A Comparative Investigation of Associative Processes in Executive-Control Paradigms

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature: ……..

ABSTRACT

The experiments reported in this thesis were conducted to examine the effects of executive-control and associative-learning processes on performance in conventional executive-control paradigms.

For this purpose, I developed comparative task-switching and response-inhibition paradigms, which were used to assess the performance of pigeons, whose behaviour is presumably based purely on associative processes, and of humans, whose behaviour may be guided by executive control and by associative processes. Pigeons were able to perform accurately in the comparative paradigms; hence, associative-learning processes are sufficient to account for successful performance. However, some task-specific effects that can be attributed to executive-control processes, and which were found in humans applying executive control, were absent or greatly reduced in pigeons. Those effects either reflect the mental operations that are performed to ensure that a specific set of stimulus-response-contingencies is applied and any contingencies belonging to a different set are suppressed, or reflect mental preparations for the possibility that the requirement to execute a certain response suddenly changes. In particular, in Chapter 3, it is shown that the benefits of repeatedly applying the same set of stimulus-response contingencies (or, in reverse, the costs of switching from one set to another) do not apply when Pavlovian processes dominate learning, which is likely the case for pigeons. Furthermore, as shown in Chapters 4 and 5, the behavioural effects of preparing for an unpredicted change in response requirements appeared to be absent when behaviour was based purely on associative processes. Instead, associatively mediated performance was primarily influenced by the stimulus-response contingencies that were effective in each paradigm. Repeating the same response in consecutive trials facilitated the performance of pigeons and associatively learning human participants in the task-switching paradigms, and performing a particular Go response increased the pigeons' likelihood of executing that response in the following trial in two response-inhibition paradigms.

In summary, any behavioural effects that can be observed at the level of abstract task requirements reflect the influence of executive-control

processes, both in task-switching paradigms and in response-inhibition paradigms.

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CHAPTER 1: INTRODUCTION

Every day, humans are faced with a multitude of decisions: to do homework or watch TV (or do both at the same time?), have a quick look out the window to decide whether to take an umbrella or sunglasses, and finally start a diet - but then who could say no to a cheeky Nando's? Multitasking, planning, impulse control - all these complex cognitive abilities are said to be governed by executive control (Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004b; Ardila, 2008; Chan, Shum, Toulopoulou, & Chen, 2008; Suchy, 2009). Because of the wide range of abilities that are ascribed to executive control, it is still difficult to pin down a unified concept of what constitutes executive control. In their review of close to a dozen definitions of executive functions, Jurado and Rosselli (2007) conclude that executive-control processes "allow us to shift our mind set quickly and adapt to diverse situations while at the same time inhibiting inappropriate behaviors. They enable us to create a plan, initiate its execution, and persevere on the task at hand until its completion. Executive functions mediate the ability to organize our thoughts in a goal-directed way." The processes of task-set shifting (or task switching), response inhibition and working-memory updating have been identified as distinguishable components of executive control (Miyake, Friedman, Emerson, Witzki, Howerter, & Wagner, 2000; Friedman, Miyake, Young, DeFries, Corley, & Hewitt, 2008).

Executive-control functions have been linked to the prefrontal cortex (Robbins, Weinberger, Taylor, & Morris, 1996; Kimberg, D'Esposito, & Farah, 1997; Roberts, Robbins, & Weiskrantz, 1998; Stuss & Alexander, 2000; Royall, Lauterbach, Cummings et al., 2002; Koechlin, Ody, & Kouneiher, 2003; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004a; Ridderinkhof et al., 2004b; Braver & Barch, 2006; Niendam, Laird, Ray et al., 2012; Stuphorn & Emeric, 2012; Friedman & Miyake, in press); therefore, the ability to control ones actions in a goal-directed way has only been attributed to humans and animals that possess a frontal cortex (or analogue thereof). There is a large body of research investigating executive-control mechanisms in non-human primates (e.g., Asaad, Rainer & Miller, 2000; Fuster, 2000; Moore, Killany, Herndon, Rosene & Moss, 2005; Isoda & Hikosaka, 2007; Johnston, Levin, Koval & Everling, 2007; Desrochers, Burk, Badre & Sheinberg, 2015) and

corvids (e.g., Lefebvre, Reader, & Sol, 2004; Kirsch, Güntürkün, & Rose, 2008; Striedter, 2013; Clayton & Emery, 2015), although the efforts to confirm executive control in other species are growing (for example, for dolphins, Marino, 2002; for sheep, Morton & Avanzo, 2011; for rats, Brown & Bowman, 2002; Dalley, Cardinal & Robbins, 2004). But for animals lacking a prefrontal cortex, it is thought that behaviour is primarily governed by associative mechanisms, which Mitchell, De Houwer, and Lovibond (2009) describe as "the formation of links between mental representations of physical stimuli […]. The links are said to be formed passively and automatically as a direct consequence of contiguous (with some restrictions) pairings of those physical stimuli." Pigeons, for example, have repeatedly demonstrated responding purely on the basis of stimulus-response associations, even under conditions where humans employ more reflective processes (e.g., Lea, Wills, Leaver et al., 2009; Wills, Lea, Leaver et al., 2009).

One current theory in cognitive research suggests that human behaviour can be mediated by both executive-control and associative processes (McLaren, Green, & Mackintosh, 1994; Gigerenzer, 2007; Ashby, Paul, & Maddox, 2011; Kahneman, 2011; Forrest, 2012; but see Mitchell, De Houwer, & Lovibond, 2009 for alternative theories). The two processes can be distinguished by the way in which they enable humans to extract information to learn about their environment: for example, category learning aided by executive control is explicit and rule-based, and information is extracted from a single dimension of a (multidimensional) stimulus (Lea & Wills, 2008). Conversely, in the automatic, nonanalytic form of associative learning, behavioural responses are associated with the perceived stimulus as a whole (Ashby & Ell, 2001; Ashby, Ennis, & Spiering, 2007; Smith & Grossman, 2008; Dreisbach, 2012; Forrest, 2012; Smith, Berg, Cook et al., 2012; McLaren, Forrest, McLaren et al., 2014; Smith, Boomer, Zakrzewski et al., 2014); a stimulus may be categorised by using all of its dimensions combined and comparing its similarity to a stimulus to which the correct response is known (Lea & Wills, 2008).

Although both executive-control and associative processes govern human behaviour, it is uncertain under which conditions each process comes to control behaviour. Executive processes are supposed to be intentional and directed at a specific action goal, whereas associative processes occur without intention

(McLaren et al., 1994; Ashby et al., 2011; Kahneman, 2011; Forrest, 2012). It is possible that both processes control behaviour in a flexible way or even occur in parallel, as it is assumed that associative processes work automatically and potentially unconsciously (Gigerenzer, 2007; Shanks & St. John, 2010; Kahneman, 2011). If this is the case, then it is less certain whether a specific human behaviour can unambiguously be attributed to the influence of executive control or to associative processes. This can have potentially detrimental implications: executive-control processes are thought to be the basis of many higher-order cognitive functions, and many psychopathological symptoms, such as major deficits in attention, pathological gambling or substance abuse, have been linked to limited or impaired executive control (e.g., Royall et al., 2002; Bekker, Overtoom, Kenemans et al., 2005; Goudriaan, Oosterlaan, de Beurs & van den Brink, 2005; Li, Milivojevic, Kemp, Hong & Sinha, 2006; Liu, Heitz & Bradberry, 2009; Winstanley, 2011; Grant, Chamberlain, Schreiber, Odlaug & Kim, 2011; Urcelay & Dalley, 2012). Core executive functions, such as an individual's ability to flexibly readjust behaviour to changing demands or inhibit inappropriate behaviour, are often assessed in clinical, developmental or neuropsychological settings (Robbins et al., 1996; Salthouse, 2005; Jurado & Rosselli, 2007; Chan et al., 2008; Suchy, 2009; Lipszyc & Schachar, 2010). However, if performance in the paradigms used for these assessments is mediated by associative learning, it becomes questionable to what degree those paradigms are in fact suitable to assess a subject's level of executive control (cf. Forrest, 2012).

Two widely used paradigms that supposedly rely on executive control are the task-switching paradigm, which measures the ability to flexibly adapt one's behaviour to changing task demands, and the stop-signal task, which measures response inhibition. In Section 1.1, I summarise the current theories and empirical evidence that performance in task-switching studies may either reflect executive-control processes or be mediated by associative processes. In Section 1.2, I provide a similar overview of the current theories and empirical evidence regarding the influence of executive control or associative processes on performance in response-inhibition tasks.

As will become evident in those sections, the current evidence for an influence of associative processes in executive-control paradigms is somewhat complicated by the fact that most empirical studies were carried out with humans or other primates, species that arguably possess executive control, so it cannot be ruled out that executive-control processes contributed to the performance of those individuals. Thus, in the later chapters of this thesis, I examine the patterns of performance in task-switching and response-inhibition paradigms that occur in pigeons, which have repeatedly demonstrated an preference to learn based on associative processes rather than analytical processing (Lea & Wills, 2008; Lea et al., 2009; Wills et al., 2009; Smith, Ashby, Berg et al., 2011; Smith et al., 2012; Maes, De Filippo, Inkster et al., 2015), and contrast them to the performance of humans supposedly relying on either associations or executive-control processes (or both).

1.1 Task Switching and the Presence of Switch Costs

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 (Monsell, 2003; Kiesel, Steinhauser, Wendt et al., 2010; Vandierendonck, Liefooghe, & Verbruggen, 2010; Dreisbach, 2012). Commonly, task-switching paradigms involve the classification of the same set of stimuli along different stimulus dimensions, for which 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 background colour is yellow, but to classify the same stimulus according to whether the pattern is vertically or horizontally orientated (whilst ignoring spatial frequency) when the background colour is red.

Evidence for humans' reliance on executive control in such paradigms is taken from the presence of 'switch costs' [1] (Monsell, 2003; Kiesel et al., 2010; Vandierendonck et al., 2010; Dreisbach, 2012): humans generally take longer and make more errors in 'switch' trials, 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 'repeat' trials, in which the same task as in the previous trial is repeated and thus the response

[1] It has to be noted that this statement is rather simplified, as the presence of switch costs on its own is not a sufficient indicator of executive control (see Forrest, 2012; Forrest et al., 2014). The clearest evidence for executive-control processes might be found in the reduction of switch costs (RISC) with increasing time for preparation (Monsell, 2003): the more time to prepare for a task switch a participant has, the smaller the cost of performing a task switch. Importantly, even when the preparation time is very long or when no time restrictions are given, switch costs do not disappear entirely, but a residual switch cost persists (Monsell, 2003) - and It is this residual switch cost that is referred to here as providing evidence for humans' reliance on executive control. The experiments performed in this thesis do not impose any restrictions on preparation time; thus, it is assumed that participants were maximally prepared for a task switch when responding. The observation that they nonetheless expressed switch costs under these conditions can be regarded as evidence for executive-control processes.

has to be made on the basis of the same stimulus dimension as before (Monsell, 2003; Kiesel et al., 2010; Vandierendonck et al., 2010; Dreisbach, 2012). 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 mental reorientation process would be necessary on switch trials but not on repeat trials, for which the task-set is already available, leading to a measurable difference in performance on these two types of trial.

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 (cf. Monsell, 2003; Kiesel, et al., 2010; Vandierendonck, et al., 2010). But 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 associative-learning processes, i.e., the retrieval of cue-stimulus-response associations (Wylie & Allport, 2000; Logan & Bundesen, 2003; Schneider & Logan, 2005). 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. It is even possible that switch costs might emerge under such conditions, if the presentation of a stimulus primed a specific stimulus-task association (Monsell, 2003) that would make it more difficult to disengage from the previous task when there is a switch.

A task-switching phenomenon often observed in addition to switch costs, namely the effects of stimulus-response congruency (Monsell, Yeung, & Azuma, 2000), might in fact as easily be explained by associative learning processes as it is in terms of executive control. As each task makes use of the

same set of multidimensional stimuli, stimulus values on individual dimensions can be defined as either congruent or incongruent in relation to the correct response towards them. If a stimulus is response-congruent, it always requires the same response regardless of the current task; learning to discriminate between different congruent stimuli thus takes the form of a component discrimination, in which the correct response depends on a single element of a multidimensional stimulus. However, when a response-incongruent stimulus is shown, the correct response varies depending on the current task in the manner of a bi-conditional discrimination. Given that there is good evidence that such discriminations are difficult to learn (Harris & Livesey, 2008), it is no surprise that on trials in which a congruent stimulus is shown, reaction time and error rate are distinctly lower compared to trials with an incongruent stimulus (e.g., Monsell, Sumner, & Waters, 2003; Meiran & Kessler, 2008; Forrest, 2012; Schneider & Logan, 2014; Schneider, 2015), and human task-switching performance can be influenced by large response-congruency effects (Monsell et al., 2000), often at a magnitude of 0.5 to three times the numerical value of switch costs (Forrest, 2012; Schneider & Logan, 2014; and even when switch costs were absent in their data, Stoet & Snyder, 2003a, 2003b).

It has to be noted that this congruency effect can be explained in terms of executive control, e.g., by postulating that, because correct response selection is achieved by firstly identifying the relevant task and then selecting the appropriate task-stimulus-response mappings (Kiesel, Wendt, & Peters, 2007; Meiran & Kessler, 2008; Schneider & Logan, 2014; Schneider, 2015), the mappings of both the competing task sets are held active in working memory and influence each other. On this account, response selection might be facilitated when both task sets include the same stimulus-response mappings (as is the case for congruent stimuli), but impaired when the same stimulus is linked to different responses in the two task sets (Schneider & Logan, 2014; Schneider, 2015). However, the associative-learning account seems to prevail (Mayr & Kliegl, 2000), especially when task-switching paradigms deal with relatively small sets of stimuli (Kiesel et al., 2007), so it is plausible that nonanalytic associative processes might 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, Goschke, & Haider, 2006, 2007; Dreisbach, 2012), 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 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: the same stimulus can occur in each task, 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 was only presented in one task. Univalent stimuli are analogous to the response-congruent stimuli mentioned above, in that they perfectly predict the correct response on its own, even when no additional information about the currently relevant task is available. Essentially, this means that there was no benefit of using task rules in Dreisbach et al.'s design. It has been shown that, under conventional task-switching conditions, switch costs are smaller when stimuli are univalent than when they are bivalent (Jersild, 1927; Spector & Biederman, 1976; Allport, Styles, & Hsieh, 1994; Rogers & Monsell, 1995; Kiesel et al., 2010). 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. Bivalent stimuli (which are analogous to

the response-incongruent stimuli mentioned above) cannot accurately predict the correct behavioural response without additional information from the task cues, and it seems that task-switch costs primarily occur in response to such stimuli. Forrest (2012) and Forrest, Monsell, and McLaren (2014), for example, used bivalent stimuli in an attempt to promote associative learning in task switching and found that, contrary to Dreisbach et al. (2006, 2007), 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. To confirm that this finding can be attributed to associative-learning mechanisms, Forrest (2012) used an associative learning algorithm (Adaptively Parametrised Error Correcting System, APECS) based on back propagation to model task-switching performance in the absence of task rules. The computational simulation also predicted small but reliable switch costs in response to response-incongruent stimuli but not to response-congruent stimuli. In summary, it would seem that human participants will exhibit switch costs in a task-switching paradigm when responding to bivalent, response-incongruent stimuli, regardless of whether they are using task-sets or simple associations between stimuli and responses, whilst switch costs in response to univalent or response-incongruent stimuli might only occur when responses are based on task rules.

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. While they showed large congruency effects in their performance, 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, in the discussion of their results, they argued 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, were criticised 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, switch costs are evidently not always present in a task-switching setting, contrary to what Forrest et al. (2014) and Forrest (2012) concluded, but may in fact be absent in the task-switching performance of nonhuman primates. Given this, instead of assuming that only human executive-control processes lead to switch costs, but executive control in monkeys does not, it might be more likely that the macaques performed task switches based on associative processes instead of executive control, and thus did not suffer switch costs.

Taken together, the above studies might point towards the possibility that task switching can involve executive control or associative learning, and that an absence of switch costs might indicate a reliance purely on associative processes. There is evidence that both humans and rhesus macaques possess

two distinct learning systems: an explicit, rule-based system reliant on executive control and an implicit, nonanalytic learning system based on associative processes (Smith et al., 2012; Smith et al., 2014), though the monkey equivalent of executive control seemed to be limited compared to human executive control (Stoet & Snyder, 2003a, 2003b; Smith, Beran, Crossley, Boomer, & Ashby, 2010; Caselli & Chelazzi, 2011; Smith et al., 2012). The results described above could be a sign that both species are able to benefit from either of the two cognitive processes in a flexible manner depending on the precise demands of the test paradigm – when subjects applied executive control to the paradigm, they exhibited switch costs, and on occasions in which their performance was marked by a lack of switch costs, associative learning prevailed.

In Section 1.3, I elaborate on the approach taken in this thesis to test this hypothesis, using pigeons as a model species.

1.2 Stop-Signal Paradigms and the Ability to Inhibit Prepared Responses

In addition to task switching, another core feature of executive control is the ability to inhibit behaviours when their execution suddenly becomes inappropriate. A widely used task to assess this ability in a range of neuropsychological, clinical or developmental contexts is the so-called Stop-Signal task (Logan & Cowan, 1984), in which subjects repeatedly perform a simple task (often under time constraint) and are sometimes, by the appearance of a stop signal, instructed to withhold executing the task-appropriate response. The ability to stop a behaviour after it has been initiated is assumed to require executive control, like the readjustment of attentional and response goals and anticipatory motor regulation, to find a balance between the focus on performing the required response and the distribution of attentional resources to enhance the detection of the signal (Verbruggen & Logan, 2009b, 2015; Elchlepp, Lavric, Chambers, & Verbruggen, 2016; Verbruggen & McLaren, in preparation).

One of the most prominent models of the mechanisms underlying response inhibition in Stop-Signal tasks is the independent horse-race model (Logan & Cowan, 1984; Verbruggen & Logan, 2008b, 2009c), which postulates that initiating a response and withholding a response are two distinct processes, and each of them is triggered by the presentation of either a stimulus demanding that response (the Go stimulus) or a signal not to respond (the Stop signal). It is thought that these two processes operate independently of each other; that is, response inhibition can be triggered immediately when the signal to do so appears, irrespective of whether or not the Go process had been initiated at that point. However, it is also assumed that once the preparation of the Go response is completed, the Go response necessarily has to be executed and can no longer be inhibited. Consequently, the two processes (one of response execution, the other one of response inhibition) engage in a "horse race" with each other. The process that is completed first determines whether a response in executed or inhibited: if the Go process finishes before the inhibition process, inhibition fails and the response is executed; if the inhibition progress finishes before the Go process, inhibition of the Go response is successful.

Interestingly, the horse-race model makes no assumptions about the involvement of executive control in response inhibition - and indeed it has been proposed that response inhibition in Stop-Signal paradigms may be partly

mediated by associative processes (cf. van Gaal, Ridderinkhof, van den Wildenberg & Lamme, 2009). In fact, assuming (as the independent horse-race model does) that the appearance of the signal to withhold a response triggers the initiation of the inhibition process immediately, associative processes might be entirely sufficient to elicit response inhibition. In several studies, Verbruggen and colleagues (Verbruggen & Logan, 2008a, 2009a; Verbruggen, Best, Bowditch, Stevens, & McLaren, 2014; Best, Lawrence, Logan, McLaren, & Verbruggen, 2016) presented evidence that a stimulus that was consistently paired with the command to withhold a response eventually elicited automatic response inhibition. They argued that the effect could occur either because that stimulus became associated with the subsequent occurrence of the stop signal (and was thus indirectly associated with stopping), or because the stimulus became directly associated with the process that stopped the response.

Executive functions are crucial for the planning of actions, which demands the ability to anticipate and select appropriate responses. The independent horse-race model only applies to inhibition in response to a signal to withhold a prepared response, and associative processes might well suffice to accomplish this kind of reactive response inhibition; proactive inhibition, by which subjects prepare for the possibility of having to inhibit a response, might be a better indicator of executive-control processes (cf. Chikazoe, Jimura, Hirose et al., 2009; Aron, 2011).

Elchlepp et al. (2016) argued that most of the mental operations that enable response inhibition are performed before the appearance of a stop signal and involve proactive adjustments of attention and response thresholds. For example, it is commonly observed that participants respond more slowly to the Go stimulus if response execution was inhibited in the previous trial (e.g., Rieger & Gauggel, 1999; Bissett & Logan, 2011, 2012), and it is thought that this post-signal slowing reflects an anticipatory adjustment of response thresholds to prevent inappropriate responding (Verbruggen & Logan, 2009c; Bissett & Logan, 2011; Elchlepp et al., 2016). On a given trial of a Stop-Signal paradigm, the requirement to perform or withhold a response leads to the activation of the respective mental action goal, i.e., to perform or inhibit a response, to facilitate the correct execution of the relevant action (Boucher, Stuphorn, Logan, Schall, & Palmeri, 2007; Verbruggen & McLaren, in

preparation). To achieve an efficient balance between quickly but inflexibly performing the Go response and efficiently detecting the appearance of the stop signal, the currently active action goal is adjusted flexibly from one trial to the next (Stuphorn & Emeric, 2012; Verbruggen & McLaren, in preparation) - similar to the mental task-set reconfiguration needed in task-switching studies (cf. Monsell, 2003). Following their evaluation of different potential causes (both controlled and situational) of post-signal slowing, Bissett and Logan (2011) concluded that this trial-to-trial adjustment is most likely based on a proactive prioritising of one action goal over the other; that is, after the occurrence of a stop signal, subjects shift their priority from the goal of performing a fast Go response to the goal of successfully detecting the stop signal. Nonetheless, there is the possibility that post-signal response slowing can occur independently of executive-control processes (Emeric, Brown, Boucher et al., 2007; Verbruggen, Logan, Liefooghe, & Vandierendonck, 2008; Bissett & Logan, 2012; see also van Gaal et al., 2009): especially when the stimulus in the current Go trial is the same as the stimulus to which a response had to be inhibited, response slowing could be an effect of stimulus-specific response priming, if that stimulus became associated with the concurrent presentation of the stop signal in the previous trial.

