidimensional) stimulus, humans may also possess a more automatic, nonanalytic form of learning, in which behavioural responses are associated with the perceived stimulus as a whole (Ashby & Ell, 2001; Ashby, Ennis, & Spiering, 2007; Dreisbach, 2012; Forrest, 2012; McLaren, Forrest, McLaren et al., 2014; Smith & Grossman, 2008; Smith, Berg, Cook et al., 2012; Smith, Boomer, Zakrzewski et al., 2014). Given that the stimulus sets used in task-switching paradigms are often small and contain easily distinguishable stimuli, performance in task-switching paradigms might be entirely the result of such associative-learning processes, i.e., the retrieval of cue-stimulus-response associations (Logan & Bundesen, 2003; Schneider & Logan, 2005; Wylie & Allport, 2000). Thus,

executive control might in fact not be necessary for task switching¹. Learning to respond correctly could be accomplished by associating the overall visual appearance of a cue-stimulus combination with a certain response (Lea & Wills, 2008). Even when large stimulus set sizes are used to prevent participants from memorising individual stimulus-response combinations, each stimulus could be categorized by using all of its dimensions in combination (including the task cue) and computing its overall similarity to a stimulus, or a prototype image for many such stimuli, to which the correct response is known.

Often, task-switching studies (e.g., Forrest, 2012; Meiran & Kessler, 2008; Monsell, Sumner, & Waters, 2003; Schneider, 2015; Schneider & Logan, 2014) observe great impairments to performance for so-called incongruent stimuli: these are stimuli that are presented in all tasks but require different behavioural responses in each task. Performance in response to these response-incongruent stimuli is typically worse when compared to response-congruent stimuli, which afford the same response in all tasks. Whilst this 'congruency effect' can be explained in terms of executive control (e.g., by postulating that, during task switching, both the competing task-sets, including their respective stimulus-response rules, are held active in working memory and influence each other; cf. Meiran, 2000), it is more readily predicted by an associative learning account when dealing with relatively small sets of stimuli (Kiesel, Wendt, & Peters, 2007), indicating that nonanalytic associative processes might

¹ One possibility we do not consider here for reasons of space, is that executive control itself is a product of a complex cognitive architecture employing essentially associative processes (see Verbruggen, McLaren and Chambers, 2014, for more on this).

routinely play a substantial part in task switching, and perhaps even in the occurrence of switch costs.

A few studies have explicitly tried to elicit an associative approach to task switching in humans (e.g., Dreisbach, 2012; Dreisbach, Goschke, & Haider, 2006, 2007), either by using paradigms in which participants were only provided with a list of the cue-stimulus-response contingencies instead of full instructions for the underlying task rules, or by withholding any information and forcing participants to learn task contingencies by trial and error. The underlying hypothesis of these experiments was that, if humans performed task switching by retrieving implicit cue-stimulus-response associations, they should not suffer from switch costs, since the responses following different stimuli would not be encoded in a way that recognises any analytic task-based hierarchies or different 'tasks' as such. Indeed, Dreisbach and colleagues only observed switch costs in humans who were aware of task rules; there was no sign of differential reaction times in task-switch and task-repeat trials when participants were trained in a way that promoted an associative acquisition of the paradigm.

Although Dreisbach et al.'s (2006, 2007) results conformed to what would be expected when solving the task based on stimulus-response associations, their design differed from traditional task-switching paradigms. Conventional paradigms such as the Stroop task (Stroop, 1935) use bivalent stimuli, so that participants require additional information about which task is currently relevant in order to categorise a stimulus accurately (for example in the form of a task cue). Dreisbach et al., however, used univalent stimuli, meaning that each stimulus on its own predicted the correct response perfectly, even when no additional information about the currently relevant task was available. Essentially, this design meant that there was no benefit to using

task rules. It has been shown that, under conventional task-switching conditions, switch costs are smaller when stimuli are univalent (Allport, Styles, & Hsieh, 1994; Jersild, 1927; Kiesel et al., 2010; Rogers & Monsell, 1995; Spector & Biederman, 1976). Therefore, the possibility remains that even an associative approach to task switching would create switch costs, but that the use of univalent stimuli in Dreisbach's studies reduced switch costs to the point at which they became too small to be of statistical significance. Since bivalent stimuli cannot accurately predict the correct behavioural response without additional information from the task cues, a paradigm that utilised such stimuli might produce more meaningful data. Forrest (2012) did use bivalent stimuli in her attempt to promote associative learning in task switching. Contrary to Dreisbach et al.'s findings, participants who solved the paradigm without knowledge of the task rules demonstrated significant switch costs, albeit considerably smaller than those for participants who solved the tasks based on task instructions (Forrest, Monsell, & McLaren, 2014; Forrest, 2012). Simulations using an associative learning algorithm (APECS) based on back propagation (Forrest, 2012) also predicted small but reliable switch costs in the absence of task rules. Meier, Lea, Forrest, Angerer, and McLaren (2013) obtained similar results: their participants expressed significant switch costs regardless of whether or not they were able to verbalise the rules underlying each of the tasks, especially when responding to incongruent stimuli with bivalent response mappings. In summary, it would seem that human participants will exhibit switch costs in a task-switching paradigm using bivalent stimuli, regardless of whether they are using task-sets or simple associations between stimuli and responses.

Unfortunately, even if careful precautions are in place and participants are thoroughly questioned about their approach to a paradigm, the use of task rules can

never be fully discounted when testing humans. Thus, it might prove difficult to assess whether executive control is indeed a necessary requirement to exhibit switch costs when using human participants. An obvious way around this problem is to test task-switching effects in animals that are presumed to be unable to rely on abstract task rules. There are a few animal studies available already that might provide some insight into what cognitive processes lead to the emergence of switch costs. Stoet and Snyder (2003a, 2003b, 2008, 2009) were the first to investigate task-switching effects in non-human primates, specifically two rhesus macaques (*Macaca mulatta*). Switch costs were minimal, and in fact absent in one animal. In the light of these results, Stoet and Snyder (2003a, 2003b) assumed that monkeys might lack at least one of the cognitive mechanisms necessary to solve task-switching paradigms in the way humans do. However, they had no doubt that macaques nonetheless applied some form of executive control and did not consider the possibility that their results might be explained by associative mechanisms.

Caselli and Chelazzi (2011), in an attempt to validate Stoet and Snyder's (2003a, 2003b) findings, exposed two rhesus macaques to a comparable task-switching paradigm. Their subjects behaved remarkably similarly to Forrest's (2012) and Forrest et al.'s (2014) humans who memorised cue-stimulus-response contingencies, in that both monkeys demonstrated small but reliable switch costs. Caselli and Chelazzi declared these effects to be comparable to those expressed by humans, claiming that both species relied on the same executive-control processes when switching tasks. Like Stoet and Snyder, they acknowledged that, compared to humans, monkeys might be more limited in the extent to which they were able to perform the necessary task-set reconfiguration, but they took the fact that their subjects not only succeeded in a task-switching paradigm but also showed the

characteristic switch costs as evidence that rhesus macaques can employ executive control similar to humans. Their methods and conclusion, however, received major critique by Avdagic, Jensen, Altschul, and Terrace (2014), who themselves successfully taught three rhesus macaques to switch tasks in a simultaneous chaining paradigm. Their subjects showed no significant switch costs in doing so, replicating Stoet and Snyder's (2003a, 2003b, 2008, 2009) results and casting doubt on Caselli and Chelazzi's. Thus, as switch costs are evidently not always present in a task-switching setting, as Forrest et al. (2014) and Forrest (2012) concluded, but may in fact be absent in the task-switching performance of nonhuman primates. Given this, do we have to assume that only human executive-control processes lead to switch costs, but executive control in monkeys does not? It might be more likely that macaques performed task switches based on associative processes instead of executive control, and thus do not suffer switch costs.