Similarly, it might be assumed that the influence of a proactive reconfiguration of action goals would be apparent in the way in which participants utilise available information about whether or not response inhibition will be required in an upcoming trial; indeed, subjects are more readily able to apply inhibitory control when they expect a stop signal on a given trial than when they expect to perform the Go response (Boulinguez, Ballanger, Granjon, & Benraiss, 2009; Verbruggen & Logan, 2009a). However, Bowditch, Verbruggen, and McLaren (2016) showed that changes in behaviour that are based on the presentation of cues that predict the likelihood of a stop signal in the upcoming trial might in fact not require any proactive adjustments of mental action goals: any implicitly formed associations with stopping can extend to such cues, in such a way that seeing the cue alone might initiate a stopping response, even before any stop signal has appeared. Thus, it is possible that even behaviour that seemingly involves proactive operations, such as improved inhibition in response to predictive cues, might be reduced to associative processes.

There is a large body of research on the ability of animals to perform reactive response inhibition, mostly performed with macaques (i.e., Emeric, et al., 2007; Hanes & Schall, 2009; Liu et al., 2009; Stuphorn, Brown & Schall, 2010) and rats (i.e., Eagle & Robbins, 2003a; 2003b; Eagle, Bari & Robbins, 2008; Eagle, Baunez, Hutcheson et al., 2008; Bari, Mar, Theobald et al., 2011; Eagle, Wong, Allan et.al., 2011; Beuk, Beninger & Paré, 2014), but also with baboons (Lacreuse, Gullstrand, & Fagot, 2016). As expected, stop-signal performance of those animals consistently adhered to the predictions of the independent horse-race model, such as faster latencies to make an incorrect response in stop-signal trials (which is incorrect) than in Go trials (which is correct), and an increased probability of incorrectly responding with increasing delay between the initial presentations of the Go stimulus and the presentation of the stop signal. However, investigations of proactive response adjustments in animals, such as post-signal response slowing (Bissett & Logan, 2012) or altered performance following the presentation of predictive cues (Bowditch et al., 2016), have been less extensive. Mayse, Nelson, Park, Gallagher, and Lin (2014) found that rats responded more slowly in Go trials following response inhibition than in Go trials following response execution. Healthy macaques also showed post-signal slowing of responses (Emeric et al., 2007), whereas macaques that experienced limited executive control as a consequence of cognitive deficits caused by chronic cocaine administration did not (Liu et al., 2009). These results might indicate that executive control does indeed play a crucial role in proactive inhibition - but since there are currently no data available about whether or not subjects lacking in executive control would consequently also not show post-signal response slowing, such an assumption is speculative at the moment. The same goes for response adjustments elicited by predictive cues: there are no data about the influence of presenting such cues on stop-signal performance governed by associative processes, which makes it difficult to assess whether such adjustments are a consequence of executive control or associations.

Regardless of whether inhibition is governed by executive control or associative processes, the literature on human response inhibition unambiguously assumes that the withholding of an action after its initiation necessitates a cognitive

response-inhibition mechanism (cf. Boecker, Gauggel, & Drueke, 2013). It is widely assumed that the appearance of a signal to inhibit a prepared response activates a global stopping process that inhibits all responses (e.g., Mostofsky & Simmonds, 2008; Verbruggen & Logan, 2009b; Kenner, Mumford, Hommer et al., 2010; Boecker et al., 2013).

However, there is less consensus about how response inhibition is achieved when (as is often the case in natural, not experimentally controlled situations) only a specific action has to be withheld, but other actions have to be executed.

In this regard, it is worth considering the Change-Signal paradigm, in which the occurrence of the signal indicates that an alternative response has to be executed instead of the usual Go response. The Stop-Signal and Change-Signal tasks can use the same stimuli and very similar procedures, and it is most commonly thought that the same global stopping process that governs response inhibition when any response should be withheld is also engaged when only the main Go response has to be withheld but a different response still has to be executed (Mostofsky & Simmonds, 2008; Verbruggen & Logan, 2009b; Kenner et al., 2010; Boecker et al., 2013). The Change-Signal task has even been described as merely a "complication of the Stop-Signal paradigm" (Logan, 1994) in that stopping the Go response is followed by an additional process of initiating an alternative response. In support of this assumption, Verbruggen and Logan (2009b) successfully applied the independent horse-race model not only to Stop-Signal paradigms but also to Change-Signal paradigms. The alternative response in Change-Signal tasks may be prepared either at the same time as the global inhibition process is initiated or, if the mental capacities for parallel processing are limited, after the inhibition process is completed (Verbruggen, Schneider, & Logan, 2008b).

However, despite considerable support for a common, global mechanism, there are voices advocating two different response-inhibition processes governing Stop-Signal and Change-Signal performance. Since one task requires the complete suppression of a response, whilst the other task requires the execution of an alternative action, response inhibition in Change-Signal paradigms may be governed by a selective inhibition mechanism that stops only the inappropriate action but permits the execution of the alternative response (De Jong, Coles, & Logan, 1995; Aron & Verbruggen, 2008; Krämer, Knight, & Münte, 2010; Schall & Godlove, 2012; Boecker et al., 2013; Gulberti, Arndt, &

Colonius, 2014). The idea of a selective inhibition mechanism draws parallels to the concept of mental task-set reconfigurations during task-switching (cf. Monsell, 2003), by which appropriate stimulus-response sets are selected but inappropriate stimulus-response sets are inhibited; therefore, the mechanism that inhibits an inappropriate response in Change-Signal paradigms might afford executive control, whereas the mechanism that merely stops any response in Stop-Signal paradigms might be sufficiently acquired via associative processes.
Lastly, it has also been considered whether Change-Signal paradigms would require the involvement of a response-inhibition mechanism at all (Verbruggen et al., 2008b). The process of initiating the alternative response might suffice to override the initiation process of the Go response, making a separate process to inhibit the initially indicated Go response unnecessary (cf. Verbruggen & Logan, 2009b). Thus, whilst Stop-Signal tasks might require a mechanism to suppress inappropriate responses, Change-Signal tasks might be accomplished without a response-inhibition mechanism. In fact, there is the interesting possibility that pigeons in particular might perform better if they are given the option to execute an action instead of having to withhold a response. Pigeons often require more time to acquire the No-Go stimulus in a Go/No-Go paradigm (for example, this has been the case in the training phase of the study reported in Ghosh, Lea, and Noury, 2004; Lea, personal communication), whereas the competing stimulus-response contingencies in dual-task paradigms or simultaneous-discrimination tasks are often acquired at the same rate (e.g., Lejeune, Macar & Zakay, 1999). In relation to the Stop-Signal and Change-Signal paradigms, pigeons might face more difficulties in suppressing any response to a stimulus than in acquiring an additional set of stimulus-response associations. In terms of the underlying mechanisms governing behaviour in the two tasks, performance differences in this direction would suggest that Change-Signal tasks afford less cognitively demanding processes than Stop-Signal tasks.

In summary, since the independent horse-race model (Verbruggen & Logan, 2009b) makes no assumptions about the involvement of specific cognitive capacities in response inhibition, the predictions of the model should apply to performance in Stop-Signal tasks regardless of whether performance is governed by executive control or associative processes. However, although it is

mostly assumed that the same global inhibition mechanism that enables the stopping of a response in Stop-Signal tasks is also engaged in Change-Signal tasks (Verbruggen & Logan, 2009b), this might not be the case. Previous research has proposed both that performance in Change-Signal paradigms might afford a higher level of inhibitory control than Stop-Signal tasks (cf. De Jong et al., 1995), and that it might require a lower level of inhibitory control (or none at all; cf. Verbruggen et al., 2008b).

In Section 1.3, I elaborate on the approach taken in this thesis to test these contradictory hypotheses by assessing the ability of pigeons to perform a Stop-Signal or a Change-Signal task.

1.3 The Influence of Associative Processes on Performance in Executive-Control Paradigms

If, as contemplated in the opening section of this chapter, human behaviour can be controlled flexibly by either executive control or associative processes, results taken from studies with humans (and also nonhuman primates, which might possess a similar executive-control system as humans) face some limitations when trying to pin down which of the two cognitive processes is momentarily involved in a given executive-control paradigm, and whether associative learning could in fact be sufficient to produce the patterns of performance generally assumed to result from executive-control processes.

A promising way to overcome this issue is to assess the performance of animals whose ability to exert executive control is severely limited compared to humans (or even monkeys), such as pigeons. Pigeons have repeatedly demonstrated an absence of analytical processing where humans show it (Lea & Wills, 2008; Lea et al., 2009; Wills et al., 2009; Smith, Ashby, Berg et al., 2011; Smith et al., 2012; Maes, De Filippo, Inkster et al., 2015), suggesting a lack of the kind of mental capabilities that would provide evidence for executive control: instead of attending to a single informative stimulus dimension, they evidently associate the stimulus as a whole with its appropriate behavioural response (Pearce, 1994; Smith et al., 2011; Smith et al., 2012). Indeed, Smith et al. (2011) proposed that the implicit, nonanalytic learning mechanism of pigeons constitutes a universal, phylogenetically old system, from which the rule-based approach found in primates emerged. Therefore, using pigeons as a model species, I explored the pattern of performance that occurs if behaviour is guided entirely by associative processes, both in a task-switching paradigm, reported in Chapters 2 and 3, and in Stop-Signal and Change-Signal paradigms, reported in Chapters 4 and 5. In all paradigms, the influence of associative processes on performance should be evident in specific ways, as summarised below.

It has to be noted that, when adapting any paradigm originating from human psychology for the use with animals, it is inevitably necessary to make a series of adaptations to the paradigm, which may lead to unwanted changes in the way subjects respond - at the worst, it may make the altered paradigm

unsuitable to detect the behavioural effects that are of interest. To ensure that the paradigms that were developed for the pigeon experiments reported in this thesis were still useful in detecting the relevant human performance effects, I tested humans in (as far as possible) identical tasks and assessed whether the desired effects were observable in their performance, both during the development of the paradigms, the results of which are reported in Chapters 2 and 4, and during the administration of the final paradigms, reported in Chapters 3 and 4.

Task Switching

Following the considerations in Section 1.1, if pigeons succeeded in solving a task-switching paradigm associatively, they might show an absence of switch costs. Instead, they might predominately be susceptible to stimulus-congruency effects or other sequential effects that would be expected to occur if performance is based on associative processes. There are very few data at present concerning pigeons' task-switching abilities. Castro and Wasserman (2016) tested pigeons in a task-switching paradigm and did indeed find an absence of any switch costs. However, as stated in Section 1.1, associatively-mediated task-switch costs might primarily emerge in response to bivalent, response-incongruent stimuli, which were not included in Castro and Wasserman's study. Forrest's (Forrest, 2012; Forrest et al., 2014) participants memorising cue-stimulus-response contingencies (and thus presumably relying on associative processes) did show switch costs in response to those stimuli. Therefore, if those humans and pigeons both employed an associative-learning approach to the paradigm, both species would be expected to show similar task-switching effects (or the absence thereof). But if the task-switching performance of pigeons indeed differed from those of humans who assumedly did not use executive control to organise tasks, then those humans could not have acquired the paradigm in the same associative way as pigeons did – which would raise the question as to what learning strategies humans do employ when they are unaware of task rules.

In Chapter 2, I report how I developed a computerised task-switching paradigm that allows the comparison of the task-switching abilities of several species. In

Chapter 3, I report the results and implications of this comparison. The results reported in Sections 3.1 and 3.2 have also been published in Meier, Lea, and McLaren (2016b).

Response Inhibition

As regards the Stop-Signal task introduced in Section 1.2, the successful acquisition of this task by pigeons would have several theoretical implications. Firstly, the predictions of the independent horse-race model (Verbruggen & Logan, 2009b) should apply to the performance of pigeons, that is, the model is expected to capture the effects of associative processes involved in response inhibition following a stop signal. Specifically, as illustrated in Figure 1.3.1, the independent horse-race model makes the following predictions (Verbruggen & Logan, 2009b):

- The probability that a response is incorrectly made in trials in which a signal is presented (henceforth referred to as Signal trials) is expected to increase with increasing interval between the presentation of the stimulus that indicates that a response should be executed and the subsequent presentation of the signal indicating to withhold that response (the stop-signal-onset interval, SSO).
- Erroneous responses in Signal trials will primarily be made before or very shortly after the signal appears, as a consequence of the process that initiates a response being completed before the inhibition process to stop the response. Consequently, mean latencies to make a response should be shorter in Signal trials compared to Go trials, in which no signal appears and the prepared response needs to be executed.
- It is further expected that the mean latency for incorrect responses in Signal trials will increase as the signal-onset interval increases.

Secondly, I aimed to discern the potential limits of associative processes in mediating proactive response inhibition, by which subjects adjust their readiness to inhibit an action independently of the occurrence of a stop signal. The proactive adjustment of attentional or response thresholds in anticipation of a Stop signal is thought to require executive control - signal-independent effects such as response slowing following a Signal trial (Bissett & Logan, 2011) should

be the result of executive-control processes. However, response adjustments that occur after receiving information about the likelihood of a signal (i.e., in the form of a cue) might be accomplished associatively; since such a cue is stochastically related to the outcome (stopping or not stopping a response), it might come to deliver associatively-mediated inhibition in a similar fashion to that observed in experiments with humans (Bowditch et al., 2016). Therefore, I assessed the occurrence of associatively mediated response adjustments following post-signal trials and in response to predictive cues.

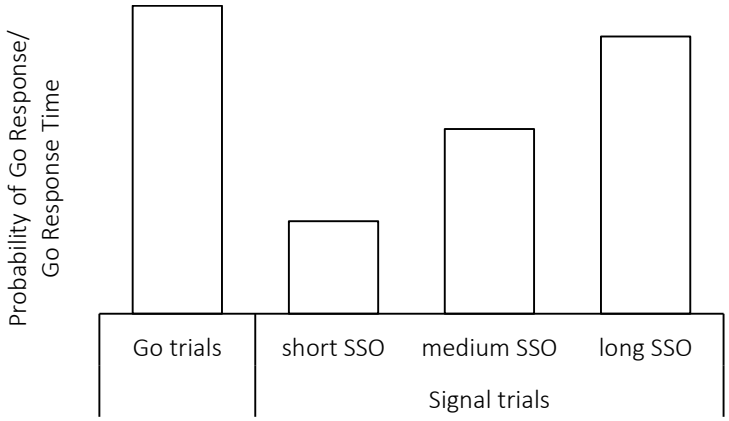

Figure 1.3.1. Expected performance in a Stop-Signal task, both measured in the probability of making a Go response and in the latencies to make the Go response, as predicted by the independent horse-race model (Verbruggen & Logan, 2009b). *SSO*: Stop-signal-onset interval, the interval between presenting the stimulus that indicates to execute a response and presenting the signal that indicates to withhold that response.

Lastly, the above assumptions about the involvement of associative processes in response inhibition might also apply to Change-Signal tasks, in which the occurrence of the signal indicates that an alternative response has to be executed, instead of signalling that any response has to be withheld. Since Stop-Signal and Change-Signal tasks often use the same stimuli and very similar procedures, it seems logical to assume that they both involve the same inhibition mechanisms. However, despite considerable support for this view, it is possible that two different response-inhibition processes govern Stop-Signal and Change-Signal performance. Since one task requires the complete suppression of a response, whilst the other task requires the execution of an alternative action, Change-Signal tasks might elicit more selective inhibition

processes than those involved in the mere stopping of a response (De Jong et al., 1995; Aron & Verbruggen, 2008; Krämer et al., 2010; Schall & Godlove, 2012; Boecker et al., 2013; Gulberti et al., 2014) potentially making the Change-Signal task more cognitively demanding (or even requiring a level of cognitive control that pigeons are incapable of). Another possibility is that associative processes might facilitate performance in Change-Signal tasks in such a way that the presentation of the Change signal immediately triggers the execution of the alternative response without the need to inhibit the Go response, so that only performance in the Stop-Signal tasks relies on a response-inhibition process, but performance in the Change-Signal task does not. Verbruggen and Logan (2009b) claimed that the independent race model fit the data from both Stop-Signal and Change-Signal paradigms, supporting the idea that they involve a common mechanism.

In Chapter 4, I report how I developed a computerised Stop-Signal and a Change-Signal paradigm that allow the comparison of the response-inhibition abilities of humans and pigeons, and report the results and implications of this comparison. In the light of the results of that chapter, in Chapter 5, I report the results of an additional study that was designed to assess the performance of pigeons in a setting that might necessitate a higher degree of response inhibition than the computer-based tasks.

CHAPTER 2: DEVELOPING A COMPARATIVE TASK-SWITCHING PARADIGM

Parts of this chapter have been published as Meier, C., Lea, S.E.G., & McLaren, I.P.L. (2016). A stimulus-location effect in discrimination learning. Journal of Experimental Psychology: Animal Learning and Cognition, 42(2), 177-186.

In this chapter, I report pilot studies conducted to establish the design of a comparative task-switching paradigm. Taking into account the results of the studies in Sections 2.1 and 2.2, I report the specifics of the final design in Section 2.3.

Constructing a paradigm that is intended to explore cognitive performance across several species (especially if these species differ in their cognitive abilities as much as humans and pigeons do) requires a series of careful choices. On one hand, the paradigm has to be simple enough to allow pigeons to acquire it easily; on the other hand, it has to be ensured that, even when simplified, the paradigm captures the corresponding human phenomena of interest. In the specific case of task-switching, the paradigms used in human experiments often incorporate semantic stimuli and verbal instructions, making them unsuitable for use with animals. The procedure described below did not rely on language-based stimuli or cues but instead used varying values of several visual dimensions, namely colour, line orientation and spatial frequency, to indicate which response should be made.

An important matter to consider was the question of how to introduce the competing task sets to the subjects. Detailed instructions could only be given to humans; pigeons would have to learn the two tasks based on trial and error. To limit the number of stimulus-response contingencies that the pigeons would have to acquire at the same time, and to ensure that both response-congruent and response-incongruent stimuli were learned at a similar rate, it seemed the most plausible to train each task in separation before exposing the pigeons to

the task-switching paradigm. However, to preserve comparability, any method of training for pigeons would also have to be applied to humans, and extensive training might have unforeseen consequences for the induction of task rules or the task-switching performance of human participants.

Specifically, as the pigeons ultimately had to be able to perform two very different discrimination tasks on the same set of stimuli, with only visual cues to guide them as to which particular feature of the stimulus was relevant for discrimination at the time, I anticipated that the pigeons might have to be exposed to the components of each task (i.e., the cues indicating the currently relevant discrimination task and the specific values of the dimension that would have to be categorised) one at a time to ensure stable performance in response to each individual feature. The pigeons might only be able to acquire the contingencies embedded in a task if each of the dimensional values that were relevant for discrimination were presented unambiguously, that is, if the stimuli varied only in that dimension during training, whilst the other dimension was held at a constant value. It might also become necessary to introduce the two cues for each of the tasks one by one.

Such detailed training, in which each individual component of the discrimination tasks is presented in isolation, might change the structure of the paradigm sufficiently to counteract any task-switching operations that usually elicit switch costs in humans. If pigeons had to be trained on a step-by-step procedure, it would have to be demonstrated that this training regime could still elicit the desired task-switching effects in humans, thus making it suitable for experimental work with pigeons. This issue was addressed in Section 2.1, by investigating the effects of very intensive training on the magnitude of switch costs and congruency effects in human participants. If, despite extensive training on each individual component of the tasks, humans nonetheless exhibited switch costs, it could be assumed that the pigeons might also show valid task-switching performance even given that they had to undergo such training.

Although I was prepared to administer the training in the detailed way described above if necessary, I chose to begin the pigeon training with the ambiguous stimuli that would ultimately be used in the task-switching paradigm, and to introduce both cues of each tasks from the start. I retained the option to restrict

the training to stimuli that varied only in the relevant dimension of the currently trained task, or to present only one task cue at the time until performance reached a stable level, or even to fade in a cue gradually from grey to its full saturation if a pigeon refused to respond to the colour of the cue.

A somewhat more complex issue arose in regard to the details of the trial procedure; specifically, the way the stimuli were presented to the subjects and a response was made. Concurrent to the work reported in this chapter, Maes et al. observed severely delayed acquisition rates in a pilot experiment to a study that would eventually be published in Maes et al. (2015). Their procedure was similar enough to the design intended for my task-switching experiments to warrant careful consideration. Section 2.2 describes a systematic comparison I conducted of the procedures that were likely the cause of learning success or failure in Maes et al.'s unpublished pilot work, and report the implications of that comparison for the design of the task-switching paradigm. Details on the trial procedure and the training methods that were ultimately employed are reported in Section 2.3.

General Methods

The following general aspects apply to all experiments reported in this chapter and in Chapter 3.

Subjects

The pigeons used in the experiments reported in this thesis had been obtained as discards from local fanciers and were housed in the Psychology animal laboratory at the University of Exeter. During testing, the pigeons were kept indoors in two group aviaries (each approximately 4.5m^2), and were maintained at or above 80% of their free-feeding weight by controlled feeding after tests. Pigeons that were not tested at the time were kept in an outdoor aviary (approximately 12m^2) with unlimited access to food. All aviaries provided *ad libitum* access to water and grit.

Human participants were drawn from the Psychology undergraduate participant pool of the University of Exeter; they took part in the experiments in exchange for course credit or monetary reimbursement of £5 per hour.

Unless stated otherwise, both humans and pigeons were naïve to the testing stimuli at the start of the experiment in which they participated.

Apparatus

The pigeons were tested in eight identical 71x50.5x43.5cm operant chambers. Each pigeon was tested in the same chamber throughout a given experiment. One of the long walls of the chamber was fitted with a 31x23.5cm (15") touch monitor (Model 1547L 1024x768pxl TFT monitor, 0.3mm per pixel, 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. Contingency control and data collection was managed using a Dell PC running Whisker (Cardinal & Aitken, 2010), with client programs written in Visual Basic 6.0.

Humans were tested at the University of Exeter either in a sound-proof, single-occupancy test room that was equipped with an Apple iMac or in a multi-testing room fitted with eight sound-proof cubicles, each equipped with a Dell PC. The human experiments were written and run in MATLAB® using the Psychtoolbox (Kleiner, Brainard, & Pelli, 2007) add-on.

Cue and Stimulus Material

Each of the two tasks was associated with two distinct cues, which were circular colour-filled disks of 200 pixels (60mm) in diameter. These were a blue or yellow disk for one task, and a red or green disk for the other task.

As shown in Figure 2.1, the stimuli were circular Gaussian patches of 200 pixels (60mm) in diameter and consisted of one of four sinusoidal grating patterns. They differed from one another in two dimensions: spatial frequency – either 2 or 12 cycles per 100 pixels – or line orientation – either horizontal or vertical.

Each of these two visual dimensions determined the correct response in one task. For example, one task might require responding to the spatial frequency of the grating pattern, e.g., if a stimulus, regardless of the orientation of the pattern, had a low spatial frequency, the correct response towards this stimulus was to choose the left reward location, while stimuli with a high spatial frequency required the subject to choose the right reward location. Conversely, in the other task, stimuli would have to be classified according to the orientation of the grating pattern, regardless of its spatial frequency. That is, if a stimulus showed a horizontal pattern, it required a response to the left reward location, while a vertical pattern indicated a response to the right location as the correct one. 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 a left response regardless of the current task. In contrast to these congruent stimuli, responses to incongruent stimuli depended on the task at hand, for example, a horizontal stimulus with a high spatial frequency pattern might require a response to the left reward location on the orientation task but a response to the right location on the spatial frequency task.

In every trial, the stimuli were always superimposed onto the cue for that trial, as illustrated in Figure 2.1.

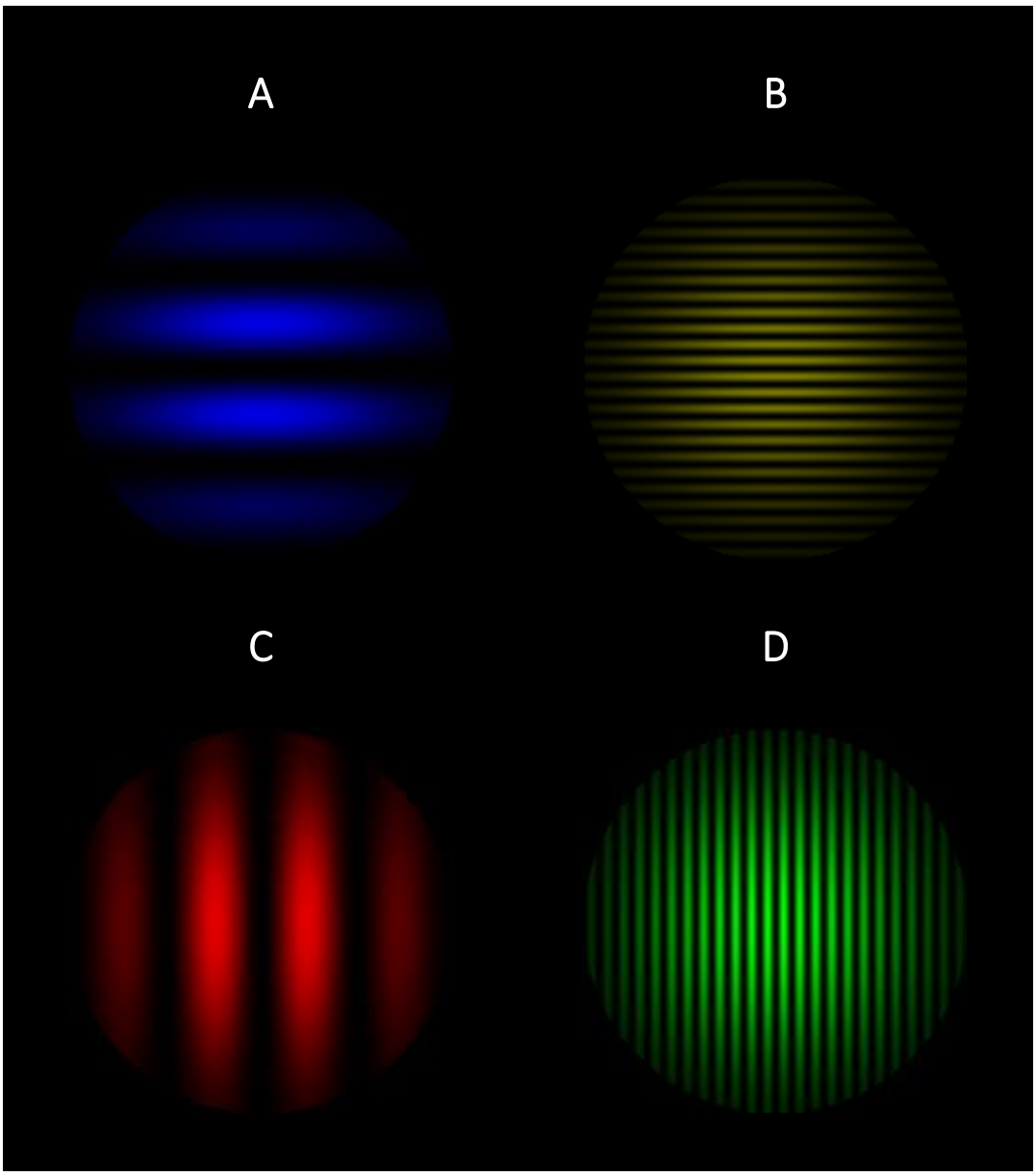

Figure 2.1. Examples of the four stimuli: *A)* low spatial frequency and horizontal orientation, *B)* high spatial frequency and horizontal orientation, *C)* low spatial frequency and vertical orientation and *D)* high spatial frequency and vertical orientation. Each stimulus was superimposed on one of the four task cues; during test, all four stimuli were paired with all four cues, resulting in sixteen different cue-stimulus combinations (four of these possible combinations are presented here for illustration). This figure appeared in Meier et al. (2016b).

2.1 The Influence of Task Training on Task-Switching Performance in Humans

To keep the procedures as similar as possible for humans and pigeons, the typical method of providing verbal instructions to human participants was discarded in favour of a practical training phase which resembled the conditioning procedures employed in animal testing. That is, participants had to infer the relevant stimulus-response associations via trial-and-error learning.
In order to establish sufficient learning in pigeons, their training might have to include introducing and training each relevant component of the task-switching paradigm individually. However, administering similarly extensive training to humans could potentially influence the size of switch costs in human participants, or the degree to which participants become aware of the two competing task sets (and let their response be guided by the task rules rather than stimulus-response contingencies) when completing the task-switching paradigm. Therefore, I examined the effects of very extensive training on human task-switching performance. If humans suffered from switch costs after prolonged experience with all task contingencies, one could be confident that such training would similarly not interfere with the expression of task-switching effects by pigeons if they employed the same processes as humans. Separately, confirming the presence of switch costs in this pilot study would help verify the validity of the paradigm and give confidence that it would be an adequate method for comparing the performance of humans and pigeons.

Methods

Participants

16 Psychology undergraduate students participated in this study.

Trial Procedure

One of the four colour cues was presented in the centre of the display at the beginning of a trial to indicate which task was relevant in that trial. Participants had to mouse-click on the cue, upon which a stimulus appeared superimposed on the cue to keep both the cue and the stimulus visible. Following a mouse-click on the cue-stimulus compound in the centre of the screen, two square

white response keys (side length of 75 pixels / 22.5mm) appeared to the left and the right side of the stimulus. Participants responded by clicking on the response key that was associated with the present cue-stimulus combination (for example, a green cue paired with a horizontal, low-spatial-frequency stimulus might require clicking the left response key). If the correct response key was chosen, the cue-stimulus compound and response keys disappeared from the screen and, for two seconds, the word "Correct!" appeared in white letters in the centre of the screen alongside a golden star presented in the location of the correct response key. Then, after an inter-trial interval of three seconds, the next trial began. If the wrong response key was clicked, the display was replaced by the word "WRONG" in white letters appearing in the screen centre for five seconds, followed by the inter-trial interval of three seconds.

Training

Participants were randomly assigned to one of two conditions:

No training. Eight participants did not receive any initial training on the tasks but were immediately presented with the full task-switching paradigm as described below.

Training. Eight participants received detailed training. They went through a series of training stages for each task separately before entering the task-switching procedure. The order in which the tasks (spatial frequency discrimination and orientation discrimination) were learned was counterbalanced across participants.

Initially, the two cues used in each task were introduced individually. Only the task-relevant dimension of the stimulus varied at this stage, while the irrelevant dimension was held constant at an intermediate level. That is, participants only responded to two distinct cue-stimulus compounds at this point: either a horizontal or vertical stimulus with a spatial frequency of 7 cycles per 100 pixels (if the first task to be learned was the orientation task), or a stimulus with a spatial frequency of either 2 or 12 cycles per 100 pixels with a diagonal line orientation of 45° from the horizontal (if the first task to be learned was the spatial-frequency task) - each one paired with only one cue colour. Once a

participant responded correctly to the two stimuli combined with one cue in at least 80% of a sequence of trials that included each stimulus at least twice (i.e., since there were two stimuli, this sequence included at least four consecutive trials), the procedure was repeated for the second cue. Then, the two task cues were combined and again trained to the same 80%-accuracy criterion. In the next stage, the training stimuli were replaced by stimuli for which the values of both dimensions were varied, in the same manner as they would appear in the task switching paradigm. This training stage was continued until participants again responded correctly in at least 80% of a sequence of trials that included each stimulus at least twice (i.e., at least eight consecutive trials). Then, that entire training procedure was repeated for the second task. After learning both tasks individually to the 80%-accuracy criterion, participants moved on to the task-switching paradigm described below.

Task-Switching Paradigm

In the task-switching part of the experiment, trials could either switch between the two tasks or repeat the previous task. The switches were partially randomised to produce a task-switch trial in one third of all trials. In the remaining (task-repeat) trials, the two cues indicating the same task alternated in successive trials so that no cue was ever presented on two consecutive trials. Participants completed 24 blocks of 25 trials. The first trial of each block was excluded from analyses as it was neither a switch nor a repeat trial. Trials following an incorrect response were also excluded from analysis because it was unclear whether the error in the previous trial had been due to performing the wrong task or due to choosing the wrong response to the given stimulus in the current task - making it impossible to assess whether the trial following the error was treated by the participant as a repeat or a switch trial.

For each pair of consecutive blocks, I analysed the participant's percentage of errors, as indicated by the first response key that was chosen (correct or incorrect), and the participant's latency to click on a response key.

After completing the task-switching paradigm, I assessed the participant's ability to describe the rules by which a correct response was defined. If a participant was able to correctly identify the contingencies between a task cue, stimulus and correct response, he or she was considered to have understood – and

applied – the underlying task rule. If a participant could not explain any relationship between stimuli, cues and the correct response, this was taken as an indication that he or she had relied on associative learning to successfully complete the task. Participants that could not be grouped into either of these categories were excluded (see below for details).

Results

Two participants in the no-training condition were unable to verbalise either of the two task rules; two further participants could name only one of the two rules. The remaining participants were able to name both rules. In the Training condition, four participants did not infer any rules, and one person named one of the two task rules. These numbers did not differ significantly between training conditions, $\chi^2(2)=1.14$, $p=.57$. To assess whether rules awareness influenced performance, I included it as a further potential predictor in addition to the type of training that had been administered. However, since there was only one participant in the Training condition who inferred one rule, I only considered those participants who had either inferred both rules or inferred no rules.

As described in Section 1.1, performance in task-switching experiments is usually affected by both switch costs and congruency effects, as participants make more errors and respond more slowly on trials in which the task switches from one trial to the next compared to trials in which the task is repeated, and when responding to a response-incongruent stimulus compared to responding to a response-congruent stimulus. The extent to which error rates and response times of the participants in the current experiment were influenced by switch costs or congruency effects was investigated with two repeated-measures ANOVAs, using Block Pairs, Trial Type (Task-Switch or Task-Repeat) and Stimulus Congruency (Congruent or Incongruent) as within-subjects factors. Training (Yes or No) and Rule Awareness (no rule inferred or both rules inferred) were considered as between-subjects variables. Where applicable, significance levels were subject to Huynh-Feldt corrections. The results of these analyses are reported in Table 2.1.1.

Table 2.1.1. Effects of training, rules awareness, switch costs, stimulus congruency and block pairs (and significant interactions between factors) on response times and error rates. Significant p values are highlighted in bold.

	Response Times				Error Rates			
	F	df	p	η_p^2	F	df	p	η_p^2
Training	1.09	1,9	.32	.11	1.33	1,9	.28	.13
Rules Awareness	1.16	1,9	.31	.11	4.07	1,9	.074	.31
Training * Rules	0.00	1,9	.99	.00	3.35	1,9	.10	.27
Trial Type (Switch Costs)	23.88	1,9	**.001**	.73	187.26	1,9	**<.001**	.95
Rules * Trial Type	0.48	1,9	.51	.05	77.33	1,9	**<.001**	.90
Stimulus Congruency	1.50	1,9	.25	.14	37.06	1,9	**<.001**	.81
Rules * Congruency	6.85	1,9	**.028**	.43	11.84	1,9	**.007**	.57
Trial Type * Congruency	0.21	1,9	.66	.02	33.20	1,9	**.001**	.79
Block Pairs	2.39	11,99	.052	.21	7.31	11,99	**<.001**	.45
Congruency * Block	0.60	11,99	.72	.06	3.75	11,99	**.001**	.29
Rules * Congruency * Block	0.60	11,99	.72	.06	2.65	11,99	**.010**	.23
Rules * Trial Type * Congruency * Block	1.52	11,99	.19	.14	2.53	11,99	**.007**	.22

The participants showed significantly worse performance in task-switch trials than in task-repeat trials (switch costs) in both response times (mean for task-switch trials: 1251ms, for task-repeat trials: 1161ms; shown in Figure 2.1.1) and error rates (mean for task-switch trials: 23.8%, for task-repeat trials: 16.0%; shown in Figure 2.1.2). Participants also showed worse performance in response to incongruent stimuli than to congruent stimuli (means for response times: 1176ms for congruent vs. 1237ms for incongruent stimuli, for error rates: 10.5% for congruent vs. 29.4% for incongruent stimuli). There are also general differences between the training groups, with those participants who had received training responding faster (mean: 1025ms) and making fewer errors (17.1%) than those who had not (means: 1239ms, 23.7%).

Figures 2.1.1 and 2.1.2 further suggest that participants performed differently depending on whether or not they had inferred the rules of the tasks, as knowledge of the two rules led to an increase in response times (mean: 1239ms) and a decrease in error rates (13.7%) compared to not knowing any of the two rules (1025ms, 27.1%). Since the purpose of this experiment was to assess the effect of training on the presence of task-switching effects, the

influence of rules awareness on the participants' performance and the magnitude of switch costs and congruency effects are not described in detail here but will be discussed in Chapter 3.

While the effect of switch costs was significant for both measures (see Figures 2.1.1 and 2.1.2), the effect of stimulus congruency was only significant for error rates (Figure 2.1.2), but not for response times (Figure 2.1.1).
Participants learned to make fewer errors as the experiment progressed, indicated by a significant influence of the factor Block Pairs on error rates, and somewhat increased in speed, as the marginal effect of Block Pairs on response times suggests. Over the course of the experiment, the effect of stimulus congruency on error rates became weaker, especially for the participants who had inferred both rules; for those participants, the interaction between switch costs and stimulus congruency also decreased over time.

Overall, training did not influence performance significantly in either response times or error rates (seen in the comparison of the "No training" column to the "Training" column in Figures 2.1.1 and 2.1.2). Likewise, participants demonstrated similar values in both measures of performance regardless of whether or not they were able to verbalise the two task rules (seen in the comparison of the rows "No rules inferred" and "Both rules inferred" in Figures 2.1.1 and 2.1.2).

Importantly, receiving training or not did not significantly alter the size of switch costs and congruency effects in participants' response times, although response times appeared to vary less overall if participants had received prior training (seen in the comparison of the "No training" column to the "Training" column in Figure 2.1.1). Training also had no effect on the size of switch costs or congruency effects in participants' error rates, or the change in response times and error rates over time.

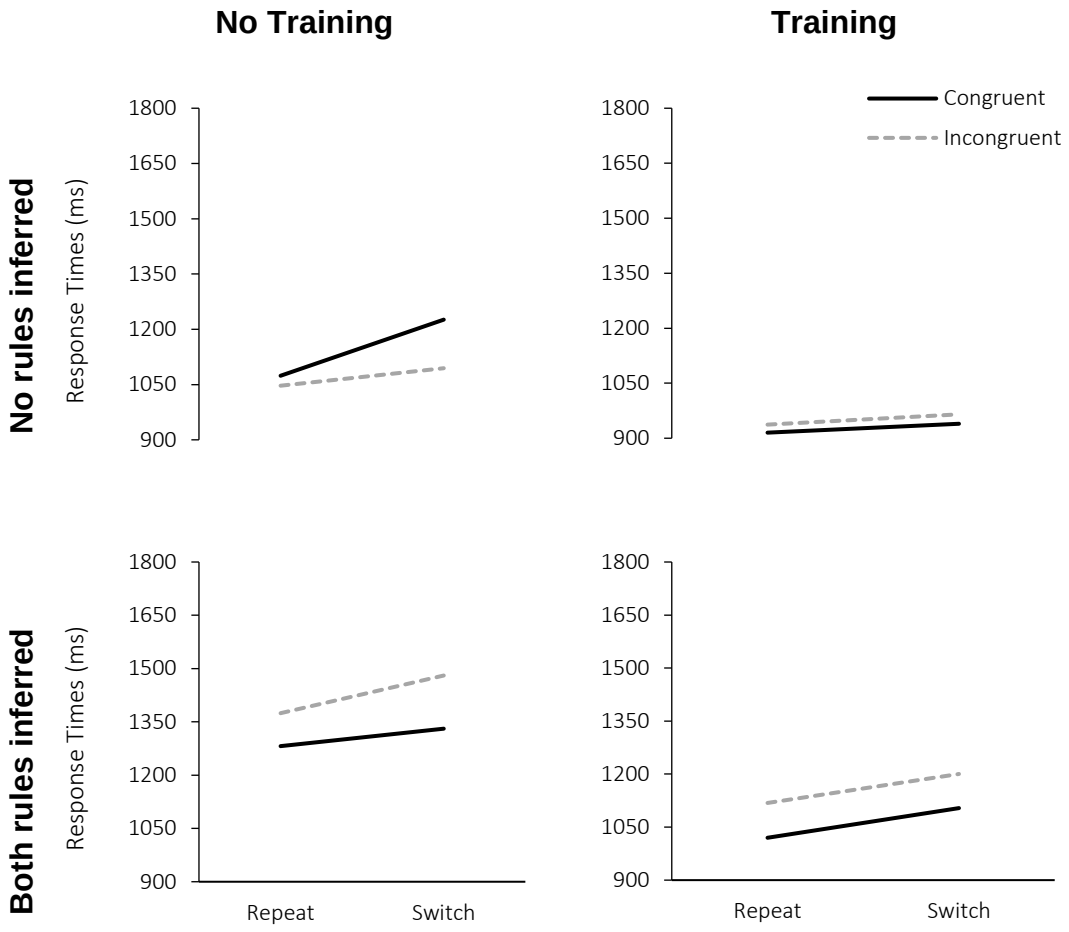

Figure 2.1.1. Response times in ms across block pairs depending on rules awareness and training. *Repeat* trials: the task in these trials was the same as in the previous trials. *Switch* trials: the task changed from the previous trial. *Congruent* stimulus: the stimulus required the same response in both tasks. *Incongruent* stimulus: the correct response to the stimulus varied between tasks.

Discussion

The above results made it evident that a task-switching paradigm employing non-semantic stimuli could generate similar task-switching effects as traditional paradigms used with human participants. Despite having to infer the correct responses from conditioning-like training, participants demonstrated substantial switch costs in both response times and error rates, and errors were greatly influenced by stimulus congruency. Therefore, it seems reasonable to assume that introducing a training phase at the start of a task-switching paradigm will not disrupt the task-switching effects that are of interest.