The logical question that follows is addressed in this paper: will animals whose ability to exert executive control is severely limited compared to humans (or even macaques) exhibit switch costs when trained in a task-switching paradigm? Or will they predominately be susceptible to stimulus-congruency effects or other sequential effects that might be expected to occur if performance is based on associative processes?

A promising candidate species in this regard might be the pigeon: pigeons have repeatedly demonstrated an absence of analytical processing where humans show it (Lea & Wills, 2008; Lea, Wills, Leaver et al., 2009; Maes, De Filippo, Inkster et al., 2015; Smith, Ashby, Berg et al., 2011; Smith et al., 2012; Wills, Lea, Leaver et al., 2009). There are relatively few data at present concerning pigeons' task-switching abilities. Meier et al. (2013) were able to show that pigeons did not exhibit any switch

costs in a task-switching paradigm using bivalent stimuli, but that they were strongly affected by congruency effects. This lack of switch costs in the pigeons was, at the time, surprising because, with the same paradigm, significant switch costs were observed for human participants who were unaware of the rules of the competing tasks - and had thus presumably relied on the same associative-learning mechanisms to acquire the cue-stimulus-response contingencies as the pigeons. But the pigeons' lack of switch costs seems robust: Castro and Wasserman (2016) also tested pigeons in a task-switching paradigm, and similarly found an absence of any switch costs. On the face of it, these two studies strongly suggest that pigeons perform task switching quite differently to humans: it is not clear how associative learning could sufficiently explain the pigeons' behaviour as well as the behaviour of participants memorising cue-stimulus-response contingencies in Forrest (2012) and Forrest et al. (2014).

Given that the sample sizes both in Meier et al. (2013) and in Castro and Wasserman (2016) are rather small (in both studies, data from eight pigeons are reported), there is some concern about the power of their results and how confidently the lack of switch costs can be accepted. In the following two experiments, we address this concern, and, to anticipate, establish that there are indeed no detectable switch costs in the performance of pigeons in a task-switching paradigm.

Furthermore, in Experiment 2, we consider another important issue that the experiments already reported in the literature did not address: in order to be confident in accepting the conclusion that pigeons produce no switch costs in task-switching paradigms, it is necessary to demonstrate not only that they can solve the problem - as was clearly the case in Meier et al. (2013) and Castro and Wasserman (2016) - but that perceptual features of the cue, stimulus or response of one trial affect performance on the next trial. Only then can we be confident that the study design

was sensitive enough to pick up any task-switch costs that might have occurred, making their absence informative. Again to anticipate, we establish that pigeons, although lacking switch costs, do nonetheless show signs of other sequential trial-order effects; that is, their performance on a given trial is affected by features of the previous trial. This enabled us to produce an associative explanation of the pigeons' performance, couched in terms of Pearce's (1987; 1994) configural theory.

EXPERIMENT 1

When adapting a paradigm intended to measure human executive control for the use with pigeons, it is important to ensure that the paradigm will still produce valid data when tested on human participants. This was done by Meier et al. (2013), and so we largely adopted those procedures here. In order to generate a valid comparative paradigm, we also have to confirm that well-known task-switching effects in humans and other animals can also be detected in pigeons. One effect that is universally observed in different species during task switching is the congruency effect (Monsell, 2003; Stoet & Snyder, 2003a, 2003b): even when switch costs were absent, subjects consistently showed poorer performance when responding to incongruent stimuli than when responding to congruent stimuli. A valid task-switching paradigm should be able to generate this effect. Therefore, if we can confirm a performance effect of stimulus congruency in pigeons, it is reasonable to assume that the paradigm is suitable for detecting any potentially present switch costs, as well.

The conventional methods of measuring task-switching performance in humans have to be adjusted to suit inter-species comparison. Switch costs are usually

assessed via the time it takes humans to respond, since the delayed reaction time on task-switch trials compared to task-repeat trials is seen as evidence that time-consuming executive-control processes were in action. With the testing apparatus currently available to us, an accurate recording of reaction times for pigeons was problematic, which made it difficult to estimate any differences in pigeons' reaction time in response to task-switch versus task-repeat trials. In addition, the time that our subjects had to respond to a stimulus could not be restricted in the same way as it is generally done in conventional human task-switching paradigms (Forrest, 2012; Kiesel et al., 2010; Monsell, 2003; Vandierendonck et al., 2010). To foreshadow, while reaction times are typically less than a second in humans (Dreisbach et al., 2006, 2007; Forrest, 2012; Monsell, 2003), our pigeons took several seconds to respond. However, in humans, switch costs and congruency effects are equally apparent in the accuracy with which the task-appropriate response is made on a given trial, as humans generally make more errors in switch trials compared to repeat trials, and in response to incongruent stimuli compared to congruent stimuli (Altmann & Gray, 2008; Rogers & Monsell, 1995; Vandierendonck et al., 2010). Recording the accuracy with which pigeons respond is easily accomplished, and, for the reasons stated above, proved to be a more suitable measure for assessing task-switching effects in our pigeons than reaction times.

We also found that it was necessary to give pigeons a relatively long and variable inter-trial interval to aid performance (cf. trial-spacing effect; Todd & Bouton, 2012). Whilst the human task-switching literature recognises that longer intervals can decrease switch costs if subjects are able to prepare for the upcoming task during the interval, this should not be an issue with cued task-switching paradigms such as the one used in the current study, because task preparation is not

possible prior to the appearance of a task cue. Nevertheless, one risk of using long inter-trial intervals might be that any carry-over effects from the previous trial or task are diminished. We address this issue in Experiment 2 when examining any potential interference from the previous trial.

Methods

Subjects

Eight pigeons (*Columbia livia*) took part in the experiment. They were obtained as discards from local fanciers. Pigeons were housed together in an indoor aviary (2 x 1 x 2.5m) and were maintained at or above 80% of their free-feeding weight. The pigeons had previously received touch-screen training, but were naïve to the testing stimuli and were required to learn the correct behaviour by trial and error.

Apparatus

The pigeons were tested in eight identical 71x50.5x43.5cm operant chambers. Each pigeon was always tested in the same chamber. One of the long walls of the chamber was fitted with a 31x23.5cm (15") touch monitor (Model 1547L 1024x768pxl TFT monitor, CarrollTouch infrared detector, ELO Touchsystems Inc.) mounted 12cm above the grid floor of the chamber. Two 2.8-Watt white houselights were mounted to either side above the screen; below the screen, mounted 4cm above the chamber floor and directly below each house light, two 6x5cm apertures gave access to grain hoppers when solenoids were activated. The food hoppers were illuminated by a 2.8-Watt light when activated and contained a 2:1 mixture of hemp seed and conditioner. A 50-Ohm loudspeaker mounted between the two food hoppers played white noise into the box and also indicated all effective pecks to target areas

on screen with an immediate feedback beep. The interior of the box was monitored by a video camera attached to the short wall of the chamber opposite the chamber door. Contingencies were controlled and data collected using a PC computer running the Whisker system (Cardinal & Aitken, 2010), with client programs written in Visual Basic 6.0.

Stimulus Materials

Stimuli were made up as circular Gaussian patches of 200 pixels in diameter. They consisted of one of four sinusoidal grating patterns that differed from one another in two dimensions: line orientation - either horizontal or vertical - and spatial frequency - either low (2 cycles per 100 pixels) or high (12 cycles per 100 pixels). The grating patterns were then superimposed on red, yellow, green or blue backgrounds. Figure 1 depicts four of the possible stimuli that resulted from these combinations.