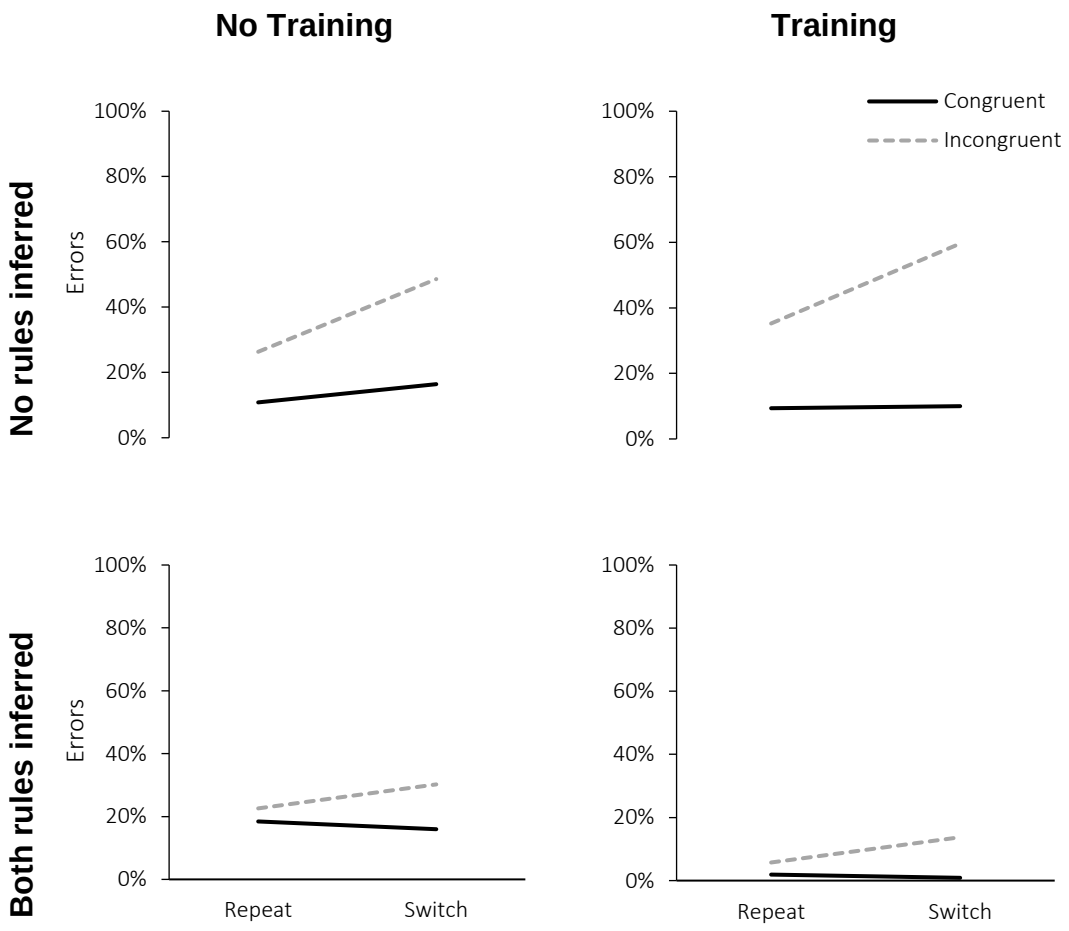

Figure 2.1.2. Error rates in % depending on rules awareness and training. *Repeat* trials: the task in these trials was the same as in the previous trials. *Switch* trials: the task changed from the previous trial. *Congruent* stimulus: the stimulus required the same response in both tasks. *Incongruent* stimulus: the correct response to the stimulus varied between tasks.

Interestingly, the error rates generally provided a clearer indication of whether a participant had inferred a task rule or not. As seen in Figure 2.1.2, the pattern of error rates over the course of the experiment differed in very distinct ways between participants who had or had not inferred the two task rules, whilst it was less obvious in their response times. Taking this observation into account (alongside other methodological limitations when assessing performance in pigeons, considered further in Section 2.2), error rates might be a more suitable measure to assess task-switching performance comparatively than response times.

As mentioned above, this section focused on significant differences in the way these main factors affected performance depending on whether or not participants had received task training prior to the task-switching paradigm. The influence of rules awareness on the participants' performance and the magnitude of switch costs and congruency effects will be discussed in detail in Chapter 3.

2.2 Stimulus Location is Included as a Stimulus Feature in Pigeons' Conditional Discrimination Learning

Concurrent to the experiments reported in this section, Maes et al. conducted pilot work for studies eventually published in Maes et al. (2015), in which pigeons and humans simultaneously learned negative and positive patterning problems in a go-left/go-right paradigm that required them to choose one of two copies of a target stimulus presented on the left or the right side of a computer screen. In the pilot work, the authors observed an unanticipated difference in learning rates between pigeons trained under two slightly different conditions. The first condition was a conventional go-left/go-right discrimination: a discriminative stimulus appeared at a central location; once a response had been made to it, two identical white response keys appeared to the left and right, and responses to the left or the right key were reinforced depending on what stimulus was presented on the centre key. The second condition was logically identical, but the response keys were replicas of the discriminative stimulus, and the stimulus in the centre disappeared. The subject's task was the same under both conditions, but the pigeons trained under the first condition learned only very slowly, whereas those trained under the second condition learned much faster.

The conclusion from this pilot work - that a simple alteration in the visual appearance of the response display determined pigeons' success or failure to acquire a discrimination problem - could have dramatic implications for the task-switching paradigm as well, as it, too, would incorporate a forced choice in response to a target stimulus. Thus, I conducted a systematic comparison between the two conditions mentioned above, and their potential influence on acquiring the tasks that were chosen for the task-switching paradigm. For completeness, and to investigate whether the difficulties in acquiring a task in one but not the other condition could be attributed to the pigeons' limited cognitive abilities or would occur in humans as well, I assessed not only the performance of pigeons but also the performance of human participants in each of the two conditions.

Methods

Subjects

Twenty-six Psychology undergraduate students and seven pigeons performed one of the two conditional discrimination tasks that would eventually be used in the task-switching paradigm.

Procedure

Trials started by displaying a coloured circle, 200 pixels (60mm) in diameter in either red, green, yellow or blue, in the centre of a computer screen. Human participants were asked to mouse-click on it, pigeons pecked it on a touch screen. Following this action, the stimulus appeared superimposed on the colour. Again, a click or peck at the stimulus was required. One of the two visual dimensions of the stimuli (spatial frequency or line orientation) determined the correct response: two pigeons and twelve human participants had to classify stimuli based on their spatial frequency, for the other subjects, discrimination was based on the orientation of the grating pattern. That is, a subject might be trained to choose left when a vertical pattern was shown and choose right when the pattern was horizontal, while another subject was trained to go left when seeing a low spatial frequency and go right for stimuli with a high spatial frequency.

Six humans and one pigeon learning the spatial-frequency discrimination and six humans and three pigeons learning the orientation discrimination experienced condition 'White Keys': the coloured stimulus remained in the centre after a response to it, and two white disks of 100 pixels (30mm) in diameter appeared to its left and right side (at a distance of 250 pixels (75mm) from the display centre to the centre of the white disk) and remained visible until a response was made. The stimulus indicated the correct response (click/peck the left or right white disk). The remaining six humans and one pigeon learning the spatial-frequency discrimination and eight humans and two pigeons learning the orientation discrimination experienced condition 'Replicas': in this condition, after responding to the stimulus, it was deleted from the display centre and reappeared on both the left and right side of the display, at a distance of 250 pixels (75mm) from the display centre to the centre of a replica. The stimulus indicated the correct response (click/peck the left or right image of the stimulus).

For pigeons, a trial ended when a correct response was made, upon which pigeons received access to a food magazine for 2.5 seconds. For humans, the trial ended as soon as they made a response; a correct response was indicated by the appearance of the word "Correct!" in the centre of a black display and a gold star at the location of the correct response, a wrong response was followed by the word "WRONG" in the display centre.

Pigeons completed a maximum of 20 daily sessions of 73 trials. Acquisition of the task was considered successful if a pigeon responded correctly on at least 80% of trials for three successive 73-trial sessions, and no further training was given once the pigeon reached this criterion. Pigeons that failed to reach this criterion under their original training condition within 20 sessions were tested on the alternative condition. Human participants completed at least 80 trials; task acquisition was considered successful when a participant answered 80% or more of a sequence of eight trials correctly. At the end of the experiment, human participants were asked whether they had noticed any relationship between a stimulus and the correct response. If they were able to report the relevant discrimination rule (e.g., horizontal stimuli required choosing the right key while vertical stimuli indicated a response to the left), it was assumed that they had relied on this rule when responding. If participants were unable to report a rule, it was assumed that they had relied on the automatic formation of stimulus-response associations to respond correctly.

To measure performance, I assessed both the number of trials required to reach the success criterion and average error rates until completing the experiment. Data were analysed for each species separately in a multivariate ANOVA with Condition (White Keys or Replicas) and Task (Orientation Discrimination or Spatial-Frequency Discrimination) as between-subjects factors. Where applicable, significance levels were subject to Huynh-Feldt corrections.

Results

Performance by pigeons and humans is illustrated in Figures 2.2.1; panel A shows average error rates and panel B shows the number of trials to reach the success criterion. For pigeons, performance levels differed between condition White Keys and condition Replicas.

All pigeons in condition White Keys failed to approach the success criterion within the 20 training sessions allowed (1460 trials), while the pigeons in condition Replicas reached the criterion significantly sooner, in a mean of 608 trials (8 sessions, *SD*=329 trials). The individual differences in task acquisition are shown in Figure 2.2.2. This difference between conditions was significant, $F(1,3)=55.1$, $p=.005$, $\eta_p^2=.95$; for these and subsequent analyses, pigeons that failed to reach the criterion were, conservatively, treated as though they had reached it in 1460 trials. Similarly, error rates were significantly lower in condition Replicas (21%, *SD*=6%) than in condition White Keys (41%, *SD*=6%), $F(1,3)=13.3$, $p=.035$, $\eta_p^2=.82$. After completion of the 20 training sessions, the pigeons that had failed task acquisition in condition White Keys were trained under condition Replicas, and learned the relevant discrimination task within 292 trials (4 sessions). As seen in Figure 2.2.2, they were faster to acquire the task and more accurate in condition Replicas than they had been in condition White Keys (number of sessions to reach criterion (20 sessions before transfer vs. 4 sessions after transfer): Wilcoxon $T=0$, $p=.068$ two-tailed; average error rate in final five sessions before transfer (37%) vs. first five sessions after transfer (22%): Wilcoxon $T=0$, $p=.068$ two-tailed).

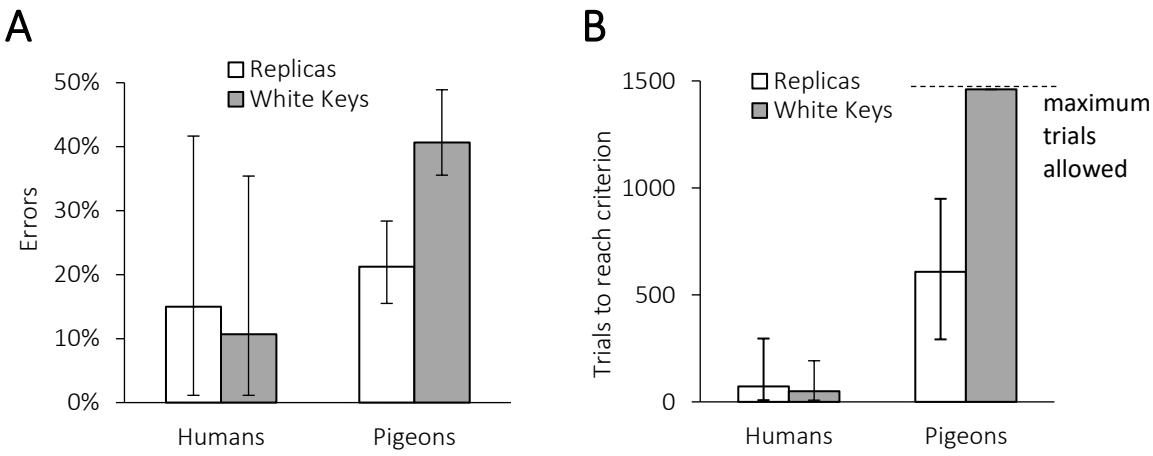

Figure 2.2.1. *A*) Error rates for humans and pigeons depending on whether subjects made a response by clicking/pecking a replica of the target stimulus (condition Replicas) or a white response key (condition White Keys). Error bars represent the individual range of errors. *B*) Trials to reach the success criterion of 80% correct trials in a sequence of eight trials for humans/three consecutive training sessions for pigeons depending on condition. Error bars represent the individual range in the number of trials to reach success criterion. *Note:* the range for pigeons in condition White Keys is not different from the mean.
This figure appeared in Meier et al. (2016a).

Two human participants, both in condition Replicas and performing the orientation discrimination, failed to reach the success criterion within 600 trials and aborted the experiment, which resulted in the loss of their data. Thus, the analyses were based on the data of 24 participants. The two excluded participants were unable to report the relevant discrimination rule at the end of the experiment; the other 24 were able to name the rule.

Humans showed no differences in acquiring a discrimination task between conditions, either in the number of trials to reach criterion, $F(1,20)=0.6$, $p=.47$, or in their error rates, $F(1,20)=0.9$, $p=.36$. However, they made more errors when they had to learn the orientation-discrimination task (mean error rate: 18%, SD=14%) compared to those humans who learned the spatial-frequency-discrimination task (mean error rate: 7%, SD=10%), $F(1,20)=5.6$, $p=.028$, $\eta_p^2=.22$. This was not the case for pigeons, $F(1,3)=1.9$, $p=.27$. Although the Condition-by-Task interaction did not reach statistical significance, $F(1,20)=3.0$, $p=.097$, Figure 2.2.3 illustrates that it was primarily humans who had to learn the orientation-discrimination task in condition Replicas who showed increased error rates compared to participants in the other conditions.

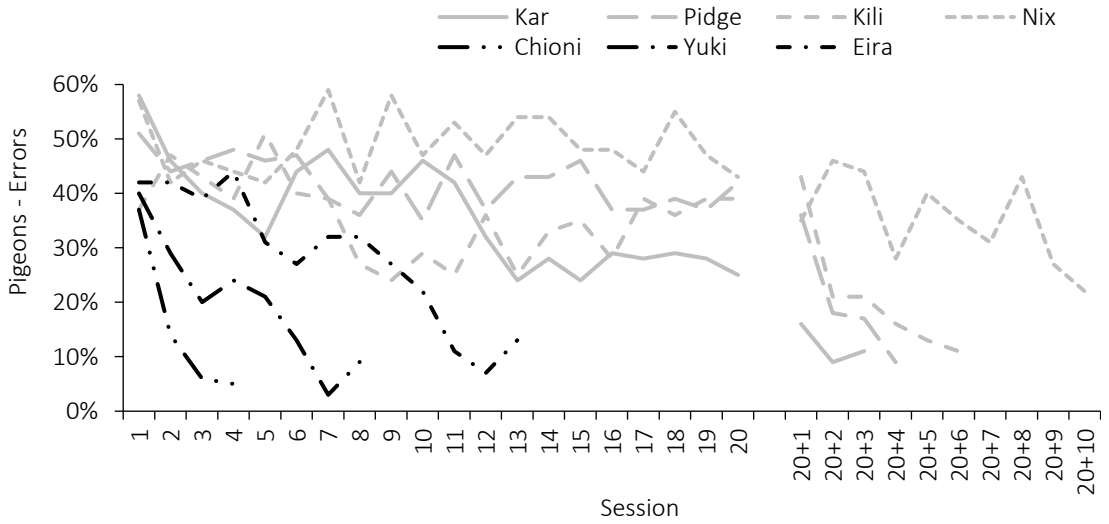

Figure 2.2.2. Pigeons' error rates across training sessions when making a response by pecking a replica of the target stimulus (condition Replicas; black lines) or a white response key (condition White Keys; grey lines). Pigeons in condition White Keys switched to condition Replicas after 20 sessions (performance after the switch shown as sessions 20+1 to 20+10). Kar and Chioni learned to discriminate spatial frequencies, the other pigeons performed the orientation-discrimination task.
This figure appeared in Meier et al. (2016a).

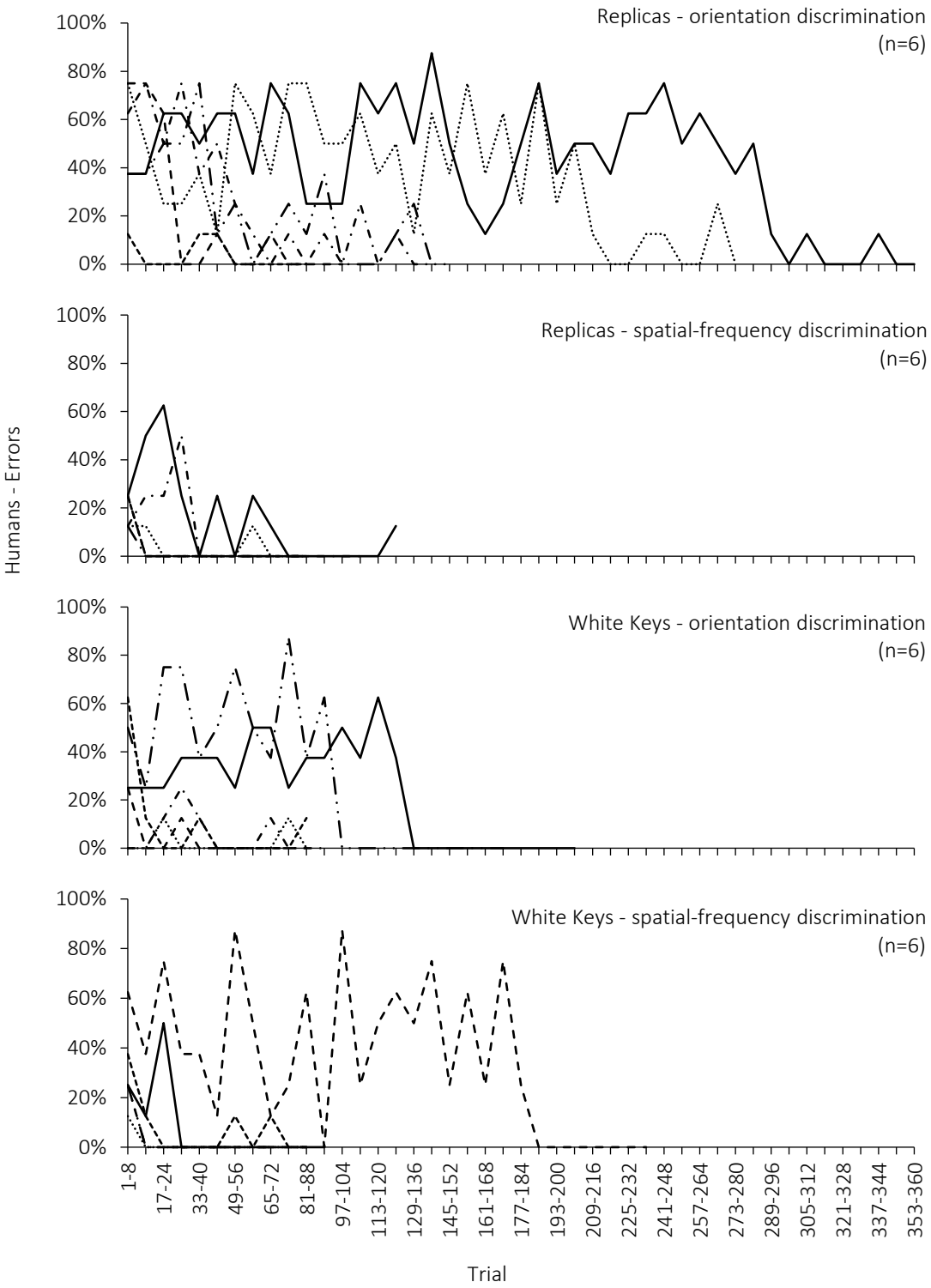

Figure 2.2.3. Individual human error rates depending on the condition that the participants completed (Replicas or White Keys) and the discrimination task that had to be learned (orientation discrimination or spatial-frequency discrimination).
This figure appeared in Meier et al. (2016a).

The species difference in learning depending on condition was confirmed by a significant Condition-by-Species interaction when analysing error rates in a univariate ANOVA including Species, Condition and Task as between-subjects factors, $F(1,23)=5.2$, $p=.032$, $\eta_p^2=.19$: again, the pigeons' performance was heavily impaired in condition White Keys compared to condition Replicas, while humans showed no difference in their error rates between the two conditions.

Discussion

As in Maes et al.'s (2015) Experiment 2A, pigeons acquired the task within a few sessions in condition Replicas. However, in condition White Keys, in which a discrimination task had to be learned by pecking one of two white response keys, pigeons had still not progressed much from chance level at the end of the twenty training sessions; but these birds progressed quickly to criterion once they had the opportunity to peck directly at a replica of the discriminative stimulus. Humans, on the other hand, showed no differences in acquiring a discrimination task depending on the way the response display was presented. This suggests that, firstly, humans and pigeons used different strategies to acquire the discrimination task and, secondly, the learning strategy employed by pigeons led to a failure to learn the task in condition White Keys.

Condition White Keys may have required pigeons to learn instrumentally, to move to the right or the left after seeing a certain stimulus in the display centre. Since the two response keys on the left and the right side of the stimulus were identical and presented simultaneously, the white key the pigeon was facing after performing the orientation behaviour did not hold any additional information as to whether the pigeons had indeed moved towards the correct location. On the other hand, when the stimulus was replicated in the response locations, as in condition Replicas and in Maes et al.'s Experiment 2A, a Pavlovian association becomes possible. There might be some intrinsic extra difficulty for a pigeon in learning an instrumental response to a stimulus at a given location compared to acquiring a Pavlovian approach. Typically, both types of learning process are considered to be active during acquisition of most tasks, with some researchers going so far as to say that "every instrumental situation is a classical conditioning situation" (Sheffield, 1965, p. 317). At least

for certain behaviours, classical conditioning results in better response formation than instrumental learning (Smith & Moore, 1966, p.138). Therefore, pigeons might have been able to acquire the discrimination task easily in condition Replicas because this condition involved a more effective classical-conditioning procedure, while pigeons in condition White Keys had to rely almost entirely on instrumental learning.

In contrast to the contingency-dependent processes that guided pigeon behaviour, humans almost certainly used verbalised rules to acquire the discrimination task in both conditions, as knowledge of the task rule was a requirement to succeed within the given time. Previous research (Galizio, 1979; Hayes, 1989; Maddox & Ing, 2005; Doll, Jacobs, Sanfey, & Frank, 2009) supports this assumption: although learning shaped by contingencies may improve performance, human behaviour is biased to be controlled by rules, even when this might be suboptimal. In the present case, simply learning the correct behaviour in response to each of the eight experienced stimuli might have resulted in more accurate performance than the rule-based approach, but nonetheless the participants did not change their approach.

However, there were some differences in the pattern of human behaviour between the two conditions that suggest that the way a response was made might have had an influence on the participants' task acquisition rates: participants in condition White Keys were able to learn either one of the two discrimination tasks quickly by deducing and applying the relevant discrimination rule. Participants in condition Replicas however made more errors and took longer to acquire the orientation-discrimination task (having to discriminate horizontal from vertical patterns) than participants in any other group. Perhaps the orientation task was more cognitively demanding, and interfered with the participants' ability to apply the task rule sufficiently in condition Replicas.