The correct response towards a stimulus depended on the currently relevant task. There were two tasks, referred to as A and B. For half the subjects, task A required responding according to the spatial frequency of the grating pattern. That is, if a stimulus, regardless of the orientation of its pattern, had a low spatial frequency, the correct response towards this stimulus was to choose response 1 (e.g., peck a response key presented on the left of the screen), while stimuli with a high spatial frequency required choosing response 2 (e.g., the response key located on the right). In task B, stimuli had to be classified according to the orientation of the grating pattern, regardless of its spatial frequency. Thus, if a stimulus showed a horizontal pattern, it required response 1, while a vertical pattern afforded response 2. For the remaining subjects, the relevant stimulus dimensions of task A and B were reversed.

Tasks were cued by colour-filled circles of 200 pixels in diameter. Each of the two tasks was associated with two distinct cues: these were blue or yellow circles for task A, and red or green circles for task B. Although blue and yellow were always both assigned to task A, the stimulus dimensions (spatial frequency or orientation) that were important for classification in that task and the location of the response key that was associated with any cue-stimulus combination were counterbalanced across pigeons. As each stimulus always contained both spatial frequency and orientation information, some stimuli always required the same response; e.g., a horizontal pattern of low spatial frequency might always require response 1 regardless of the current task. In contrast to these congruent stimuli, incongruent stimuli required opposite responses in the two tasks. For example, a horizontal stimulus with a high spatial frequency pattern might require response 1 in the orientation task but response 2 in the spatial-frequency task.

Procedure

The procedure described below is illustrated in Figure 2. Each trial began with the presentation of a white circular observing key (100 pixels in diameter) presented in the centre of a black display to focus attention to the screen. Following two pecks at the observing key, it was replaced by one of the four task cues. The pigeons had to peck the cue twice, after which a stimulus appeared superimposed on the cue colour so that information of both the cue and the stimulus were presented simultaneously in the centre of the display. Examples of what these combined cue-stimulus images looked like can be seen in Figure 1. Pecking on the cue-stimulus combination resulted in its deletion from the centre of the screen and its immediate reappearance 200 pixels to both the left and the right side of the display centre. A response was made by

choosing the correct response location (left or right) that was associated with the present cue-stimulus combination and pecking on the stimulus presented in that location. Two successive pecks at the correct location resulted in the activation of the corresponding food magazine for 2.5 seconds and the end of the trial. Pecks at the incorrect key had no scheduled consequences. The inter-trial-interval to the next presentation of the observing key lasted 15 to 30 seconds.

Training

Pigeons received training on each task separately before attempting the task-switching paradigm. The order in which the tasks were learned was counterbalanced across individuals. There were daily training sessions, each administered in three blocks of 24 trials in such a way that the eight possible combinations of the two cues of the task currently being trained and the four stimuli were shown three times per block. The first block of each session included a 25th trial (a repeat of the first trial of the session, as the first trial was not included in the analysis of daily performance), resulting in 73 trials per day in total. The order of cue-stimulus combinations was randomized within blocks. After successfully acquiring one task, subjects proceeded to training on the competing task. For each task, discrimination of the stimuli was considered successful if the subject responded correctly on at least 80% of trials within a daily training session, for at least three consecutive sessions. The pigeons acquired their first task in a mean of eight sessions; the second task was learned in a mean of six sessions. Once performance in the second task reached criterion, pigeons received further training sessions on the first task until they passed criterion again, followed by retraining sessions for the second task. The number of sessions on each task was gradually reduced until pigeons were able to switch between tasks from one

day to the next and still perform at or above 80% correct responses in each session. Finally, pigeons received three sessions consisting of four blocks of 24 trials each, in which the task changed from one block to the next, to ensure that they were able to switch between the two tasks within the same session. The entire training was completed in a mean of 46 sessions.

Test

Once each task had been trained separately to criterion, subjects entered the task-switching part of the experiment, in which task A and task B trials were intermingled. The task sequence was partially randomized to produce a switch trial in one third of trials. Task cues always changed from the previous trial in switch trials. Because there were two cues for each task, it was possible to alternate between the relevant task cues on repeat trials to avoid the possibility that the same cue was presented on two consecutive trials. The pigeons received 20 sessions of 73 trials each, a total of 1460 trials.

Results

Our main dependent variable is error rate when choosing a response key, though, for completeness, we also recorded the latency from the onset of the response display to the peck at the correct response key resulting in the operation of the food magazine. Trials immediately following an incorrect response were excluded, in case a wrong response indicated that subjects had been unable to execute the relevant task of that trial, in which case the next trial could not be regarded as either a switch or a repeat trial. The first trial of each session was also excluded, as it was neither a switch nor a repeat trial.

Pigeons' error rates were generally low ($M=8.8\%$, $SD=3.1$); since the pigeons had received substantial training, this overall error rate was significantly better than 50% chance performance, $t(7)=37.57$, $p<.001$.

The significance of any task-switching effects was investigated by a repeated-measures ANOVA using Trial Type (Task-Repeat or Task-Switch trial), Stimulus Congruency (Congruent or Incongruent) and Sessions as within-subject factors. Where appropriate, significance levels were subjected to Huynh-Feldt correction. The results of this analysis are summarised in Table 1 and illustrated in Figure 3.

The effect of the factor Trial Type was non-significant: as seen in Figure 3, pigeons demonstrated no sign of any switch costs (Task-Repeat: 9.1% vs. Task-Switch: 8.9%). However, Stimulus Congruency strongly influenced performance, as pigeons showed increased error rates when responding to an incongruent stimulus compared to responding to a congruent stimulus (Incongruent: 14.3% vs. Congruent: 3.6%; both values are significantly different from 50% chance performance, $t(7)=41.52$ and $t(7)=22.18$, respectively, adjusted $p<.002$).

Stimulus Congruency did not interact with Trial Type, and pigeons showed no indication of increased error rates when switching tasks in response to stimuli of either congruency (switch costs on congruent trials: -0.6% , $p=.301$; on incongruent trials: 0.2% , $p=.850$). The pigeons did not show any significant changes in their error rates across sessions, nor did the progression in the experiment affect the magnitude of switch costs or congruency effects.

As expected, reaction times of pigeons were slow, and too variable to show consistent congruency effects (Incongruent: 6919ms vs. Congruent: 7109ms; $F(1,7)=2.17$, $p=.184$) or switch costs (Task-Repeat: 7047ms vs. Task-Switch: 6981ms; $F(1,7)=3.27$, $p=.113$).

In light of the remarkable absence of any switch costs in the pigeons' performance, the accuracy data were also examined by estimating a Bayes factor using the Bayesian repeated-measures ANOVA function in JASP (Love, Selker, Marsman et al., 2015). The estimated Bayes factor (Congruency / Trial Type + Congruency) suggested that the data were 0.091:1 in favour of the null hypothesis, that is, the data are 11.04 times more likely to occur under a model assuming only an effect of Stimulus Congruency rather than a model including Trial Type as a second factor.

Finally, in addition to the first-order transitions from trial N-1 to trial N, we also assessed the potential influence of second-order transitions from trial N-2 on performance on trial N with a repeated-measures ANOVA including first-order (Task-Repeat and Task-Switch trials) and second-order transitions (Task-Repeat and Task-Switch trials). We found no significant effects, all $p > .13$.

Discussion

Experiment 1 demonstrated that pigeons were able to perform well in our version of the task-switching paradigm. Their error rates were well below chance, and they exhibited a very strong congruency effect. Nevertheless, they did not show any hint of switch costs. The lack of any switch costs for the congruent stimuli supports Dreisbach et al.'s (2006, 2007) claim that an associative acquisition of task-switching paradigms can eliminate switch costs for univalent stimuli. The lack of any switch cost for the incongruent stimuli, however, is inconsistent with Forrest (2012) and Forrest et al.'s (2014) claim that switch costs could appear in response to incongruent stimuli when associative learning was in play. This inconsistency is exacerbated by

the fact that Forrest et al. (2014) provided simulations to back up their claim. We shall return to this point later.

For the moment our main concern is to increase the power of our design to detect any task-switch costs in pigeons under these conditions, and, failing that, to demonstrate that our procedures are sufficiently sensitive to detect other common sequential effects, such as cue-repetition, stimulus-repetition or response-repetition effects. Experiment 2 addresses these issues.

EXPERIMENT 2

Whilst Experiment 1 replicated the findings of previous task-switching studies with nonhuman animals, it could not clarify the apparent presence of 'switch costs' in human performance that presumably occurred as a consequence of associative processes (as in Meier, et al., 2013). In Experiment 2, we closely examined other trial-order effects for pigeons to understand how associative processes might influence the emergence of costs on task-switch trials in the performance of humans but not in that of pigeons.

The design in Experiment 1 was carefully controlled to adhere to what is thought to be best practice in the task-switching literature. For example, we took measures to address the common issue of separating the costs of switching a task from the costs of switching a cue. If a given task is indicated by the same cue on each trial, every task-repeat trial coincides with a repetition of the relevant task cue, while every task-switch trial also implies a change of the task cue. Previous studies have shown that this is a major contributor to the magnitude of switch costs (Altmann, 2006; Logan & Bundesen, 2003; Logan & Bundesen, 2004; Mayr & Kliegl, 2003; Monsell

& Mizon, 2006; Schneider & Logan, 2005), and, as a result, every effort is made nowadays to avoid presenting the same cue on consecutive trials. In Experiment 2 we relaxed this constraint: half of the task-repeat trials were now accompanied by a repeat of the task cue. This should increase the similarity of the current trial to the previous trial, facilitating the retrieval of the associated response performed on that previous trial and perhaps leading to better performance on task-repeat over task-switch trials.

Moreover, any benefit of immediate repetition should also extend to other features of the cue-stimulus compound – thus, we should observe improved performance when not only the same cue but also the same stimulus is presented in both the current and the previous trial, compared to trials in which the stimulus dimensions are visually different from the stimulus of the previous trial. More precisely, performance should peak on trials that repeat all components of the previous trial, i.e., those in which the cue, the stimulus and the required response are the same as in the immediately preceding trial. This benefit should be visible when comparing performance in such trials to performance in task-switch trials, and especially so if the stimulus of that trial is the same as in the previous trial but the required response can change - which is only possible for incongruent stimuli.

To summarise, given that pigeons might show costs to performance on task-switch trials compared to task-repeat trials with a cue repetition, but not when compared to task-repeat trials with a cue change (as in Experiment 1), the paradigm introduced in Experiment 1 was extended in Experiment 2 to include task-repeat trials with cue repetitions. Separately, we extended the analyses to not only investigate cue-repetition effects, but also effects of repeating the same stimulus (with the same or a different response) on two consecutive trials.

Methods

Subjects

Fourteen pigeons took part in the experiment. Eight of the pigeons were those that had previously taken part in Experiment 1. They had proceeded to a similar experiment (not reported here) before entering Experiment 2. The other six pigeons had also experienced both of these experiments, but in reversed order (which excluded them from being part of the sample of Experiment 1), before entering Experiment 2.

Procedure

Experiment 2 used the same apparatus, stimulus material and (for the six novel pigeons) training procedure as described in Experiment 1. The only difference was that, at test, for the 2/3 of trials that were repeat trials, the relevant task cue was picked randomly so that in half of the repeat trials the cue changed from the previous trial (task-repeat trials) and in the other half the cue repeated (cue-repeat trials). Pigeons received 10 sessions of 73 trials each.

Results

The same trial-exclusion criteria used in Experiment 1 applied. Pigeons' error rates were low ($M=11.8\%$, $SD=5.8$), since the pigeons had received considerable training, and this overall error rate was significantly better than 50% chance performance, $t(13)=24.74$, $p<.001$.

The results were analysed by means of a repeated-measure ANOVA using Trial Type (Cue-Repeat, Task-Repeat or Task-Switch trial), Stimulus Congruency and

Sessions as within-subject factors. Where applicable, significance levels were subjected to Huynh-Feldt correction. The results of this analysis are summarised in Table 2 and illustrated in Figure 4.

Figure 4 shows that, once again, pigeons did not suffer from switch costs. As in Experiment 1, pigeons demonstrated no decrease in performance on Task-Switch trials (Cue-Repeat: 11.9%, Task-Repeat: 11.9%, Task-Switch: 11.1%). However, Stimulus Congruency strongly influenced performance, with increased error rates when an incongruent stimulus was presented compared to when a congruent stimulus was shown (16.4% vs 6.8%); this effect was entirely unaffected by a change in tasks or cues, difference between Task-Switch and Task-Repeat (Cue-Repeat) trials in response to incongruent vs congruent stimuli: 0.9% vs -0.8% (0.7% vs 1.0%). Pigeons also did not experience any significant changes in their error rates or switch cost across sessions.

Again, the accuracy data were also examined by estimating a Bayes factor using the Bayesian repeated-measures ANOVA function in JASP (Love et al., 2015). The estimated Bayes factor (Congruency / Trial Type + Congruency) suggested that the data were 0.024:1 in favour of the null hypothesis, that is, the data are 41.78 times more likely to occur under a model assuming only an effect of Stimulus Congruency rather than a model including Trial Type as a second factor.

In addition to the first-order transitions from trial N-1 to trial N, we assessed the potential influence of second-order transitions from trial N-2 to trial N with a repeated-measures ANOVA including first-order (Cue-Repeat, Task-Repeat and Task-Switch trials) and second-order transitions (Cue-Repeat, Task-Repeat and Task-Switch trials). We found no significant effects, all $p > .18$.

To test the assumption that performance is better on trials that repeat all components (i.e., cue, incongruent stimulus and required response) of the previous trial compared to performance in task-switch trials in which the incongruent stimulus of that trial is the same as in the previous trial but the required response changes, we conducted a repeated-measures ANOVA including only incongruent stimuli, using Stimulus Repeat (repeating the same incongruent stimulus or switching from one incongruent stimulus to the other incongruent stimulus) and Trial Type (Cue-Repeat, Task-Repeat or Task-Switch trial) as within-subject factors. Where appropriate, significance levels were subjected to Huynh-Feldt correction. As illustrated in Figure 5, there was a highly significant interaction between the two factors ($F(2,26)=13.6$, $p<.001$, $\eta_p^2=.51$), but no significant main effect of either factor (both $p>.26$). Pigeons showed very low error rates on cue-repeat trials in which the incongruent stimulus repeated, and elevated error rates on switch trials in which the incongruent stimulus repeated. Conversely, when the stimulus on the previous trial shared no elements with the current stimulus (i.e., when the two opposing incongruent stimuli were shown on subsequent trials), error rates were very low when the task switched (and thus the required response was the same in both trials), and increased when the task repeated (and thus the required response changed) in cue-repeat and task-repeat trials. Thus, we have succeeded in demonstrating sequential effects in the data from this experiment, confirming that our procedures are sensitive to trial-order effects, and so have the potential to detect switch costs.

Discussion

Just as in Experiment 1, our pigeons did not show any switch costs. Instead, Figure 5 reveals a reliable pattern of pigeons tending to respond more accurately on

Cue-Repeat/Stimulus-Repeat, Task-Repeat/Stimulus-Repeat and Task-Switch/Stimulus-Change trials, and to make more errors on Cue-Repeat/Stimulus-Change, Task-Repeat/Stimulus-Change and Task-Switch/Stimulus-Repeat trials. Taken together, pigeons primarily showed increased error rates on those trials in which the correct response was opposite to the one required by the previous trial; conversely, they benefited from a repetition of the previously required response.

Such an outcome would be expected if there was a tendency to return to the same response location that produced reinforcement in the previous trial rather than change to a different response alternative. Indeed, pigeons may have a tendency to do so (cf. Schneider, 2008; Schneider & Davison, 2005; Stubbs, Fetterman, & Dreyfus, 1987; Morgan, 1974, had earlier shown a similar result with rats).