Indeed, two people in condition Replicas failed to infer the rule of the orientation task altogether (and consequently did not show any improvement in performance over the course of the experiment), whereas all participants in condition White Keys were able to report the relevant discrimination rule at the end of the experiment. Thus, condition White Keys might facilitate rule

deduction in some way, making even the apparently more difficult orientation-discrimination rule obvious to participants at an earlier point.

Alternatively, the way a stimulus is presented in Condition Replicas might make the deduction of the correct discrimination rule more difficult, to the point at which it even prevents some participants from inferring the rule within the duration of the experiment. Indeed, many participants in Condition Replicas reported, when questioned about their strategy for solving the task at the end of the experiment, that the presence of two stimulus replicas in the response display confused them, and many tried to detect slight differences, for example in brightness or hue, in the two identical stimulus copies, hoping that such a perceived difference might help them choose the correct response. Obviously, this search strategy could not succeed – and participants would continue to be unable to solve the task unless they changed their strategy either by considering alternative hypotheses about the discrimination rule, or by switching to a contingency-based learning approach. Levine (1971) discovered that it can be difficult, if not impossible, for humans to discover even an easy sorting rule when it is very different from the kind of hypotheses that have worked previously to infer a rule. Thus, the participants in Condition Replicas who started out searching for differences between the two stimulus replicas might have been unable to abandon this unsuccessful hypothesis about the correct discrimination rule in favour of a hypothesis that accepts the stimulus replicas as being identical. If this is the case, then the only option that remained to enable those participants to solve the task correctly was to allow learning to be shaped not only by rules but also by the observed contingencies between the display and the correct response. Comparable conclusions have been drawn previously, e.g. by Hayes, Brownstein, Zettle, Rosenfarb, and Korn (1986), who argued that the assumed bias towards rule-governed behaviour in humans (Maddox & Ashby, 2004; Maddox & Ing, 2005; Smith et al., 2010) can possibly be overcome more easily than previously thought: human performance may be shaped by an interaction between contingency-shaped and rule-governed behaviour, especially when the rules originally governing behaviour were unreliable or incomplete, as might be the case with self-generated rules. Participants in condition Replicas may initially have failed to deduce the appropriate task rule, which led to higher errors in responding than in condition White Keys, especially in the more difficult orientation-discrimination task.

Ultimately, this failure to learn via a rule-governed approach might have caused a shift in control of behaviour from rules to contingencies - learning the discrimination based on contingencies may then have helped to infer the correct task rule later on in the experiment, so that all successful participants were able to report the discrimination rule at the end of the experiment. This possibility holds an important implication: if condition Replicas can elicit contingency-based learning in humans - even if this learning system is later replaced by the application of rules -, it might be the preferable design when attempting to inhibit rules awareness in human participants.

Combining the results from pigeons and humans, a design in which the cue-stimulus compounds are presented as response keys emerged as the preferable design in the quest to investigate associative processes during task switching.

2.3 Procedures for a Comparative Task-Switching Paradigm

The experiments reported in Sections 2.1 and 2.2 established that a paradigm utilising coloured task cues and stimuli of varying Gaussian grating patterns in different spatial orientations could sufficiently elicit typical task-switching effects in humans, and that these stimuli were reliably discriminated from each other by both humans and pigeons. Further, administering detailed training on each component of the stimuli and task cues did not appear to affect humans' task-switching performance; thus, comparability between the procedures for humans and pigeons can be achieved by administering a stepwise conditioning-like training (that is, training each task on its own until reliable performance is achieved before combining the two tasks in a task-switching setting) to both human participants and pigeons. Finally, the most effective way to ensure stable acquisition of the two discrimination tasks by pigeons appeared to be presenting the stimulus compounds in the place of the response keys (instead of the centre of the screen with non-informative response keys). This method also seemed suitable for promoting associative learning in human participants.
The resulting procedure and training regime for both pigeons and humans are reported below.

Trial Procedure

Pigeons

The procedure used for the pigeon experiments is illustrated in Figure 2.3.1. Each trial began with the presentation of a white circular start key (100 pixels / 30mm in diameter) presented in the centre of a black display to focus attention on the screen. Following two pecks at the start key, it was replaced by one of the four task cues. A red or green key indicated one task, and a blue or yellow key signalled the competing task. Although blue and yellow were always assigned to a task together, the stimulus attributes (spatial frequency or orientation) that were important for classification in that task and the reward location that was associated with any cue-stimulus combination were counterbalanced across pigeons and across humans.

The pigeons had to peck the cue once, after which one of the four stimuli appeared superimposed on the cue colour so that both the cue and the stimulus were presented simultaneously in the centre of the display, as illustrated above in Figure 2.1.

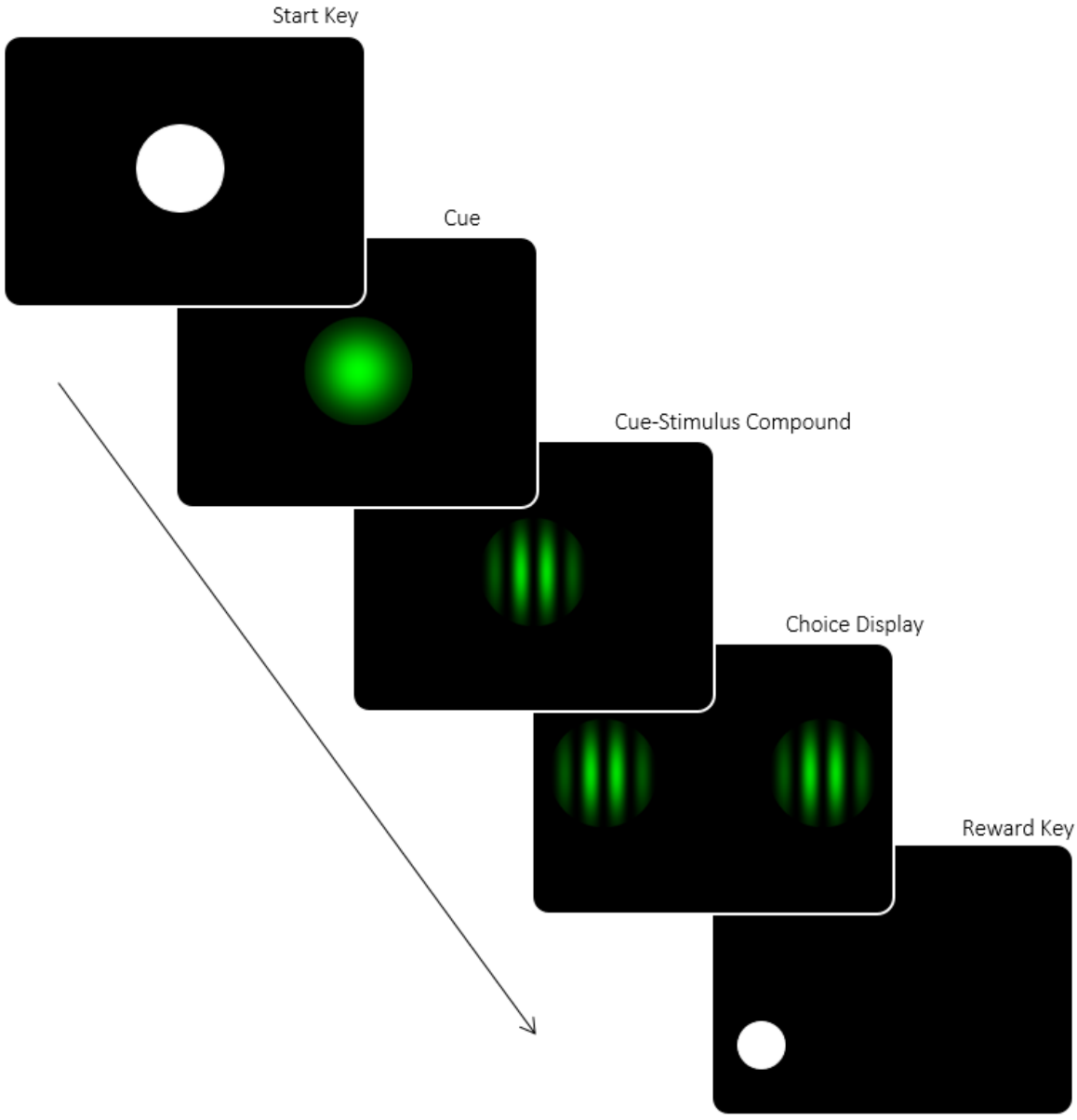

Figure 2.3.1. Procedure of a task-switching trial as experienced by pigeons. Pecking the reward key in the final display triggered the release of a food magazine.
For humans, the start key was omitted. Further, a correct response towards the choice display resulted in the word "Correct!" being displayed in the centre of a black screen, next to a gold star presented in the correct response location; an incorrect response resulted in the word "WRONG" displayed in the centre of a black screen.
This figure appeared in Meier et al. (2016b).

Pecking on the cue-stimulus combination resulted in its deletion from the centre of the screen and its immediate reappearance 200 pixels (60mm) to both the left and the right side of the display centre. A response was made by pecking at the stimulus presented in the location (left or right) that was associated with the present cue-stimulus combination. 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 stimulus in the incorrect location had no scheduled consequences. The inter-trial-interval to the next presentation of the observing key lasted 15 to 30 seconds.

Humans

For humans, a trial started immediately with the presentation of one of the four task cues. Participants had to mouse-click once on the cue, after which one of the four stimuli appeared superimposed on the cue so that both the cue and the stimulus were visible simultaneously in the centre of the display. One mouse-click on the stimulus resulted in its deletion from the centre of the screen and its immediate reappearance 200 pixels (60mm) to both the left and the right of the display centre. A response was made by mouse-clicking the stimulus presented in the location (left or right) that was associated with the shown cue-stimulus combination. If the correct response location was chosen, the stimuli in both response locations disappeared from the screen and a golden star appeared in the correct location next to the word "Correct!" in white letters for two seconds, then the next trial began. If the wrong response location was clicked, the entire display turned black and the phrase "WRONG!" in white letters was shown for five seconds before the next trial began.

Training

Pigeons

Seven pigeons received cue-training sessions before the start of the task-switching training. In these sessions, the observing key was presented and, after pecking that key, one of the four cues to be used in the task-switching paradigm appeared in the centre of the screen. Upon pecking the cue twice, a reward key appeared to either the left or the right side of the display. Pecking this reward key delivered 2.5 seconds of access to the food magazine mounted

below that key. Cue-training sessions continued until a pigeon reliably pecked at the cue in 80% or more trials of a session. Following the cue training, the pigeon received training on the first task. For all but one of the seven birds, this training took the following form: the saturation of the cue-stimulus compounds that had to be discriminated was initially reduced to 20% of the full colour; this was done because the pigeons, although responding well to a white key, initially refused to respond to the cues when the cue colours were fully saturated. If performance in a block of 24 trials exceeded 80%, the cue saturation was increased by 20% in the following block in that training session. If performance in the entire session of three blocks exceeded 80%, the cue saturation was increased by 20% in the following session. For example, if a pigeon's session started with a cue saturation of 40%, and the pigeon responded reliably in all three blocks of that session (leading to the saturation being increased to 60% in the second block and to 80% in the third block of that session), the next session would start at a saturation level of 60%. Once the pigeon was able to perform at or above 80% accuracy overall (and above 70% for each of the four stimuli) in three consecutive sessions that only contained fully saturated cues, training for the first task was considered successful. The same procedure was applied to train the second task, with the difference that the initial cue saturation for the cues of this task was set at 40%. Following the successful acquisition of the second task, the pigeon received refresher training on the first task, at full cue saturation, until it performed at or above 80% overall accuracy in two consecutive sessions. This was repeated for the second task. The alternating training of the two tasks continued until the pigeon was able to change between the two tasks from one day to the next and perform at 80% accuracy or above in each task for four consecutive days. Then, it received at least three further sessions in which the two tasks alternated between blocks (there were four blocks of 24 trials in each of these sessions). If the pigeon performed to the 80% criterion in these sessions, it was moved on to the task-switching paradigm.

The seventh pigeon in this group (Nelson) experienced a slightly altered training procedure: it responded very well towards the coloured cue-stimulus compounds, so that it was not necessary to gradually increase the saturation of the cue in order to maintain reliable responses. Thus, this pigeon experienced the fully saturated cue-stimulus combinations from the onset of the training; all

other criteria for successful completion of a task-training stage were the same as described above.

A second group of six pigeons was recruited at a later point. As the previous group, these pigeons started their training with cue-training sessions, but the brightness of the three red, green and blue colour components of each cue were initially set to maximum level (i.e., the RGB code of the cues were set to RGB[255,255,255]), which made the cues white. If the pigeon pecked at the cue in every trial of a given session, the brightness of the irrelevant colour components was reduced exponentially for each cue in the following session, so that the real cue colour was faded in across sessions. For example, the red cue was faded in by subsequently presenting coloured cues with the following RGB values: [255,255,255], [247,247,255], [239,239,255], [223,223,255], [191,191,255], [127,127,255], [063,063,255], [000,000,255]. This step-wise fade-in procedure applied to all cues at the same time, so that the pigeons always experienced the same level of colour brightness for all four cues.
The cue-training stage was considered successful if the pigeon responded in every trial towards the cues when the brightness was set at 100%. Following this cue training, the six pigeons received training on their first task; similar to Nelson's training regime, the cue saturation was set at 100% from the beginning of the training. Training of the two different tasks continued as outlined above for the first group of pigeons, and all pass criteria to proceed to the next training stage were identical.

Finally, another pigeon (Kili) was recruited for this experiment. It received the same gradual cue introduction as the first group in that the saturation of the cue-stimulus compounds was increased over training sessions, starting at 20% saturation for the first task and 40% saturation for the task that was trained second. In addition, it started the training sessions for each task with stimuli that only varied in the task-relevant dimension; the second dimension was held constant at an intermediate value to the two values that had to be discriminated in the competing task. That is, Kili was first trained on the orientation-discrimination task: it experienced stimuli (at reduced cue saturation) that were either horizontally or vertically orientated, and had a spatial frequency of 7 cycles per 100 pixels. The cue saturation was increased as described for the

first group of pigeons until Kili performed accurately in response to these training stimuli combined with the two fully saturated task cues in two consecutive sessions. Following this training, Kili completed further sessions in which the ambiguous stimuli (varying both in orientation and in spatial frequency) were presented until it was able to perform at or above 80% accuracy in three consecutive sessions. The same procedure applied to the training of the second task: initially, the stimuli only varied in spatial frequency, whilst the orientation of the grating was kept constant at 45° from the horizontal pane. Upon successful performance in response to these stimuli paired with fully saturated cues in two consecutive sessions, Kili completed further sessions in this task with the ambiguous stimuli until it was able to perform at 80% accuracy or above in three consecutive sessions. Then, it received alternating training on each task in the same way as the other pigeons.

Humans

Humans were trained in the two tasks in four blocks within the same session. The first training block contained at least 32 trials of one task. Then, the second task was trained in the second block for at least 32 trials. After this, the first task was repeated in block 3 for a minimum of another 16 trials. In the fourth and final training block, participants again experienced at least 16 trials of the second task. A block was terminated when subjects reached the criterion of 80% or more correct responses in a sequence of eight or more consecutive trials that included each of the four stimuli at least twice. Humans did not experience any adjustments of cue saturation or brightness. The only instructions humans received were how to respond (via mouse-clicks) and to try to "respond as quickly as possible whilst making as few mistakes as possible".

Data Collection

A final point for consideration was the way in which performance would be assessed. The conventional methods of measuring task-switching performance in humans had 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 in Exeter's animal cognition laboratories, the recording of reaction times for pigeons could be inaccurate; often, the system was not sensitive enough to record every peck that a pigeon attempted, so that the pigeon had to peck repeatedly until a response was recorded, which would distort actual response times. This 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 subjects have to respond to a stimulus cannot be restricted in the same way in animal studies as it is generally done in conventional human task-switching paradigms (Monsell, 2003; Kiesel et al., 2010; Vandierendonck et al., 2010; Forrest, 2012). As a result, reaction times can range from milliseconds in humans (Monsell, 2003; Dreisbach et al., 2006, 2007; Forrest, 2012) to several seconds in animals (Stoet & Snyder, 2003a, 2003b, 2008; Caselli & Chelazzi, 2011; Avdagic et al., 2014). 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, because humans generally make more errors in task-switch trials compared to task-repeat trials, and in response to incongruent stimuli compared to congruent stimuli (Rogers & Monsell, 1995; Vandierendonck et al., 2010). Recording the accuracy with which pigeons respond is easily accomplished, and, for the reasons stated above, might be a more suitable measure for comparison between species than reaction times. Nonetheless, to establish the validity of our paradigm, I recorded each subject's latency to make a response, although I did not restrict the time that participants had to respond, in an effort to preserve the comparability between species.

In summary, by taking into account the findings of the pilot studies reported in Sections 2.1 and 2.2, the task-switching paradigm constructed in this section can be expected to adequately elicit task-switching effects in humans and enable a comparison of such effects between humans and pigeons.

CHAPTER 3: DO ASSOCIATIVE PROCESSES CAUSE SWITCH COSTS IN A TASK-SWITCHING PARADIGM?

Parts of this chapter have been published as Meier, C., Lea, S.E.G., and McLaren, I.P.L. (2016). Task-switching in pigeons: Associative learning or executive control? Journal of Experimental Psychology: Animal Learning and Cognition, 42(2), 163-176.

In Chapter 2, I report the design of a comparative task-switching paradigm to investigate whether pigeons, whose behaviour is assumed to be governed entirely by associative processes, would suffer the same task-switching effects (namely task-switch costs and stimulus-congruency effects) as humans reportedly do (Monsell, 2003).

Forrest (2012) suggested that task-switch costs might be mediated by associative processes: in her experiments, participants who learned to perform a task-switching paradigm by learning its stimulus-response contingencies suffered small but reliable costs to performance when switching between the two existing task rules, even when the participants did not apply these rules. But is this observation proof that such switch costs are the result of associative processes? If they are, will pigeons demonstrate switch costs in their task-switching performance, as well? So far, only one other research group has investigated the task-switching performance of pigeons, and found that pigeons showed a lack of switch costs (Castro & Wasserman, 2016), apparently contradicting Forrest's (2012; Forrest et al., 2014) assumption. However, their sample size was rather small, which may raise some concern about the power of their results and how confidently the observed lack of switch costs can be accepted. Indeed, small sample sizes might have been the reason for the rather inconclusive results following from the studies of Stoet and Snyder (2003a, 2003b), Caselli and Chelazzi (2011) and Avdagic et al. (2014) regarding the expression of switch costs in macaques. Therefore, in order to be able to draw any meaningful conclusions from pigeons' performance in the comparative task-switching paradigm developed in Section 2.3, it had to be shown that it could adequately capture any potentially present task-switching effects, even when

sample sizes are small, which is often the case in studies of animal cognition that require long training periods (as was also the case here).
One effect that is universally observed in different species during task switching is the response-congruency effect (Kiesel et al., 2007; Forrest, 2012; Schneider, 2015), and it can be assumed that a valid task-switching paradigm would be able to generate this effect. The magnitude of a congruency effect was not investigated by Castro and Wasserman (2016), which makes it difficult to assess whether their pigeons did not express switch costs because of an inherent absence thereof in the pigeons' performance, or because their paradigm lacked the power to make a reliable statement about any task-switching effects in general.

To anticipate the results of Section 3.1, the paradigm was successfully acquired by pigeons and elicited the common task-switching effects in humans. I conducted further systematic investigations of the influence of associative processes on task-switching performance in pigeons and humans in an attempt to find an explanation for the behavioural patterns that were observed in Section 3.1: in Section 3.2, I investigated the influence of the perceptual features of task cue, stimulus or response of one trial on performance in the next trial to establish whether pigeons and humans would express the type of trial-to-trial effects that commonly occur in associative learning. In Section 3.3, I tested the hypothesis that human participants generally do not solve the task-switching paradigm via associative learning, but instead apply some form of abstract rule that they extract from the perceived cue-stimulus-response contingencies, even if that rule is imperfect or cannot adequately be described by the participant.

3.1 Task-Switching Performance of Pigeons and Humans

In this section, the task-switching paradigm developed in Section 2.3 was put to the test. Firstly, I aimed to verify the occurrence of both switch costs and congruency effects in human participants, which have previously been found to affect performance of humans regardless of whether their behaviour was based on task sets or on stimulus-response contingencies (Forrest, 2012). Although the paradigm used in Section 2.1 did elicit robust task-switching effects in humans, the final paradigm was sufficiently different from that initial design to again raise this concern. Thus, I included a sample of human participants in this experiment to confirm that the final paradigm adequately captured task-switching effects in humans.

Secondly, I also investigated the occurrence of these effects in pigeons' performance. Congruency effects have been reported for both humans and macaques tested in a task-switching setting (Monsell, 2003; Stoet & Snyder, 2003a, 2003b; Vandierendonck et al., 2010; Caselli & Chelazzi, 2011; Forrest, 2012; Avdagic et al., 2014), and can be attributed to associative processes during stimulus processing (Kiesel et al., 2007); this assumption was discussed in more detail in Section 1.1. The logical conclusion here is that congruency effects will affect the task-switching performance of all species, regardless of their cognitive capacity to apply task rules. More importantly, I investigated the extent to which the task-switching performance of pigeons was influenced by switch costs, especially in response to incongruent stimuli, to which the correct response depends on the currently relevant task (cf. Section 1.1). If the switch costs expressed by humans who did not apply task rules to solve the paradigm were mediated by the same associative processes that govern pigeon behaviour, then the same costs should be observed in the pigeons' performance.

Methods

Subjects

Twenty-seven Psychology undergraduate students and eight pigeons completed this experiment.