It is plausible that the response location in itself became integrated into the cue-stimulus compound that pigeons associated with a reward; instead of instrumentally learning the correct behaviour (go left or right) afforded by a stimulus, pigeons might have associated the perceived combination of cue, stimulus and location as a whole with reinforcement (Meier, Lea, & McLaren, in press), and idea that is consistent with instance theory explanations of task switching (Logan, 1988) and the idea of event files (Hommel, 1998). As a consequence, the two response locations in which the stimulus was simultaneously presented in the choice display became aversive or appetitive depending on the opportunity to receive a reward by avoiding or approaching them. It is plausible that the spatial location of the reinforced stimulus in the previous trial became as strong a determinant of behaviour as other elements like the cue colour, or the spatial frequency or orientation of the stimulus (Campos, Debert, da Silva Barros, & McIlvane, 2011; Iversen, Sidman, & Carrigan, 1986; Lionello & Urcuioli, 1998; Lipkens, Kop, & Matthijs, 1988; Sidman, 2009).

This is especially likely considering that, while spatial frequency or orientation can change depending on the visual angle from which they are perceived (for example, spatial frequencies decrease as one approaches them), the spatial position in which a pigeon held its head immediately before it received a reward is not so susceptible to variation.

The pigeons' general response-repetition benefit is in contrast to the response-repetition effects commonly observed in human task-switching: while humans also experience a benefit of repeating a response on task-repeat trials, being required to repeat the previous response on task-switch trials often incurs a cost to performance (Hübner & Druey, 2006; Kleinsorge, 1999; Kleinsorge & Heuer, 1999; Mayr & Bryck, 2005). This fact might provide further evidence that pigeons' performance is not governed by the same cognitive processes that govern human task-switching performance. We will elaborate on this point in more detail in the general discussion.

It is worth noting that the observed response-repetition effect also has implications for the validity of our paradigm: as mentioned above, we chose to administer a long inter-trial interval to aid performance. Using longer intervals could have introduced the risk of reducing any carry-over effects from the previous trial or task, so that any potential task-switch costs for pigeons became too small to be of significance. Despite the long ITI, however, the pigeons demonstrated large trial-to-trial effects that captured the sequential influence of the preceding trial; thus, it is plausible to assume that any sequential effects of the task would also have been apparent.

GENERAL DISCUSSION

The main question that this article is concerned with is whether task-switching and the commonly observed costs of performing a task switch are necessarily the product of executive-control functions such as task-set reconfiguration, or whether task-switch costs can occur when performance is primarily mediated by associative learning.

Previous work suggested that, when human participants solve a task-switching paradigm by learning cue-stimulus-response contingencies, switch costs might be eliminated when responding to response-congruent stimuli (Dreisbach, 2012; Dreisbach et al., 2006, 2007). Similarly, pigeons did not show any switch costs when responding to congruent stimuli. Since the stimulus that is presented signals the required response unambiguously, no information about the currently relevant task is required to perform accurately – hence, congruent stimuli should favour stimulus-response learning over the costly retrieval and reconfiguration of task-sets.

More interestingly though, when responding to response-incongruent stimuli, humans consistently suffer from switch costs, even when they lack task awareness (Forrest et al., 2014; Forrest, 2012; Meier et al., 2013). These results have been simulated in associative models, which equally predicted small but reliable switch costs under pure associative-learning conditions; this has led Forrest (2012) and Forrest et al. (2014) to conclude that performance costs in task-switch trials might not necessarily be mediated by complex executive-control processes but could also emerge as a product of the automatic retrieval of cue-stimulus-response associations. Unfortunately, research on the task-switching abilities of animals is equivocal with respect to this assumption: none of the several independent studies on rhesus macaques could convincingly demonstrate switch costs in the monkeys' performance (Avdagic et al., 2014; Stoet & Snyder, 2003a, 2003b, 2008, 2009). Similarly, the

present paper and previous research using pigeons (Castro & Wasserman, 2016; Meier et al., 2013) found no evidence that associative processes may lead to switch costs in response to incongruent stimuli - pigeons did not show any evidence of reduced performance when the tasks switched on trials with incongruent stimuli. Therefore, an alternative explanation for the occurrence of switch costs under some circumstances but not others may be required. One, perhaps the most likely, explanation is that switch costs emerge only when executive-control processes, such as task-set reconfiguration, are afforded by subjects relying on abstract task rules, but that when performance is governed by associative processes and subjects do not rely on task-sets, no task-switch costs ensue. The implication of this would be that, while pigeons (and macaques) behaved entirely associatively and thus lacked switch costs, any switch costs that were present in previous studies with humans indicate that the performance of those subjects was governed by executive-control processes, or at least different processes to those used by our pigeons.

In the case of the pigeons, we have some evidence that this assumption is true, since pigeons were strongly affected by stimulus congruency. It has previously been suggested (i.e., Kiesel et al., 2007, Schneider, 2015) that this congruency effect is governed by an automatic retrieval of stimulus-response contingencies rather than executive-control processes. In the current context, it also provides evidence that the pigeons' behaviour was controlled by specific stimulus features, and that interference between the competing cue-stimulus-response contingencies did in fact affect their performance more than abstract task-sets. Further evidence for this fact is the clear benefit of response repetitions for pigeons. Response-repetition effects have also been shown by task-switching humans (Hübner & Druey, 2006; Kleinsorge, 1999; Kleinsorge & Heuer, 1999; Mayr & Bryck, 2005), but with an important difference: to

humans, repeating the same response on two consecutive trials is only beneficial to performance on task-repeat trials – but on task-switch trials, having to repeat the previous response often comes at a cost. As mentioned earlier, the universal benefit to pigeons most likely stems from associative processes and the integration of stimulus location as another feature of the perceived cue-stimulus compound. In contrast, the observed costs of response repetitions in task-switch trials for human performance are most logically explained by the influence of task-sets (i.e., Kleinsorge, 1999): a change in a relevant task dimension that requires a recoding operation generalises to response selection, and in effect facilitates response alteration rather than response repetition.

Whilst one possibility is that the switch costs reported in previous human studies were always due to executive control, another is that there was some associative component - especially given that computational-modelling accounts (Forrest et al., 2014; Forrest, 2012) confirm the possibility of the presence of switch costs under associative-learning conditions. How can we distinguish between these two possibilities? In order to address this question, is it worth looking at how Forrest (2012) explains the presence of switch costs in her APECS models. Switch costs could in part be an expression of the closer associative connection between cues that indicate the same task: if the same stimulus-response links in an associative network are repeatedly activated in the presence of certain task cues, this activation can strengthen the link between these cues themselves, resulting in an associative cue equivalence. This equivalence in turn selectively facilitates the retrieval of a stimulus-response link on trials with equivalent cues, that is, task-repeat trials.

The crucial point may be that pigeons represent the various components of a trial quite differently to humans. Forrest's explanation relies on the assumption that

task cues are encoded as one of several components of a trial - as are the stimuli, or even the separate stimulus dimensions. Pigeons, however, may perceive the presentation of cue and stimulus as a single cue-stimulus compound. To the eye of a pigeon, a horizontal, low-spatial-frequency stimulus presented on a green task cue may be very different from a horizontal, low-spatial-frequency stimulus presented on a red cue, even though both combinations require the same response. Thus, in a way, even Forrest's associative algorithms obey a task structure in that the cues are regarded as providing separable information to the stimuli - to the pigeon, cues and stimuli may be indivisible elements of the same image.

Keeping in mind the response-repetition effects on the pigeons' performance, this analysis can be taken even further to postulate that what the pigeons may do is not only to represent cue colour, stimulus orientation and spatial frequency as a compound, but also to encode whether this compound is to the left or right of the centre of the screen. We hypothesize that they employ Pavlovian processes to learn the problems we set them in this paper, and that the trial-to-trial sequential effects brought about by the application of these processes (see Figure 5) can be shown to result in very small to no switch costs. To illustrate this idea, we can give a concrete example specific to the paradigm used in this paper, by using one of the current, well validated models of Pavlovian conditioning in pigeons, specifically that due to Pearce (1987). In this model, pigeons (and other animals) learn by associating configurations of stimuli with outcomes, and these associations then generalize to other configurations that share elements with the trained configuration. Pearce gives a simple rule for generalization, which is:

1. $G(\text{generalization}) = NS \times NS / TA \times TB$

where NS is the number of elements shared by stimulus configurations A and B , TA is the total number of elements in A and TB the total number of elements in B . In essence, this captures the idea that generalization between two configurations, A and B , is governed by the product of the proportion of A elements in B and the proportion of B elements in A .

We shall make use of this idea, but because we are interested in sequential effects, i.e., the influence of trial $N-1$ on trial N , we will not require the learning rule specified by Pearce except to note that we assume that, for any given trial involving incongruent stimuli, when pigeons are performing on this problem, all these stimuli are at approximately the same level of associative strength, such that increments in this strength as a result of a trial will be approximately equal. We do not consider congruent stimuli here because typically performance is at near asymptotic levels for these stimuli, making any such increment very small. We assume that the increment is small, but non-negligible for incongruent stimuli, which allows us to perform a perturbation analysis of the sequential effects that can be expected on Pearce's model.

Our analysis also assumes that the pigeons are learning to approach the correct configuration, say AWL , where A is the cue, W the stimulus, and L denotes this is the left-hand key, and avoid the wrong configuration, which in this case would be AWR , where the R denotes the right-hand key. Thus, we take it that they learn a stimulus configuration using spatial location as one of the elements making up this configuration. We will consider the merits of this assumption later, but for now we show how our perturbation analysis would proceed and generate an estimate of the switch costs to be expected on the basis of this model using our paradigm.

There are four cues, which we call A, B, C, D, where A and B denote one task and C and D the other. There are also four stimuli, W, X, Y, Z, and we take W and X to be the incongruent stimuli. We denote spatial location by L and R, and this means that we have eight different configurations involving stimulus W. An example of two that could occur on the same trial would be AWL and AWR, and we assume that AWL is the correct choice on this trial. All these elements are, for simplicity, assumed to have equal salience.

We are now in a position to proceed with our analysis. So, for example, if we are considering a trial on which cue A plus stimulus W occur and are correctly chosen on the Left, we would represent this as AWL+. As this combination would become more strongly associated with reward, its associative strength with reward would increase from its current value V to $V+\partial$, where ∂ is the small increment to associative strength that occurred on that trial. In Pearce's model, this increment to associative strength will generalize, meaning that the effective increment to the other choice location on this trial, AWR (sharing 2 of a total of 3 elements with AWL), will be $2/3 \times 2/3 = 4/9$ of ∂ following Equation 1. If the next trial is a repeat of the one that has just occurred, we can estimate how much better the pigeon will be on that trial as a result of this increment. The extra associative strength for the correct configural stimulus is ∂ , the extra for the incorrect stimulus is $4\partial/9$, hence the net gain is $5\partial/9$. Table 3 shows this calculation and the other possible trial-to-trial transitions beginning with AWL+ on trial N-1.

The calculations based on this analysis can be illustrated in a graph equivalent to Figure 5 (see Figure 6). To construct Figure 6, we used the negative of the values in the final column of Table 3, because a positive value in the table equates to fewer errors on that trial. The correspondence between this model and our data is

immediately apparent. On the basis of the model, it is possible to work out the expected switch costs: the average of Cue-Repeat and Task-Repeat trials is $-.11\delta$; the average of Task-Switch trials is $+.11\delta$; hence, the difference (the switch cost) is predicted to be $.22\delta$. Given that δ is itself a small increment, and this is multiplied by a factor considerably less than 1, we can now see why the switch costs in our pigeons can be so small, even though there are measurable sequential effects in both our data and the model².

It only remains to explain why Forrest et al. (2014) observed switch costs (albeit smaller than usual) in their participants, if they were solving the problem associatively. We follow Forrest et al. in assuming that the human participants were learning to associate a combination of cue and stimulus with a left or right response, and not encoding all these components as one compound. We also follow the analysis there and in Forrest (2012) by assuming that humans developed cue equivalence, as discussed earlier, in the same way that APECS (an algorithm based on back propagation) did. With these assumptions, it is possible to generate an estimate of the switch costs using Pearce's (1987) generalisation rule. It comes to $.50\delta$, i.e. more than double the estimate for the pigeons. The role of cue equivalence in generating this result is worth elaborating. Our simulation using Pearce (1987) for the pigeons is not actually affected by incorporating equivalence, but the instrumental version for humans is, and in this case increases the estimated switch costs. Thus, part of our

² While this model explains the results of the present study rather well, we make no claims about the applicability of the model to other task-switching studies conducted with nonhuman animals, like Castro and Wasserman's (2016), Stoet and Snyder's (2003a) or Avdagic et al.'s (2014).

answer may well lie in the fact that pigeons solve these problems using Pavlovian processes and humans instead solve them instrumentally when denied any task rules or task sets (cf. Meier et al., in press). This is an issue that we intend to pursue further in the future, but, for the moment, it suggests that the lack of any detectable switch costs in pigeons in our experiments may have been due to their reliance on a Pavlovian-conditioned approach in solving the problem, and that an instrumental solution was responsible for the small but detectable switch cost reported by Forrest et al. (2014).

To conclude, we were able to show that, whilst task switching is possible without the involvement of executive control, the occurrence of switch costs is not inevitable under associative-learning conditions, as our pigeons evidently suffered no costs to performance when switching from one task to another. Nonetheless, despite an absence of task-switch costs for pigeons, the previous trial affected their performance on the next trial. By incorporating this finding into Pearce's (1987) model of stimulus categorisation, we conclude that pigeons acquired our task-switching paradigm via Pavlovian processes, which resulted in an absence of switch costs. Further, Pearce's model also allowed us to make inferences about the reliable occurrence of switch costs when no task-sets are available to humans (Forrest et al., 2014) and in simulations using an associative learning algorithm (APECS) based on back propagation (Forrest, 2012), suggesting that they are likely due to instrumental learning and the establishment of an equivalence between cues that signal the same task.

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Table 1. *Experiment 1:* Results of a repeated-measures ANOVA on error rates, using Trial Type (Task Repeat or Task Switch), Stimulus Congruency (Congruent or Incongruent) and Sessions as within-subject factors.

	F	df	MSE	p	η_p^2
Trial Type	0.10	1, 7	.007	.766	.014
Stimulus Congruency	75.62	1, 7	.026	<.001	.915
Trial Type * Congruency	0.49	1, 7	.006	.508	.065
Sessions	1.06	19, 133	.029	.399	.132
Sessions * Trial Type	0.78	19, 133	.006	.725	.100
Sessions * Congruency	1.60	19, 133	.005	.064	.186
Sessions * Trial Type * Congruency	1.17	19, 133	.006	.311	.143

Table 2. *Experiment 2:* Results of a repeated-measures ANOVA on error rates, using Trial Type (Cue Repeat, Task Repeat or Task Switch), Stimulus Congruency (Congruent or Incongruent) and Sessions as within-subject factors.

	F	df	MSE	p	η_p^2
Trial Type	0.62	2, 26	.012	.525	.046
Stimulus Congruency	42.20	1, 13	.046	<.001	.764
Trial Type * Congruency	0.75	2, 26	.012	.480	.055
Sessions	1.44	9, 117	.009	.177	.100
Sessions * Trial Type	1.05	18, 234	.009	.410	.075
Sessions * Congruency	1.07	9, 117	.010	.388	.076
Sessions * Trial Type * Congruency	1.14	18, 234	.011	.321	.081

Table 3. Perturbation analysis of task-switching in pigeons based on Pearce (1987).