Paradigm

The apparatus and stimulus material is described in Chapter 2. After completing the training procedure described in Section 2.3, subjects completed the full task-switching paradigm, in which trials of the two previously separately trained tasks were intermingled. The task sequence was partially randomized to produce a switch trial in one third of the trials; for trials in which the previous task repeated, the two task cues for that task alternated so that the same cue was never shown consecutively on two trials. Pigeons received 20 sessions of 72 trials (three runs of 24 trials, amounting to 1460 trials per pigeon); in each run, the four combinations of spatial frequency and orientation were presented three times per task. Humans completed 24 blocks of 24 trials (resulting in 576 trials per person), with each of the four combinations occurring trice per task per block. After each block, participants had the option to take a short break. As the first trial of each block or session would be neither a task-switch nor a task-repeat trial, it could not be included in any analysis; thus, a 73rd trial for pigeons and a 25th trial for humans was added at the start of each session and block; the cue and stimulus of this dummy trial were selected at random.

At the end of the task-switching procedure, human participants were interviewed about their ability to describe the rules that defined a correct response, to determine the approach they had used to solve the paradigm. The interview questions are attached in Appendix A1. If a participant was able to correctly identify the contingencies between a task cue and certain stimulus characteristics, he or she was considered to have understood and successfully applied the underlying rule. If a participant could not explain any relationship between stimuli, cues and the correct response, this was taken as an indication that he or she had not relied on the corresponding task rules when making a response in the task-switching paradigm. Participants who reported that they had always applied the same one of the two rules (for example, they said that they made a response based on the spatial orientation of the stimulus in all trials), or said that they had made up their own solving strategies, were excluded from further analyses.

Results

Trials immediately following an incorrect response were excluded from analysis because it was unclear whether the error in the previous trial had been due to performing the wrong task or due to choosing the wrong response to the given stimulus in the current task - thus making it impossible to assess whether the trial following the error was treated by the subject as a task-switch or a task-repeat trial.

Table 3.1.1. Results of repeated-measures ANOVAs on error rates of Rules-Aware participants, Rules-Ignorant participants and pigeons, using Trial Type (Task Repeat or Task Switch), Stimulus Congruency (Congruent or Incongruent) and Test Blocks/Sessions as within-subjects factors. Significant p values are highlighted in bold.

	Error Rates			
	F	df	p	η_p^2
Rules-Aware Participants (n=8)				
Trial Type	17.38	1, 7	**.004**	.713
Stimulus Congruency	51.84	1, 7	**<.001**	.881
Trial Type * Stimulus Congruency	7.27	1, 7	**.031**	.510
Test Blocks	7.31	23, 161	**<.001**	.511
Blocks * Trial Type	2.86	23, 161	**.008**	.290
Blocks * Stimulus Congruency	2.74	23, 161	**.003**	.282
Blocks * Trial Type * Stimulus Congruency	1.16	23, 161	.317	.142
Rules-Ignorant Participants (n=9)				
Trial Type	17.43	1, 8	**.003**	.685
Stimulus Congruency	267.02	1, 8	**<.001**	.971
Trial Type * Stimulus Congruency	16.28	1, 8	**.004**	.671
Test Blocks	1.30	23,184	.178	.140
Blocks * Trial Type	1.03	23,184	.432	.114
Blocks * Stimulus Congruency	1.00	23,184	.461	.111
Blocks * Trial Type * Stimulus Congruency	1.08	23,184	.377	.118
Pigeons (n=8)				
Trial Type	0.10	1, 7	.766	.014
Stimulus Congruency	75.62	1, 7	**<.001**	.915
Trial Type * Stimulus Congruency	0.49	1, 7	.508	.065
Test Sessions	1.06	19, 133	.399	.132
Sessions * Trial Type	0.78	19, 133	.725	.100
Sessions * Stimulus Congruency	1.60	19, 133	.064	.186
Sessions * Trial Type * Stimulus Congruency	1.17	19, 133	.311	.143

The subject species and the human participants' rule use had a main effect on performance, $F(2,22)=46.78$, $p<.001$, $\eta_p^2=.81$, and influenced the expression of the two task-switching effects of interest and their interaction significantly, all $p\leq.004$. Therefore, all analyses were carried out separately for humans (split according to the number of rules participants could name) and for pigeons. The extent to which humans and pigeons were influenced by any task-switching effects was investigated in repeated-measures ANOVAs using Trial Type (Task-Repeat or Task-Switch trial), Stimulus Congruency (Congruent or Incongruent) and Blocks/Sessions as within-subjects factors. Where appropriate, significance levels were subjected to Huynh-Feldt correction. The results of these analyses are summarised in Table 3.1.1 and illustrated in Figure 3.1.1.

Pigeons

Pigeons' error rates were generally low (8.8%, *SD*=3.1), since the pigeons had received substantial training. This overall error rate was significantly better than expected by chance, $t(7)=37.57$, $p<.001$, $\eta_p^2=.99$.

As seen in Figure 3.1.1, pigeons demonstrated no indication of suffering switch costs in their error rates (task-repeat: 9.1% vs. task-switch: 8.9%). However, the influence of Stimulus Congruency on performance was greatly visible, 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%).

This observation was confirmed by a non-significant effect of the factor Trial Type and a significant influence of Stimulus Congruency (Table 3.1.1). The two factors did not interact with each other - 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 also 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, the response times of pigeons were slow and too variable to show consistent congruency effects (6919ms for incongruent stimuli vs.7109ms for

congruent stimuli, $F(1,7)=2.17$, $p=.184$) or switch costs (7047ms for task-repeat trials vs. 6981ms for task-switch trials, $F(1,7)=3.27$, $p=.113$).

In light of the remarkable absence of any switch costs in the pigeons' performance, the accuracy data were also examined 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 are 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 than under a model including Trial Type as a second factor.

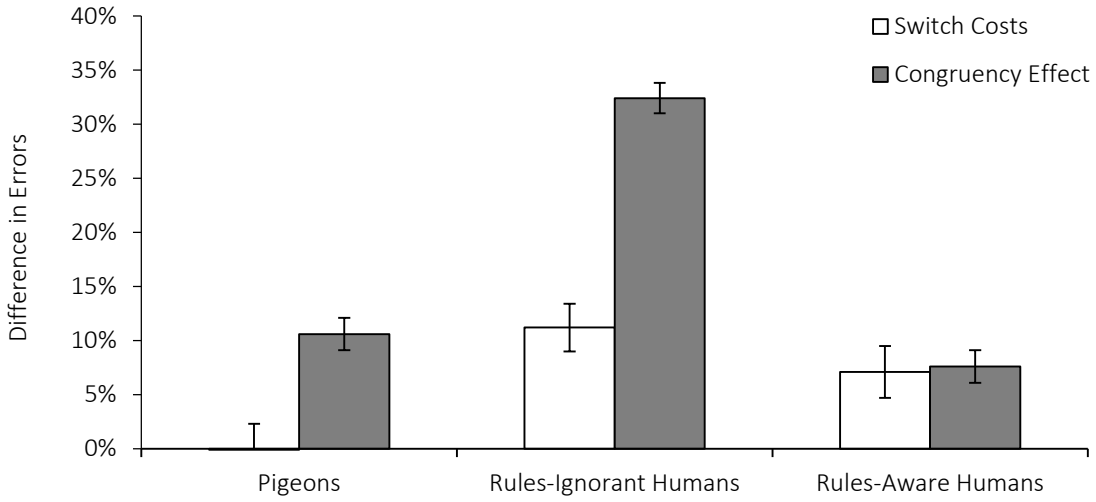

Figure 3.1.1. Switch costs (difference in error rates of switch trials and task-repeat trials) and congruency effect (difference in error rates of trials containing a congruent stimulus and trials containing an incongruent stimulus) for pigeons, humans who were unaware of any underlying task rules (Rules-Ignorant) and humans who inferred the task rules (Rules-Aware). Error bars represent standard errors.

Humans

Twenty-three of the 27 human participants completed the training phase described in Section 2.3 and proceeded to the task-switching phase after an average of 131 training trials (the other four participants did not reach the pass criterion of the training in 600 training trials and aborted the experiment). Eight

participants were able to verbalize the rules for both tasks (orientation and spatial frequency) at the end of the experiment, and it can be assumed that they had relied on these rules to solve the paradigm (the 'Rules-Aware' group). A further six participants reported having discovered one of the two rules (for example, they said that horizontal stimuli generally required clicking the left response key, but that sometimes this strategy did not succeed) or having made up their own solving strategies. Because of the ambiguity as to what cognitive strategy these participants relied on to solve the tasks, their data were not included in any further analyses. The remaining nine participants stated that they had not been aware of any relationships between specific stimuli and the correct response, or that the relations they had assumed appeared to change throughout the experiment; these participants claimed that their responses had not been governed by any specific rules throughout the experiment (this group will therefore be referred to as the 'Rules-Ignorant' group). Note that, although the definition of what constituted a Rules-Aware person was quite strict in comparison to the relatively relaxed definition of what constituted a Rules-Ignorant participant, the behavioural differences between two groups that are reported below seem substantial enough to validate the definitions.

Overall error rates were significantly lower for the Rules-Aware group (9.5%, *SD*=5.0) than the Rules-Ignorant group (30.3%, *SD*=5.5), $t(15)=8.16$, $p<.001$, $\eta_p^2=.82$. Both groups made significantly fewer errors than expected by chance, Rules-Aware: $t(7)=22.85$, $p<.001$, $\eta_p^2=.99$; Rules-Ignorant: $t(8)=10.82$, $p<.001$, $\eta_p^2=.94$.

The effect of the factor Trial Type was consistently present in both human groups (errors in task-repeat vs. task-switch trials: Rules-Aware: 8.4% vs. 17.2%; Rules-Ignorant: 26.4% vs. 39.4%). Stimulus Congruency strongly influenced performance of humans, as both groups showed increased error rates when responding to an incongruent stimulus compared to responding to a congruent stimulus (Rules-Aware participants: 17.6% vs. 8.0%; Rules-Ignorant participants: 51.5% vs. 14.2%). Numerically, the stimulus-congruency effect on error rates was equally large as the effect of a task switch for Rules-Aware participants (both were around 9%), and about three times larger than switch costs for Rules-Ignorant participants; previous literature found that the

congruency effect on error rates could be two to three times larger numerically than switch costs if participants employed task rules (Forrest, 2012; Schneider, 2015) and around three to eight times the size of switch costs if humans based their response on stimulus-response contingencies (Forrest, 2012). The two factors interacted significantly in Rules-Ignorant and Rules-Aware participants; as seen in Figure 3.1.2, switch costs were mainly present when responding to an incongruent stimulus rather than to a congruent stimulus. Most notably, Bonferroni post-hoc comparisons show that, for Rules-Ignorant participants (much like Forrest's, 2012, participants learning cue-stimulus-response contingencies), the difference in errors between task-repeat and task-switch trials was only significantly different from zero when responding to an incongruent stimulus (switch costs on incongruent trials: 26.8%, p=.002; on congruent trials: -0.8%, p=.771); for Rules-Aware participants, performing a task switch produced higher error rates both on trials with an incongruent stimulus and a congruent stimulus (switch costs on incongruent trials: 12.7%, p=.006; on congruent trials: 4.8%, p=.022).

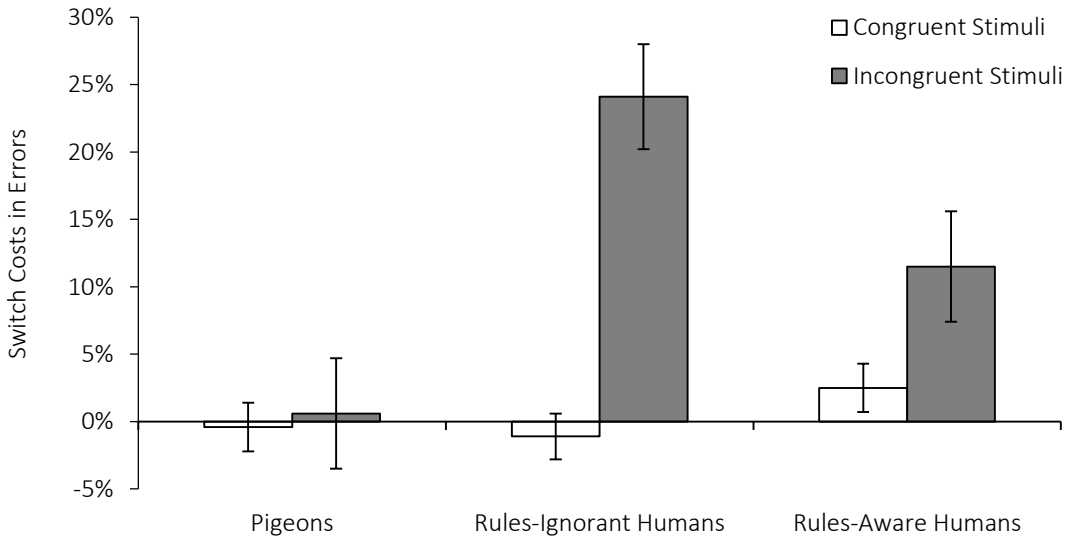

Figure 3.1.2. Switch costs (difference in error rates of switch trials and task-repeat trials) for those trials in which a congruent stimulus or an incongruent stimulus was presented, for pigeons, humans who were unaware of any underlying rules (Rules-Ignorant) and humans who inferred the rules (Rules-Aware). Error bars represent standard errors.

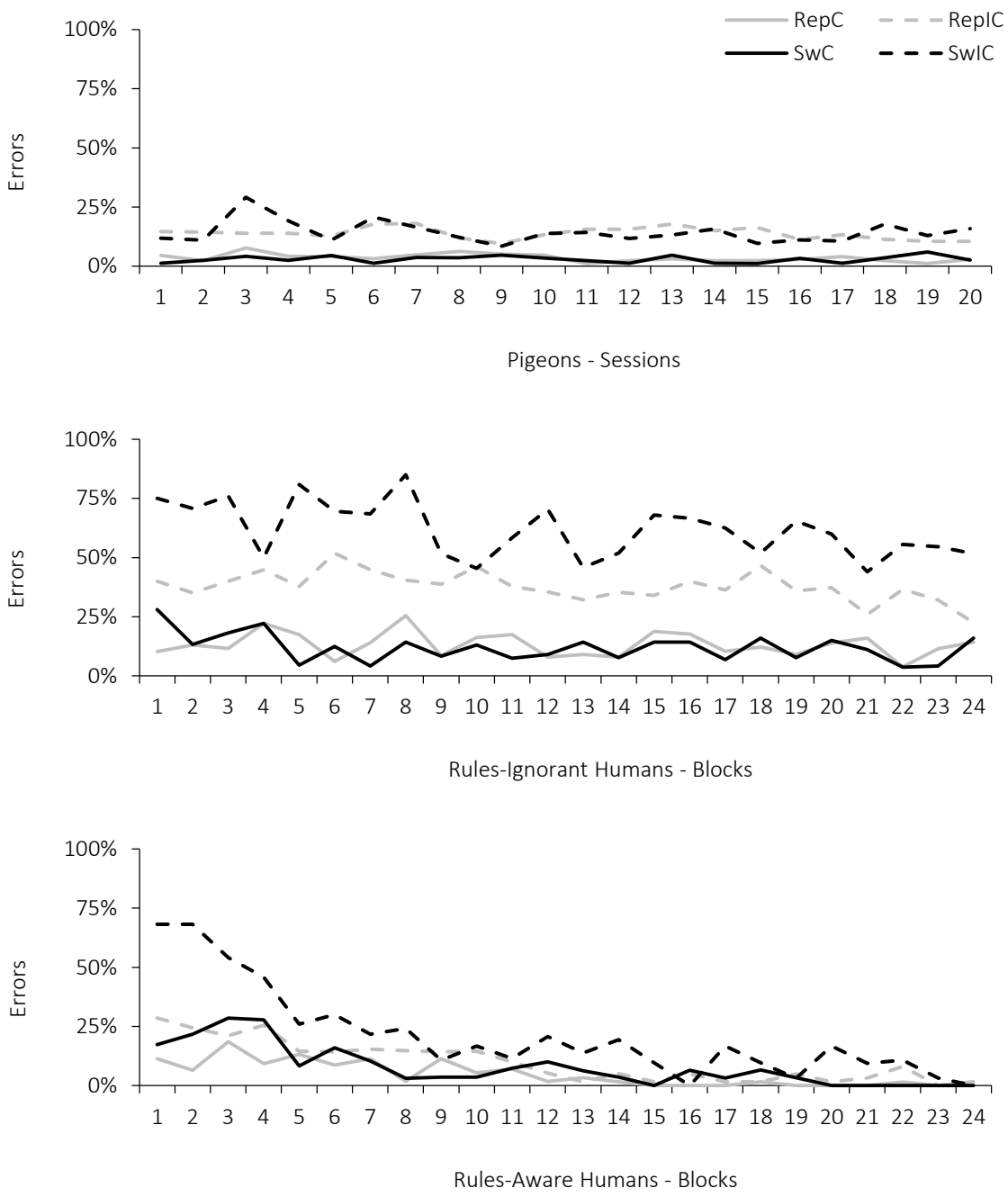

Figure 3.1.3. Error rates across the 20 test sessions for pigeons and the 24 test blocks that human participants (both Rules-Ignorant and Rules-Aware) completed. *Rep*: Repeat trials; the task in these trials was the same as in the previous trials. *Sw*: Switch trials; the task changed from the previous trial. *C*: Congruent stimulus; the stimulus required the same response in both tasks. *IC*: Incongruent stimulus; the correct response to the stimulus varied between tasks.

The sequence of Test Blocks had a reliable effect on error rates for the Rules-Aware group, as they learned to make fewer mistakes over the course of the experiment. This improvement led to a significant reduction over blocks in both switch costs and congruency effects. Participants in the Rules-Ignorant group did not show any significant changes in their error rates across test blocks, nor

did the progression in the experiment affect the magnitude of switch costs or congruency effects. This result also supports the idea that Rules-Aware and Rules-Ignorant participants approached the paradigm differently. The differences across test blocks (and sessions for pigeons) between the three groups of subjects are illustrated in Figure 3.1.3.

To verify the external validity of the paradigm, I also examined participants' latency to click on a response key. Following convention, only trials that followed a correct response and were also answered correctly were considered in this analysis. The effects reported above for error rates were replicated in the participants' response times: Rules-Aware participants were slower to respond in task-switch trials versus task-repeat trials (986ms vs. 840ms; $F(1,7)=12.08$, $p=.010$, $\eta_p^2=.633$) and to incongruent stimuli versus congruent stimuli (956ms vs. 869ms; $F(1,7)=15.82$, $p=.005$, $\eta_p^2=.693$). Unlike for error rates, switch costs in response times did not differ when responding to incongruent stimuli versus congruent stimuli (switch costs: 138 vs. 155ms; $F(1,7)=0.30$, $p=.60$). Rules-Ignorant participants also showed impairments due to a task switch compared to a task repeat in response times (820ms vs. 772ms; $F(1,8)=12.69$, $p=.007$, $\eta_p^2=.613$). Surprisingly, the effect of stimulus congruency was not sufficiently reliable in their reaction times (848ms for incongruent stimuli vs. 744ms for congruent stimuli; $F(1,8)=5.08$, $p=.054$); however, responding to incongruent stimuli significantly enhanced switch costs compared to responding to congruent stimuli (switch costs: 81ms vs. 16ms; $F(1,8)=6.86$, $p=.031$, $\eta_p^2=.462$). The human task-switching literature reports that the effect of stimulus congruency on response times can be between 0.5 to three times the numerical value of task-switch costs if the participants are employing task rules (e.g., Forrest, 2012; Schneider, 2015), and were found to be about six to ten times the magnitude of switch costs in reaction times if the participants based their responses on stimulus-response contingencies (Forrest, 2012). In the two groups of participants in this experiment, the numerical difference in response times due to the congruency effect was around 1.5 times the difference in response times between task-repeat and task-switch trials. Although the main focus of my experiments were error rates, and not response times as in conventional task-switching studies on humans, these results confirm that the

paradigm used in this experiment can reliably detect task-switching effects in humans across several measures of performance.

To confirm that there were reliably different patterns in error rates between the three groups of subjects, a Kruskal-Wallis Test estimating the influence of the Group (Rules-Aware participants, Rules-Ignorant participants, pigeons) on the dependent variables Switch Costs and Congruency Effect was carried out. It revealed a significant difference between groups regarding Switch Costs, $\chi^2(2)=8.51$, $p=.014$. Bonferroni post-hoc comparisons confirmed that switch costs were similar in size in Rules-Aware and Rules-Ignorant participants, $p=.236$, and differed between Rules-Aware participants and pigeons, $p=.003$. However, this difference was not statistically reliable when comparing pigeons and Rules-Ignorant participants, $p=.059$. The Congruency Effect also differed across groups, $\chi^2(2)=18.05$, $p<.001$, in that Rules-Ignorant humans were affected to a greater extend by stimulus congruency than the other two groups (both $p\leq.003$ compared to either group; pigeons compared to Rules-Aware participants: $p=.083$).

Discussion

A major concern in developing a comparative task-switching paradigm was ensuring that the paradigm could successfully be acquired by pigeons whilst preserving validity when tested with human participants. The human participants in this study demonstrated persistent switch costs, and they did so regardless of whether or not they had been aware of the underlying task rules. The confirmation of switch costs in humans supported the validity of this paradigm to accurately assess task-switching performance even when subjects were not verbally instructed and were not restricted in the time they had to respond. It provides some confidence that there is value in the observation that pigeons, on the other hand, did not suffer from switch costs in the task-switching paradigm despite being able to perform at a high level of accuracy.
The fact that the congruency of a stimulus persistently affected performance in both humans and pigeons further confirmed that the paradigm was able to capture task-switching effects in both species. Thus, the task-switching

paradigm developed in Section 2.3 appears to be a useful tool for comparing task-switching performance across species.

Humans who were able to report the rules underlying the two tasks experienced substantial switch costs. This result is in line with the conventional assumptions (Monsell, 2003; Vandierendonck et al., 2010) about task-switching performance in humans: these Rules-Aware participants relied on identifying and shifting between the competing task rules in order to make a response, and the switch costs observed in their performance likely resulted from their reliance on executive control. Although both Rules-Aware and Rules-Ignorant participants showed similar levels of performance in the first task-switching block, the performance of Rules-Aware participants improved drastically and had reached a high level of accuracy by the final block; this process probably resulted from the discovery of the two task rules.

Pigeons performed at a very high level of accuracy without incurring any costs to performance on switch trials. This observation supports Dreisbach et al.'s (2006, 2007) claim that an associative acquisition of task-switching paradigms leads to a lack of switch costs. By acquiring information about the correct behavioural response to each experienced combination of cue and stimulus via associative learning, pigeons succeeded in this paradigm despite their assumed inability to organise stimuli in task sets.

Although it is appealing to claim that the observed switch costs in humans indicate the application of task sets while a lack of switch costs in pigeons implies a reliance on associative processes, matters may not be this simple. In assuming that rule-based and contingency-governed learning are clearly dissociable processes and that humans are able to apply either one flexibly depending on current cognitive demands, one would expect to find persistent switch costs in the data of some humans - those who could verbalise task rules - and a lack of switch costs in other humans - those who were unaware of rules -, in the same way as switch costs were sometimes present or absent in rhesus macaques (Stoet & Snyder, 2003a, 2003b; Caselli & Chelazzi, 2011; Avdagic et al., 2014), who are believed to possess a comparable dissociation of an explicit and an implicit learning mechanism (Smith et al., 2012). This is indeed the case in the human participants - but only when considering switch costs in response

to congruent stimuli, which are only present in Rules-Aware participants but not in Rules-Ignorant participants. Similar to the univalent stimuli used by Dreisbach et al. (2006, 2007), the congruent stimuli in the paradigm always signalled the same unambiguous correct response, regardless of the task that was currently cued.

However, both Rules-Aware and Rules-Ignorant participants showed reliable switch costs when responding to incongruent stimuli, to which the correct response depended on the currently relevant task - so these costs occurred not only in participants who knew of the existence of the two different task rules, but also in those who stated they had been unaware of any tasks and had presumably relied on implicit, contingency-driven learning to solve the paradigm. This is an extraordinary observation - and it combines the seemingly contradictory findings of Dreisbach et al. (2006, 2007) and Forrest (2012) in an impressive way. Dreisbach et al. (2006, 2007) explained a lack of switch costs in response to univalent stimuli (that require only one response) as being the result of contingency learning: Rules-Ignorant participants were sensitive to the consistent stimulus-response contingencies of the congruent stimuli, which enabled them to perform accurately without having to incorporate the presented task cue, or having to "switch tasks". Complementary to this idea, Forrest (2012) argued that switch costs could appear in response to incongruent stimuli, and express 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 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, i.e., task-repeat trials. It might be puzzling that an associative cue equivalence would only affect performance in trials with incongruent stimuli but not extend to congruent stimuli, but this issue could be addressed by arguing that the associative strength between a congruent stimulus and the correct response sufficed to elicit a fast, correct response, so that the presentation of the task cue did not hold any additional information in these trials (i.e., there was a ceiling effect), whereas the task cue was crucial to learning the correct response to an incongruent stimulus.

In summary, the lack of any switch costs in response to congruent stimuli (shown by both Rules-Ignorant humans and pigeons) supports Dreisbach et al.'s (2006, 2007) claim that an associative acquisition of task-switching paradigms can eliminate switch costs for univalent stimuli. However, Forrest's (2012; Forrest et al., 2014) claim that switch costs could appear in response to incongruent stimuli when associative learning was in play seems to apply only to associatively learning humans - pigeons showed no switch costs in response to incongruent stimuli. This inconsistency is even more puzzling considering that Forrest provided simulations to back up her claim. Does it have to be assumed that the associative processes determining human behaviour differed from those in pigeons, since they evoked switch costs in humans but not in pigeons? This seem irrational; there are other explanations for this discrepancy that seem more plausible.

One possibility is that pigeons do in fact suffer switch costs, but that some aspect of the design of the paradigm is masking it. Perhaps the differences in switch and repeat trials were counteracted by a preference for novelty that is often observed in pigeons (e.g., in matching to sample, see Wright & Delius, 2005). Pigeons might have preferentially responded to trials in which there is some change in stimulation (either in the form of a different stimulus or a different response) compared to the previous trial, and avoided those in which both the stimulus and the response location were the same as in the preceding trial. The latter, for incongruent stimuli, is only possible on repeat trials, so, other things being equal, performance on those trials should then on average be worse than on switch trials. A disadvantage for repeat trials over switch trials for incongruent stimuli could cancel out any switch costs in those trials, which by definition comprise a disadvantage for switch trials over repeat trials. This possible explanation for the lack of switch costs in the pigeons' data is addressed in Section 3.2, by examining a range of sequential effects, such as cue-repetition, stimulus-repetition and response-repetition effects that occur with the given task-switching paradigm.

However, a much more interesting possible cause for the pigeons' lack of switch costs is that pigeons simply do not suffer any such costs. That is, they do not exhibit any difficulty in switching from one hypothetical task to another, even when the discrimination involves incongruent stimuli. This possibility would in turn have other implications: for example, pigeons might lack switch costs

because they do not develop the associative cue equivalence that Forrest (2012) and Forrest et al. (2014) held responsible for causing switch costs in the associatively mediated performance of humans. This possible explanation is investigated in more detail in Section 3.2. Alternatively, one might have to assume that there are genuinely no switch costs in associatively-mediated task switching, and that the switch costs in both human groups were due to rule use in some sense, perhaps if humans form rules that they cannot verbalise but which still control behaviour. This would fit rather well with theories that explain switch costs in terms of task-set reconfiguration (Monsell & Mizon, 2006) but would go against any theories that attempt to explain switch costs in associative terms (e.g., Logan & Bundesen, 2003, Forrest et al., 2014). This explanation is considered in Section 3.3.

3.2 Why do Pigeons Show an Absence of Switch Costs?

In Section 3.1, pigeons performed at a high level of accuracy without suffering any switch costs. In contrast to this, humans were persistently impaired by switch costs when information from task cues was needed to make a correct response, even when they reported not to have "switched" between different tasks. This obvious difference in the magnitude of switch costs in response to incongruent stimuli expressed by Rules-Ignorant participants and pigeons required further investigation. If Rules-Ignorant participants and pigeons both acquired the task-switching paradigm based on the same associative mechanisms, both groups would be expected to show similar task-switching effects in their performance, plausibly in the way hypothesised by Forrest (2012) and Forrest et al. (2014).

There are a number of potential causes for the discrepancy observed in Section 3.1. It might be the case that participants in the Rules-Ignorant group did not rely on associative learning to acquire the contingencies of each cue-stimulus-response pairing. Even though Rules-Ignorant participants did not describe the correct classification rules during the post-experiment interview, they might have relied on other rule-based solving strategies to make a response (and perhaps the way in which the questionnaire was structured discouraged them from mentioning those strategies). Alternatively, if Rules-Ignorant participants did solve the paradigm via associative learning, it is possible that the apparent lack of switch costs in the pigeons' performance was in fact due to the specifics of the paradigm. Although the current paradigm might have reliably detected switch costs that occur as a consequence of associative processes in humans, it might have led to an absence of the same in the performance of pigeons. In this section, I investigate the lack of associatively mediated switch costs in pigeons despite their apparent presence in humans. Complementary to this, in Section 3.3 I address the potential causes of switch costs in humans despite a lack of them in pigeons.

The study design in Section 3.1 was carefully controlled to adhere to what is thought to be best practice in the task-switching literature. For example, a common issue is that 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. This is a major contributor to the magnitude of switch costs (Logan & Bundesen, 2003; Mayr & Kliegl, 2003; Logan & Bundesen, 2004; Schneider & Logan, 2005; Altmann, 2006; Monsell & Mizon, 2006) and as a result every effort is made nowadays to avoid presenting the same cue on consecutive trials. However, Forrest (2012) demonstrated that, even when cue repetitions are avoided, humans might still learn to equate the different cues that signal the same task, which in turn facilitates the associative retrieval of a stimulus-response link on trials with equivalent cues. The establishment of cue equivalence might be paralleled by a kind of within-category association referred to as "clumping" in the concept-learning literature (cf. Bateson & Chantrey, 1972; Delius, Ameling, Lea, & Staddon, 1995); pigeons acquire it, if at all, with great difficulty (cf. Fersen & Lea, 1990).

Consequently, if an associative equivalence of the two task cues is the effective cause of switch costs, pigeons might not express any costs because, to them, the two cues remain distinct features with separable informational value. If this is the case, then it might be possible to facilitate the retrieval of a stimulus-response association by increasing the perceptual similarity of the current trial to the previous trial; allowing the cue to repeat on subsequent trials might lead to better performance on task-repeat over task-switch trials and the emergence of switch costs in the performance of pigeons. If so, there should also be a notable difference in performance between task-repeat trials in which the cue repeats, and task-repeat trials in which the cue changes. Accordingly, this chapter examines the pigeons' task-switching performance when the task-switching paradigm is extended to include task-repeat trials involving cue repetitions.

Any benefit of immediate repetition might also extend to other features of the cue-stimulus compound – for example, trials in which not only the same cue but also the same stimulus as in the previous trial are presented. Similarly, performance might peak in trials in which the stimulus and the correct response location are the same as in the immediately preceding trial, especially compared to performance in task-switch trials in which the stimulus is the same

as in the previous trial but the required response changes - which is only possible for incongruent stimuli.

It has to be noted that, although in associative terms it is more plausible to assume that a repetition of the features of a cue-stimulus compound would lead to a benefit for performance, the opposite effect might occur, as well, and might in fact contribute to the lack of switch costs for pigeons. As noted in Section 3.1, pigeons might show an absence of switch costs in this paradigm due to a preference for novel cue-stimulus-location combinations. For example, after pecking the correct location of a stimulus and receiving a reward, pigeons might show a tendency to avoid responding to that location in the following trial, which would induce errors if the same task and stimulus are repeated. The resulting performance benefit of task-switch trials over task-repeat trials might cancel out any otherwise observable benefits of repeat trials over switch trials.

These two contrasting hypotheses about the influence of repetitions during associatively mediated task-switching are also addressed in this section: I investigate the effect (if any) that repeating the same incongruent stimulus (and repeating or changing the correct response location) on two consecutive trials has on the performance of pigeons and Rules-Ignorant participants.

Methods

Subjects

Thirty-seven Psychology undergraduate students and fourteen pigeons took part in the experiment. Eight of the pigeons were those that had previously taken part in the experiment reported in Section 3.1. They had proceeded to a similar experiment (reported in Appendix A5.A) before entering this experiment. 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 Section 3.1), before entering this experiment.

Paradigm

The apparatus and stimulus material is described in Chapter 2. The procedure for this experiment was almost identical to that reported in Section 3.1, with the difference that, 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 72 trials each. Humans completed 20 blocks of 24 trials.

After completion of the task-switching procedure, human participants completed an on-screen questionnaire (Appendix A2) that assessed their ability to describe the rules that defined a correct response. The questions were open, asking participants to explain whether they had used a particular stimulus dimension when choosing a response and how this dimension (or the combination of several, if participants indicated that they had paid attention to more than one stimulus dimension) helped to determine the required response. Participants who responded that they had not attended to any of the suggested stimulus dimensions were asked to describe any solution strategy they might have used. Participants who were able to correctly identify the contingencies between the task cues and stimulus dimensions were considered to have inferred the underlying rules. If a participant could not explain a correct relationship between stimuli, cues and the correct response, this was taken as an indication that he or she had not relied on task rules to solve the paradigm. Participants who reported that they had always applied the same one of the two rules (for example, they said that they made a response based on the spatial orientation of the stimulus in all trials) or that they had made up their own solving strategies were excluded from further analyses.

Results

The subject species and the human participants' rule use had a main effect on performance, $F(2,34)=41.51$, $p<.001$, $\eta_p^2=.71$, and influenced the expression of the two task-switching effects of interest and their interaction significantly, all $p<.001$. Therefore, as in Section 3.1, all analyses were carried out separately for Rules-Ignorant participants, Rules-Aware participants and pigeons. The same trial-exclusion criteria as reported in Section 3.1 applied to this experiment. The data were analysed by means of repeated-measures ANOVAs using Trial Type (Cue-Repeat, Task-Repeat or Task-Switch trial), Stimulus Congruency and Test Blocks/Sessions as within-subjects factors. Where applicable, significance levels were subjected to Huynh-Feldt correction. The

results of these analyses are summarised in Table 3.2.1 and illustrated in Figure 3.2.1.

Table 3.2.1. Results of repeated-measure ANOVAs on error rates of Rules-Aware and Rules-Ignorant participants and pigeons, using Trial Type (Cue Repeat, Task Repeat or Task Switch), Stimulus Congruency (Congruent or Incongruent) and Test Blocks/Sessions as within-subjects factors. Significant p values are highlighted in bold.

	Error Rates			
	F	df	p	η_p^2
Rules-Aware Participants (n=12)				
Trial Type	14.31	2, 22	**<.001**	.565
Stimulus Congruency	45.28	1, 11	**<.001**	.805
Trial Type * Stimulus Congruency	9.64	2, 22	**.002**	.467
Test Blocks	7.32	19, 209	**<.001**	.400
Blocks * Trial Type	1.06	38, 418	.398	.088
Blocks * Stimulus Congruency	2.32	19, 209	**.014**	.174
Blocks * Trial Type * Stimulus Congruency	1.45	38, 418	.140	.117
Rules-Ignorant Participants (n=11)				
Trial Type	7.55	2, 20	**.005**	.430
Stimulus Congruency	62.45	1, 10	**<.001**	.862
Trial Type * Stimulus Congruency	21.96	2, 20	**<.001**	.687
Test Blocks	1.21	19, 190	.252	.108
Blocks * Trial Type	1.01	38, 380	.466	.091
Blocks * Stimulus Congruency	0.76	19, 190	.756	.070
Blocks * Trial Type * Stimulus Congruency	0.60	38, 380	.968	.057
Pigeons (n=14)				
Trial Type	0.62	2, 26	.525	.046
Stimulus Congruency	42.20	1, 13	**<.001**	.764
Trial Type * Stimulus Congruency	0.75	2, 26	.480	.055
Test Sessions	1.44	9, 117	.177	.100
Sessions * Trial Type	1.05	18, 234	.410	.074
Sessions * Stimulus Congruency	1.07	9, 117	.388	.076
Sessions * Trial Type * Stimulus Congruency	1.14	18, 234	.321	.081

Stimulus-repetition effects were analysed via 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-subjects factors. Where applicable, significance levels were subjected to Huynh-Feldt correction.

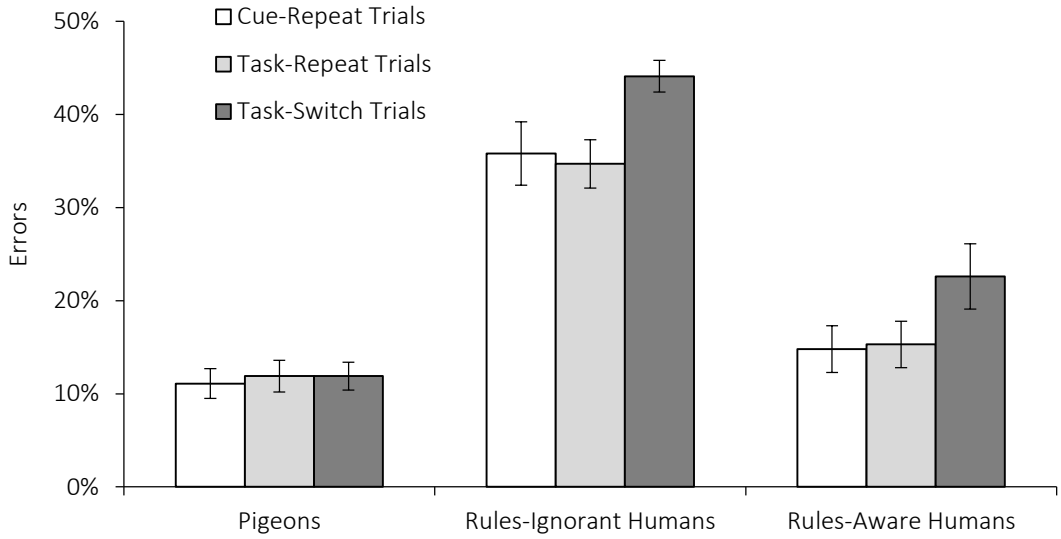

Figure 3.2.1. Error rates on cue-repeat, task-repeat and task-switch trials, for pigeons, humans who were unaware of any underlying rules (Rules-Ignorant) and humans who inferred the rules (Rules-Aware). Error bars represent standard errors.

Pigeons

Pigeons' error rates were low (11.8%, *SD*=5.8), and this overall performance was significantly better than expected by chance, $t(13)=24.74$, $p<.001$, $\eta_p^2=.98$.

Figure 3.2.1 shows that, once again, pigeons did not suffer switch costs. As in Section 3.1, pigeons demonstrated no decrease in performance on task-switch trials (cue-repeat: 11.1%, task-repeat: 11.9%, task-switch: 11.9%). 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, congruency effects or switch costs across sessions.

As in Section 3.1, the accuracy data were examined 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 are 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 than under a model including Trial Type as a second factor.

Stimulus-repetition effects are illustrated in Figure 3.2.2. There was a highly significant interaction between the two factors Stimulus Repetition and Trial Type, $F(2,26)=13.6$, $p<.001$, $\eta_p^2 =.51$, but no significant main effect of either factor, both $p>.26$. Pigeons showed very low error rates in cue-repeat trials in which the incongruent stimulus repeated (and the required response was also the same as in the previous trial), and elevated error rates in task-switch trials in which the incongruent stimulus repeated (and the required response changed from the previous trial). Conversely, when the stimulus on the previous trial shared no elements with the current stimulus (i.e., when the two different incongruent stimuli were shown on subsequent trials), error rates were very low when the task switched (and thus the required response was the same as in the previous trial), and increased when the task repeated (and thus the required response changed) in cue-repeat and task-repeat trials. This pattern of responding indicates that the pigeons had a bias to repeat the response that was correct in the previous trial.

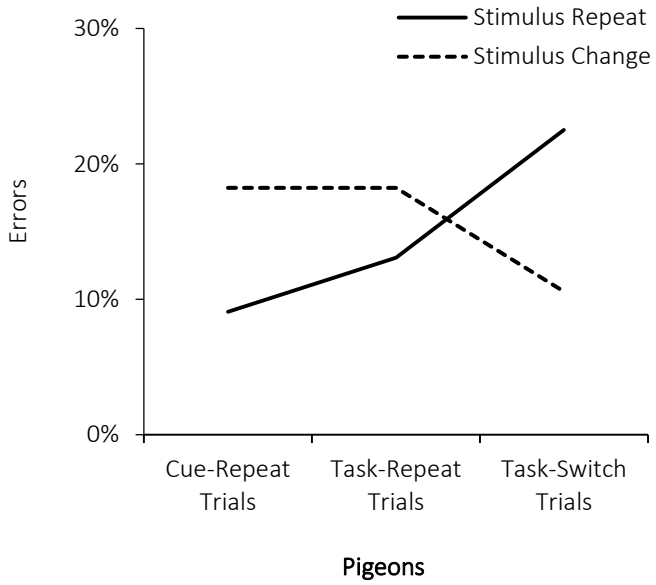

Figure 3.2.2. Pigeons' error rates in trials in which an incongruent stimulus is presented and is the same as in the immediately preceding trial (Stimulus Repeat) or follows a trial in which the other incongruent stimulus appeared (Stimulus Change), depending on Trial Type.
This figure appeared in Meier et al. (2016b).

Humans

Twenty-five of the 37 human participants completed the training phase outlined in Section 2.3 and proceeded to the task-switching test phase after a mean of 196 training trials (the other 12 participants did not reach the pass criterion during 600 trials of training and aborted the experiment). Twelve participants were able to verbalise the rules for both tasks (orientation and spatial frequency) at the end of the experiment and it was assumed that they had relied on the rules to solve the paradigm (the Rules-Aware group). Eleven participants claimed that their responses had not been governed by the application of any specific rules (the Rules-Ignorant group). The remaining two participants reported having discovered one of the two rules or having made up their own solution strategies. Their data were not included in any further analyses.

Overall error rates were significantly lower for the Rules-Aware group (14.5%, SD=8.0) than the Rules-Ignorant group (34.3%, SD=5.7), $t(21)=6.80$, $p<.001$, $\eta_p^2=.69$. These error rates were significantly lower than expected by chance for

both groups, Rules-Ignorant: $t(10)=9.13$, $p<.001$, $\eta_p^2=.89$; Rules-Aware: $t(11)=15.47$, $p<.001$, $\eta_p^2=.96$.

The effect of the factor Trial Type was clearly present in both human groups. Bonferroni post-hoc comparisons revealed a considerable increase in error rates in both human groups in response to task-switch trials compared to task-repeat trials (Rules-Aware: 22.6% vs. 15.3%, $p=.004$; Rules-Ignorant: 44.1% vs. 34.7%, $p<.001$), and for Rules-Aware participants also compared to cue-repeat trials (22.6% vs. 14.8%, $p=.004$; Rules-Ignorant: 44.1% vs. 35.8%, $p=.086$). Cue-repeat and task-repeat trials yielded comparable performance rates ($p=1.0$ for both groups), which somewhat contradicts previous findings in the literature (e.g., Logan & Bundesen, 2003; Mayr & Kliegl, 2003; Logan & Bundesen, 2004; Schneider & Logan, 2005; Altmann, 2006; Monsell & Mizon, 2006), though admittedly the procedures used here were rather different to those of standard task-switching experiments.

Stimulus Congruency strongly influenced performance, as both human groups showed increased error rates when an incongruent stimulus was presented compared to when a congruent stimulus was shown (Rules-Aware: 24.2% vs. 10.9%; Rules-Ignorant: 50.9% vs. 25.4%). The factors Trial Type and Stimulus Congruency interacted significantly in both human groups; that is, switch costs were present almost exclusively when a response had to be made to an incongruent stimulus, difference between task-switch and task-repeat (cue-repeat) trials: Rules-Aware: 14.1%, $p<.001$ (13.8%, $p=.006$); Rules-Ignorant: 22.6%, $p<.001$ (21.7%, $p=.006$), but were absent when subjects responded to a congruent stimulus, difference between task-switch and task-repeat (cue-repeat) trials: Rules-Aware: 0.5%, $p=1.0$ (1.8%, $p=1.0$); Rules-Ignorant: -3.7%, $p=.691$ (-5.1%, $p=.070$).