	Previous configuration	Correct choice	Incorrect choice	Difference (correct-incorrect)
Cue Repeat + stimulus repeat	AWL+	AWL	AWR	5 δ /9
Task Repeat + stimulus repeat	AWL+	BWL	BWR	3 δ /9
Task Switch + stimulus repeat	AWL+	CWR	CWL	-3 δ /9
Cue Repeat + stimulus change	AWL+	AXR	AXL	-3 δ /9
Task Repeat + stimulus change	AWL+	BXR	BXL	-1 δ /9
Task Switch + stimulus change	AWL+	CXL	CXR	1 δ /9

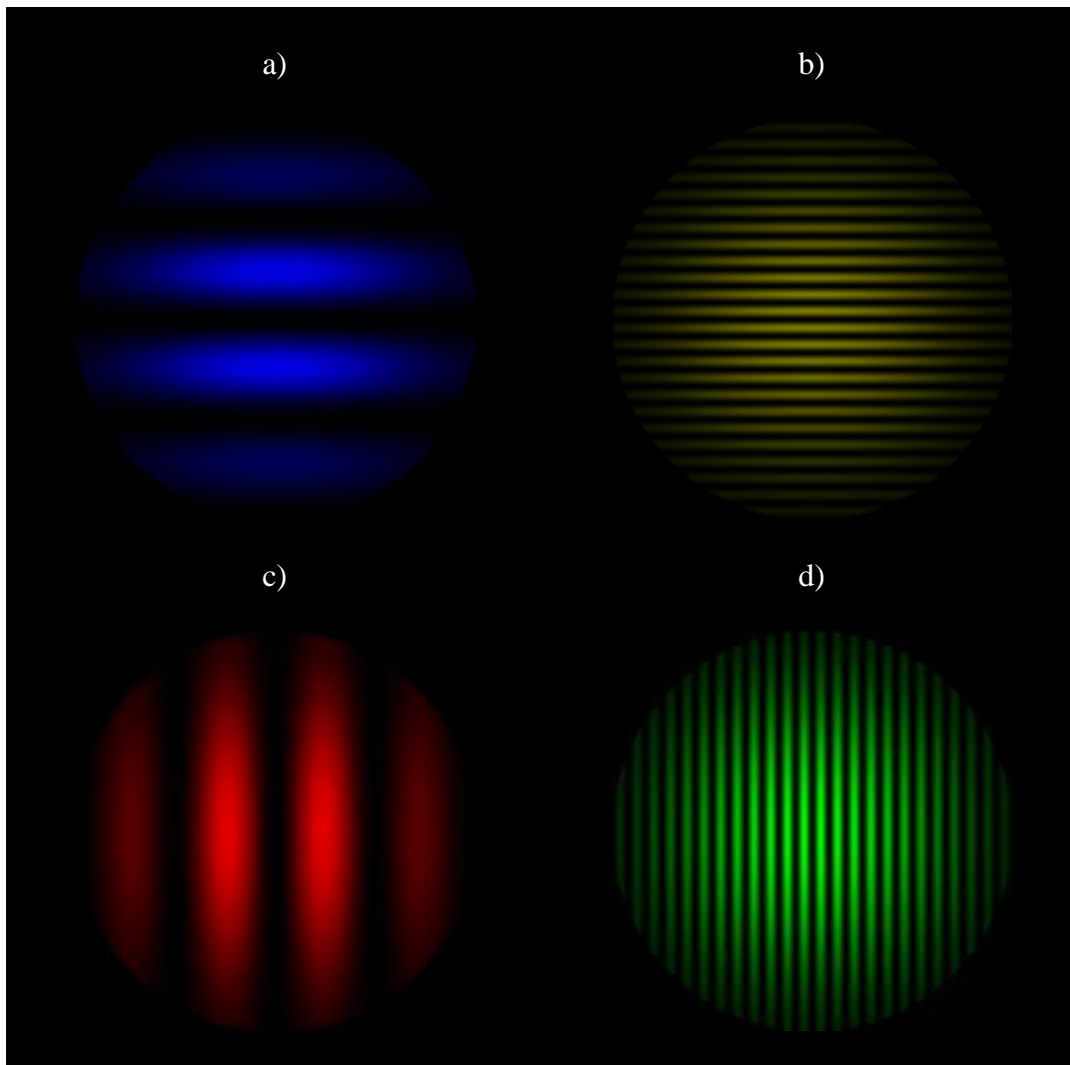


Figure 1. Examples of the four stimuli used in Experiment 1 and 2; a) low spatial frequency and horizontal orientation, b) high spatial frequency and horizontal orientation, c) low spatial frequency and vertical orientation and d) high spatial frequency and vertical orientation. Each stimulus was superimposed on one of the four cues; during test, all four stimuli were paired with all four cues, so that a pigeon experienced sixteen different cue-stimulus combinations (four of these possible combinations are presented here for illustration).

Please refer to the online version of this article for the colour image.

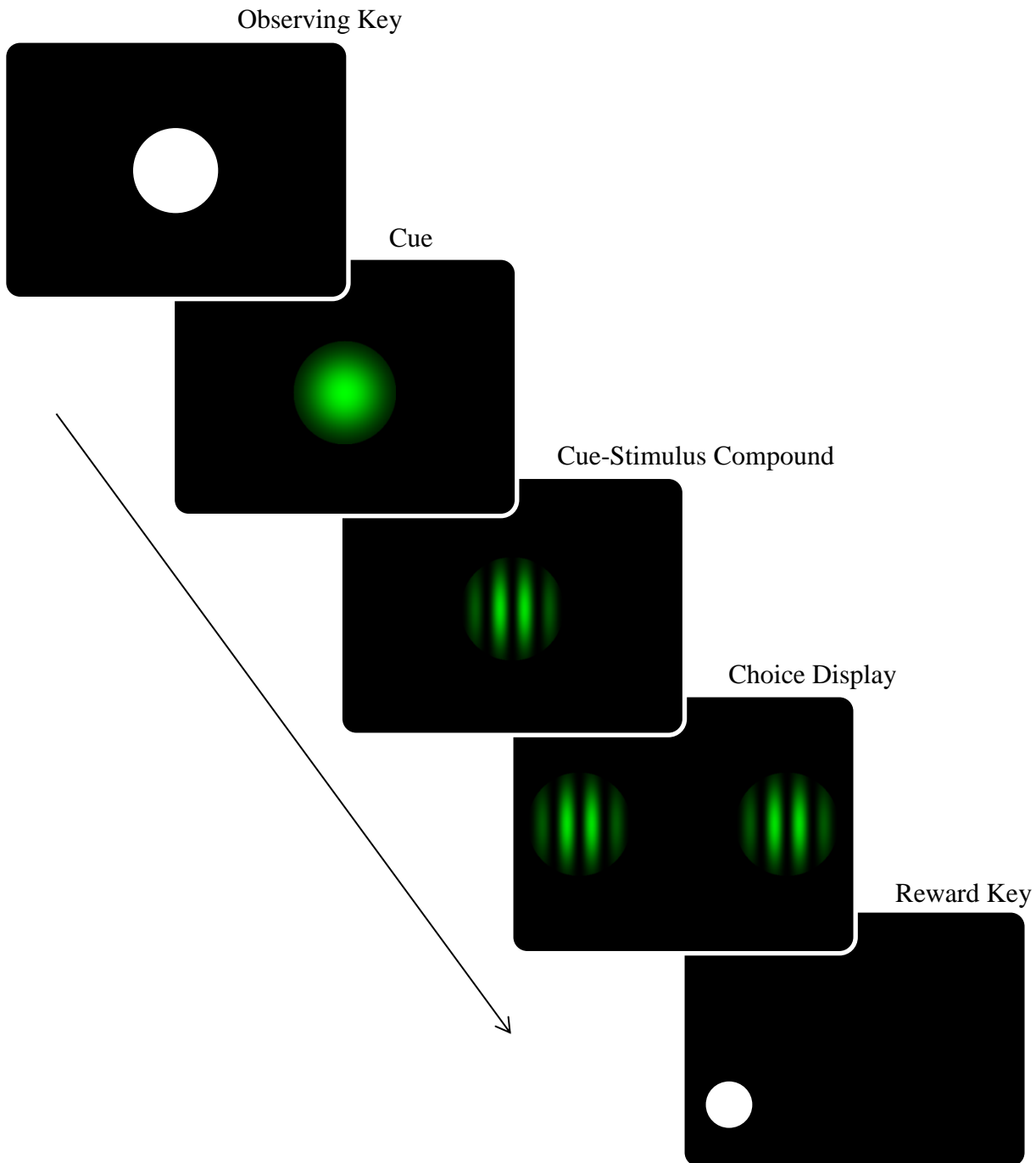


Figure 2. Procedure of Experiment 1. Please refer to the online version of this article for the colour image.

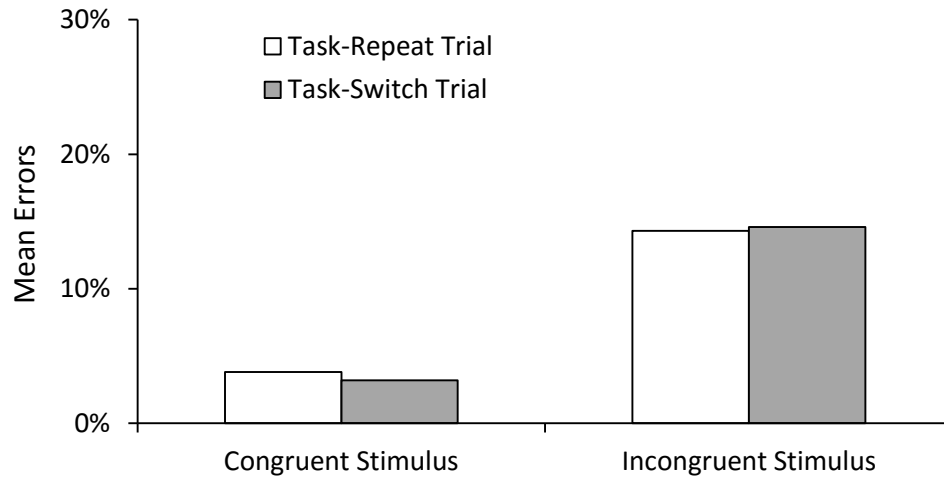


Figure 3. *Experiment 1:* Mean error rates depending on Trial Type (Task-Repeat and Task-Switch trials) and Stimulus Congruency (trials containing a congruent stimulus and trials containing an incongruent stimulus). Please refer to the text and Table 1 for mean differences and measures of variance.

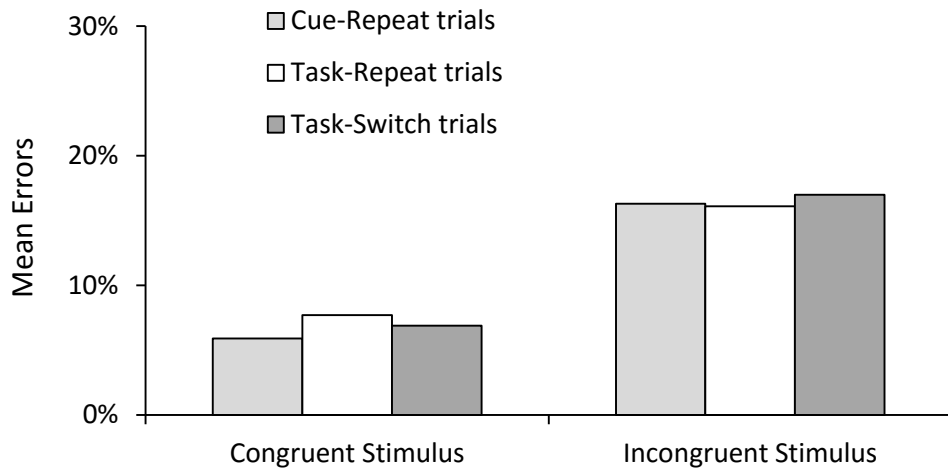


Figure 4. *Experiment 2:* Mean error rates depending on Trial Type (Task-Repeat and Task-Switch trials) and Stimulus Congruency (trials containing a congruent stimulus and trials containing an incongruent stimulus). Please refer to the text and Table 2 for mean differences and measures of variance.

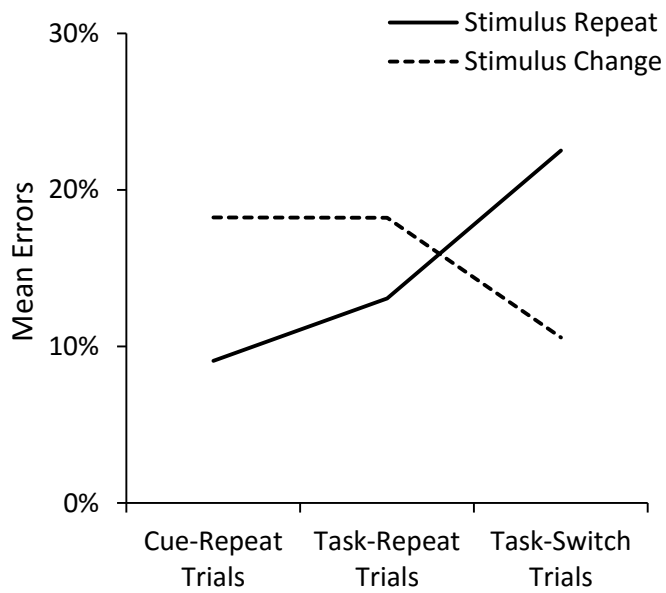


Figure 5. *Experiment 2:* Mean error rates in trials in which an incongruent stimulus is presented and is the same as in the immediately preceding trial (Stimulus Repeat) or follows a trial in which the other incongruent stimulus appeared (Stimulus Change), depending on Trial Type. The pattern suggests a benefit of response repetitions (see text for details).

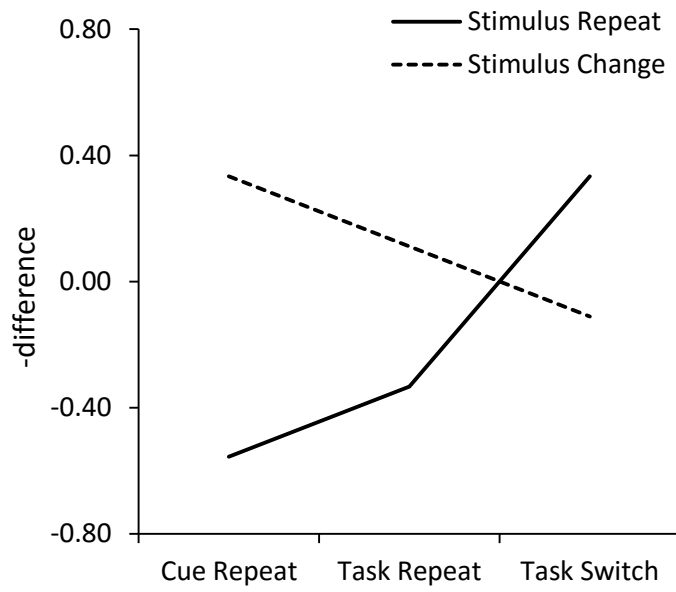


Figure 6. Plot of the perturbation analysis of task-switching in pigeons based on Pearce (1987). The dependent variable is the negative of the difference score reported in Table 3. Higher scores mean more errors.