The sequence of blocks had a reliable effect on error rates for the Rules-Aware group only. Those participants learned to make significantly fewer mistakes as the experiment progressed, while participants belonging to the Rules-Ignorant group did not show any significant changes in their error rates over time (Group-by-Block interaction: $F(19,399)=3.16$, $p<.001$, $\eta_p^2=.13$). In Rules-Aware participants, the congruency effect decreased significantly over the course of

the experiment, while it remained similar across time for Rules-Ignorant humans (Group-by-Block-by-Congruency interaction: $F(19,399)=1.70$, $p=.034$, $\eta_p^2=.08$). The magnitude of switch costs remained unchanged over time in both groups.

Stimulus-repetition effects are shown in Figure 3.2.3. Regardless of whether or not humans were aware of task rules, they consistently showed a main effect of Trial Type (Rules-Ignorant group: $F(2,20)=41.6$, $p<.001$, $\eta_p^2=.81$; Rules-Aware: $F(2,22)=25.8$, $p<.001$, $\eta_p^2=.70$). In both groups, this difference was due to increased error rates in response to task-switch trials (in the case of Rules-Ignorant participants to above the 50% chance level) compared to cue-repeat and task-repeat trials (Bonferroni post-hoc comparisons: all $p\leq.001$). For Rules-Aware participants, performance was similar in cue-repeat and task-repeat trials, $p=.35$, while Rules-Ignorant participants made significantly fewer errors in cue-repeat trials, $p=.008$. Although the main effect on performance of the factor Stimulus Repeat only reached significance for Rules-Ignorant participants, $F(1,10)=5.35$, $p=.043$, $\eta_p^2=.35$ (Rules-Aware group: $F(1,11)=0.03$, $p=.88$; Group-by-Stimulus-Repeat interaction: $F(1,21)=1.55$, $p=.23$), both groups were influenced by a significant Stimulus-Repeat-by-Trial-Type interaction, Rules-Ignorant group: $F(2,20)=14.81$, $p\leq.001$, $\eta_p^2=.60$; Rules-Aware: $F(2,22)=10.15$, $p=.001$, $\eta_p^2=.48$. This interaction was visible in higher error rates in task-switch trials in which an incongruent stimulus was repeated compared to task-switch trials in which a change in stimulus occurred, whereas stimulus repeats yielded lower error rates than stimulus changes in both cue-repeat and task-repeat trials.

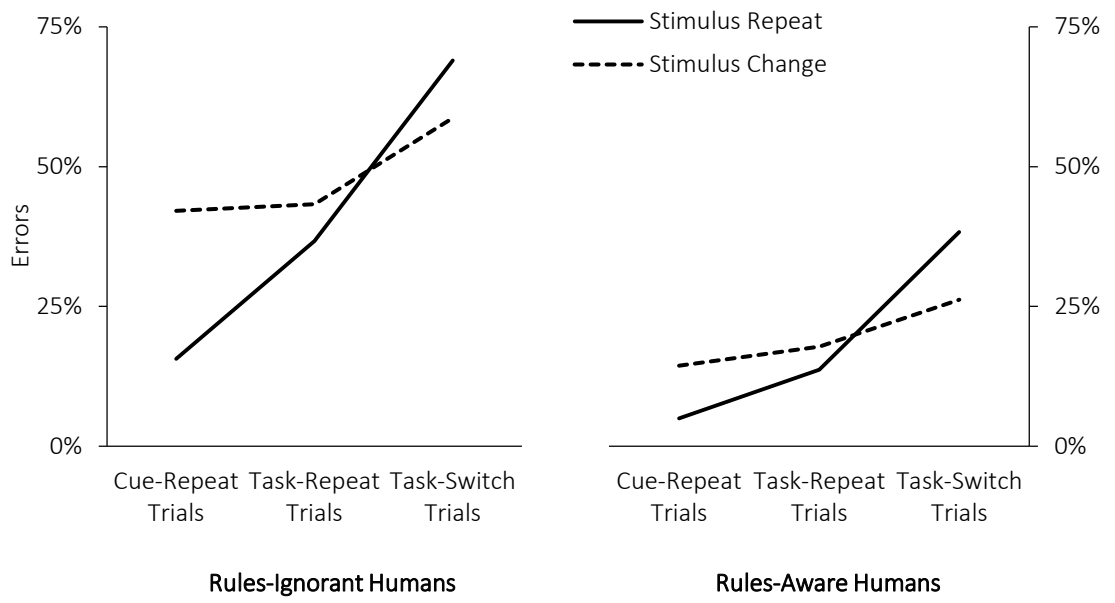

Figure 3.2.3. Rules-Ignorant and Rules-Aware participants' error rates in trials in which an incongruent stimulus was presented and was the same as in the immediately preceding trial (Stimulus Repeat) or follows a trial in which the other incongruent stimulus appeared (Stimulus Change), depending on Trial Type.

Discussion

In this chapter, the paradigm of Section 3.1 was extended to include cue-repeat trials. Even though cue repetitions on task-repeat trials normally contribute considerably to switch costs in both response times and error rates (e.g., Altmann, 2006; Forrest, 2012; Mayr & Kliegl, 2003; Monsell & Mizon, 2006), this was not the case in this experiment: overall switch costs in human participants did not differ in size when subtracting error rates in task-repeat trials or cue-repeat trials from error rates in task-switch trials (and the difference was in fact numerically smaller for cue-repeat trials). This result was not entirely unforeseeable; for example, Altmann (2006) reported that, although cue-repetitions largely increased switch costs in response times, such an increase was only observed in error rates if the cue-stimulus interval was rather long, but was absent when the cue-stimulus interval was short. Mayr (2006) even reported reduced switch costs in error rates due to cue-repetitions, whereas they increased switch costs in the participants' response times.

Just as in Section 3.1, pigeons did not show any switch costs, and Bayesian analyses confirmed that it is highly unlikely that switch costs were present but undetected. Instead, pigeons showed a reliable pattern of responding more accurately on Cue-Repeat/Stimulus-Repeat, Task-Repeat/Stimulus-Repeat and Task-Switch/Stimulus-Change trials, and of making 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 in the previous trial; conversely, they benefitted when a repetition of the previously emitted response was required. 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. This finding contradicts the hypothesis that pigeons might avoid approaching the same stimulus-location combination in subsequent trials, and instead leads to suggest that pigeons might in fact have a tendency to repeat a rewarded response (cf. Stubbs, Fetterman, & Dreyfus, 1987; Schneider & Davison, 2005; Schneider, 2008; Morgan, 1974, had earlier shown a similar result with rats).

In the light of such a strong response-repetition effect, 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 (Lea, 2016), an 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. Indeed, the spatial location of the reinforced stimulus in the previous trial might become as strong a determinant of behaviour as other elements like the cue colour, or the spatial frequency or orientation of the stimulus (Iversen, Sidman, & Carrigan, 1986; Lipkens, Kop, & Matthijs, 1988; Lionello & Urcuioli, 1998; Sidman, 2009; Campos, Debert, da Silva Barros, & McIlvane, 2011). 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.
Moreover, this explanation gives insight into whether the pigeons could develop the level of cue equivalence that Forrest (2012) hypothesised and modelled for her associatively learning participants. Forrest's explanation relies on the assumption that task cues are encoded as one of several separable components of a trial - as are the stimuli, or even the separate stimulus dimensions. But if, to pigeons, even the precise location in which a stimulus is presented is a discriminative part of that stimulus, then pigeons may also perceive every combination of a 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 from the stimuli - to the pigeon, cues and stimuli may be indivisible elements of the same image.

Although switch costs had the greatest impact on the performance of humans, both Rules-Ignorant and Rules-Aware participants on average made fewer errors on trials that required that the previously correct response was repeated compared to the same trial type but with a change in the correct response (i.e., Cue-Repeat/Stimulus-Repeat trials led to better performance than Cue-Repeat/Stimulus-Change trials, Task-Repeat/Stimulus-Repeat trials led to better performance than Task-Repeat/Stimulus-Change trials and Task-Switch/Stimulus-Change trials led to better performance than Task-Switch/Stimulus-Repeat trials); that is, they benefitted from a response repetition on both task-repeat and task-switch trials. While a response-repetition benefit on task-repeat trials is reliably observed in human task-switching, repeating the same response as before on a task-switch trial usually imposes a cost to accuracy or speed (i.e., Rogers & Monsell, 1995; Kleinsorge, 1999; Schuch & Koch, 2004; Hübner & Druey, 2006). One might wonder as to why this established effect was not replicated in this experiment, at least by the

Rules-Aware participants, but this issue will be returned to later - for the moment, the results of the Rules-Ignorant participants are of greater interest.

On the one hand, like Rules-Aware humans, the Rules-Ignorant participants exhibited pronounced switch costs in response to incongruent stimuli - but, unlike Rules-Aware participants, their error rates on task-switch trials were much higher than expected by chance, implying that Rules-Ignorant participants systematically chose the wrong response in these trials. On the other hand, Rules-Ignorant participants showed a huge performance benefit when both the task cue and the stimulus were repeated in two consecutive trials compared to repeat trials in which either the cue or the stimulus (or both) changed, which makes it possible that their behaviour may have been partly guided by associative processes. These findings confirm that, although they had not learned the cue-stimulus-response contingencies as well as the pigeons had, it is unlikely that Rules-Ignorant participants based their responses on the same task rules (albeit without being able to verbalise them) as those used by Rules-Aware subjects, to whom it was irrelevant for performance whether the same or the other task cue was shown on a task-repeat trial.

A likely explanation for the observed behaviour of Rules-Ignorant participants is that responses were based on the perceived changes in the visual aspects of the stimulus seen on the current trial compared to the stimulus seen on the previous trial. More precisely, if the present stimulus shared many visual features with the stimulus seen on the preceding trial, the response that was previously labelled as correct was repeated. The more the visual features of the stimulus changed from one trial to the next, the more likely the response opposite to the one that was correct on the previous trial was to be chosen. A strategy of responding that is based on tracing the similarity of stimuli from one trial to the next would lead to the wrong response in Task-Switch/Stimulus-Repeat trials (which afforded a response change but would, according to the afore-mentioned heuristic, be answered with a response repeat) and Task-Switch/Stimulus-Change trials (which afforded a response repeat but would, if following this heuristic, be answered with a response change), whilst producing the correct response in all other trials (cf. Kleinsorge, 1999; Ruthruff, Remington & Johnston, 2001). As a consequence, Rules-Ignorant humans would express

persistent switch costs, even if participants were unaware of the existence of different tasks.

Apart from the possibility that Rules-Ignorant participants were guided by a heuristic sensitive to the particular sequence of trials, there are other explanations for the observed results, and it is very well plausible that the pattern found at the group level is the result of a multitude of strategies. For example, many participants reported that they suspected that either the orientation of the pattern or its spatial frequency determined the correct response at times, but that it was impossible to predict when a certain dimension was relevant, leading these participants to, as they claimed, respond "randomly" or change their strategy frequently throughout the experiment (which ultimately led to their classification as "Rules-Ignorant"). Almost all Rules-Ignorant participants reported that the colour of the stimulus seemed irrelevant to them - a good indication that, even though they might have noticed that orientation and spatial frequency determined which response was required, Rules-Ignorant participants were unable to infer when a switch in the determining dimension would occur. A clue as to why participants might have considered the relevance of the stimulus dimensions but not the cues might lie in the training that was administered prior to the task-switching phase: during training, participants had a more direct exposure to the two task sets, but the cues were irrelevant at that stage. As long as the participants focussed on the relevant stimulus dimension, performance during training would be adequate and possibly discourage any analysis of the task cues. It could even be argued that the subjects would not need to be aware of the precise response requirements for each dimensional value (e.g., horizontal patterns require a left response and vertical ones a right response): as long as they are focussing on the correct stimulus dimensions, participants would be able to correctly adjust their responses according to the experienced stimulus-response combination of the previous trial.

Regardless of what precisely caused Rules-Ignorant participants to systematically choose the wrong response on task-switch trials, it is apparent that the presence of switch costs in their performance was not the result of a mental task-set reconfiguration on task-switch trials. Nonetheless, the sensitivity

to a switch in "tasks" could imply that the behaviour of these participants was guided by a rule rather than by the experienced cue-stimulus-response contingencies. Rules-Ignorant participants might have based their responses on a self-generated heuristic, even when this strategy led to suboptimal performance. This possibility is explored in the experiment reported in Section 3.3, in which I investigated the precise nature of the solving strategy that Rules-Ignorant participants developed to solve the task-switching paradigm.

3.3 Why do Humans Show Switch Costs?

In Section 3.2, I investigated the lack of switch costs in pigeons despite their presence in humans and concluded that Rules-Ignorant participants likely did not depend on the same associative strategies to solve the task-switching paradigm as pigeons. This section addresses potential causes for the expression of switch costs by Rules-Ignorant humans.

As stated in Section 3.2, it is possible that the performance of Rules-Ignorant participants was not determined by the experienced contingencies of the paradigm: it might be that, due to a failure to infer a rule that would predict the correct responses sufficiently well, the Rules-Ignorant participants continued to test different hypotheses as to what the underlying task rule might be, instead of responding to the experienced stimulus-response contingencies. The rule-based learning system of humans might generally be so pre-potent that participants find it difficult to overcome it. Striking evidence for this has been reported by Levine (Levine, 1971; Fingerman & Levine, 1974), who observed that humans were unable to detect even a very simple classification rule after experiencing a number of more complex rules, a phenomenon Levine referred to as "non-learning". This trait might even be unique to humans compared to other primate species. Even the most optimistic view of the capabilities of rhesus macaques does not grant monkeys the full capacity of executive control available to humans (Stoet & Snyder, 2003a, 2003b; Smith et al., 2010; Caselli & Chelazzi, 2011; Smith et al., 2012). Thus, some of the task-switching paradigms used in primate studies could have been too complex to be solvable by means of their limited hypothesis-testing learning strategy, allowing the (in their case) more successful process of associative learning to dominate behaviour. The cognitive limitations of macaques' rule-based approach might in fact enable macaques to utilise the two strategies very flexibly, whereas humans might have to overcome a predisposed tendency to rely on their highly optimised rule-based approach.

The behaviour of Rules-Ignorant participants might be explained by a simple heuristic: "repeat the response that was correct on the previous trial if the current stimulus (possibly ignoring the cue) looks similar to the previous one,

and change the response if the current stimulus looks different from the previous one". As illustrated in Table 3.3.1, this heuristic would apply to all congruent-to-congruent-stimulus transitions (25% of all trials) and to incongruent-to-incongruent-stimulus transitions on cue- and task-repeat trials (16.7% of all trials), and it would lead to chance performance in congruent-to-incongruent-stimulus and incongruent-to-congruent-stimulus transitions (resulting in a correct response on approximately 25% of all trials). Thus, even if participants memorised the correct response to congruent stimuli, when considering only incongruent stimuli, applying the heuristic to trials in which an ambiguous incongruent stimulus was presented would generate an average accuracy of approximately 67%. More importantly, it would lead to large task-switch costs despite an absence of separate task sets.

Alternatively, Rules-Ignorant participants, though stating that they had not noticed any reliable connections between a stimulus dimension and the correct response, might nonetheless have been aware of the predictive nature of the two separate stimulus dimensions, but failed to use the information provided by the task cues to deduce when a certain dimension would be relevant for categorisation, so that a switch in tasks would always occur unexpectedly. Without this information, both of the stimulus dimensions are unreliable predictors. However, each one predicts the correct response in 75% of all trials (i.e., in all congruent trials, which make up 50% of all trials, and in half of the incongruent trials, which make up another 25% of all trials). Additionally, since a task switch occurred on only a third of trials, the task sequence was biased towards task repetitions, so that focussing on the same stimulus dimension would be more successful than frequently changing ones focus from one to the other dimension. Some participants only inferred one of the two task rules (the data of those participants were previously discarded), which indicates that this success rate might be sufficient for participants to abandon the search for a further, possibly more effective, response strategy. It is remarkable that participants might have nonetheless detected that each stimulus dimension was relevant at times (in such a way as that they suspected that sometimes the spatial frequency and sometimes the orientation of a stimulus determined which response was correct), but were unable to utilise them optimally.

Table 3.3.1. Success of a sequential heuristic (see text for details) for each transition from a certain cue-stimulus combination in trial N-1 to a certain combination in trial N. *Key*: cues: a/A - cues indicating one task (red/green); b/B - cues indicating the competing task (blue/yellow); congruent stimuli (requiring the same response in the two tasks): H/L - Horizontal Orientation/Low Spatial Frequency; V/H - Vertical Orientation/High Spatial Frequency; incongruent stimuli (requiring a different response in the two tasks): V/L - Vertical Orientation/Low Spatial Frequency; H/H - Horizontal Orientation/High Spatial Frequency; R1/R2 - the two required responses (left/right); ✓ - heuristic would result in correct responding; X - heuristic would result in wrong responding; O - heuristic would result in 50% accuracy.

			Trial N-1															
Cue			a	A	a	A	b	B	b	B	a	A	a	A	b	B	b	B
	Stimulus		H/L	H/L	V/H	V/H	H/L	H/L	V/H	V/H	V/L	V/L	H/H	H/H	V/L	V/L	H/H	H/H
		Correct Response	R1	R1	R2	R2	R1	R1	R2	R2	R1	R1	R2	R2	R2	R2	R1	R1
Trial N																		
a	H/L	R1	✓	✓	✓	✓	✓	✓	✓	✓	O	O	O	O	O	O	O	O
A	H/L	R1	✓	✓	✓	✓	✓	✓	✓	✓	O	O	O	O	O	O	O	O
a	V/H	R2	✓	✓	✓	✓	✓	✓	✓	✓	O	O	O	O	O	O	O	O
A	V/H	R2	✓	✓	✓	✓	✓	✓	✓	✓	O	O	O	O	O	O	O	O
b	H/L	R1	✓	✓	✓	✓	✓	✓	✓	✓	O	O	O	O	O	O	O	O
B	H/L	R1	✓	✓	✓	✓	✓	✓	✓	✓	O	O	O	O	O	O	O	O
b	V/H	R2	✓	✓	✓	✓	✓	✓	✓	✓	O	O	O	O	O	O	O	O
B	V/H	R2	✓	✓	✓	✓	✓	✓	✓	✓	O	O	O	O	O	O	O	O
a	V/L	R2	O	O	O	O	O	O	O	O	✓	✓	✓	✓	X	X	X	X
A	V/L	R2	O	O	O	O	O	O	O	O	✓	✓	✓	✓	X	X	X	X
a	H/H	R1	O	O	O	O	O	O	O	O	✓	✓	✓	✓	X	X	X	X
A	H/H	R1	O	O	O	O	O	O	O	O	✓	✓	✓	✓	X	X	X	X
b	V/L	R1	O	O	O	O	O	O	O	O	X	X	X	X	✓	✓	✓	✓
B	V/L	R1	O	O	O	O	O	O	O	O	X	X	X	X	✓	✓	✓	✓
b	H/H	R2	O	O	O	O	O	O	O	O	X	X	X	X	✓	✓	✓	✓
B	H/H	R2	O	O	O	O	O	O	O	O	X	X	X	X	✓	✓	✓	✓

A clue as to how participants accomplished this might be found in the training administered ahead of the task-switching phase. Before participants engaged in the task-switching paradigm, they were exposed to both tasks separately for at least 48 trials on each. Although the training did not influence the magnitude of task-switching effects in the experiment reported in Section 2.1, it might have increased attention to both task dimensions prior to the test phase. But since the task cues that were simultaneously presented with each task during training

did not hold any information at that point, they might not have been processed, and might have been too ambiguous during test to be considered informative. Some evidence for this possibility might be found in the results of the experiment reported in Section 2.2, in which only one task had to be learned: only those participants who inferred the discrimination rule of the task performed at a good level of accuracy. This leads to the suggestion that the participants in the task-switching experiments in this chapter might also have inferred the relevant dimension of at least the first discrimination task they encountered (the training of each task was methodologically identical to the paradigm in Section 2.2), which enabled them to complete the training of that task at high accuracy. Given that none of the participants explicitly reported the contingencies of the first task, it is plausible that the introduction of the second task (requiring attention to the so far ignored stimulus dimension) in subsequent training blocks led participants to abandon the initially inferred task rule and searched for a more applicable rule. Perhaps, after realising that both dimensions determined the correct response at different times, the participants started applying the "choose the opposite response" heuristic to a single stimulus dimension at the time - and when the comparison failed, they changed the focal dimension in the subsequent trial.

In an attempt to pinpoint the causes of switch costs in the performance of Rules-Ignorant humans, I considered the two potential causes for increased error rates in task-switch trials mentioned above in this section.

Firstly, to investigate the influence of the initial training phase on rule deduction, I included a no-training group that did not receive any task-specific training before the task-switching phase. Separate exposure to the two relevant tasks prior to the task-switching test might facilitate awareness of the tasks but not the task cues, enabling participants to flexibly apply both rules – although the switch occurs unpredictably. Without an initial training phase, the opportunities to infer the task rules are reduced, which might eliminate switch costs that are caused by an unexpected failure of the previously relevant rule.

Secondly, to explore the possibility that participants base their responses on the visual similarity of the stimuli of two subsequent trials, the sequence of trials was controlled in such a way that performance would be at chance level if participants were guided by a heuristic like "choose the opposite response to

the one that was previously correct if the current stimulus looks different from the previous one". If switch costs in the performance of Rules-Ignorant participants are the consequence of comparing the visual similarity of two consecutive stimuli, controlling the sequence in which stimuli are presented would lead to performance at 50%, and might discourage the use of this response strategy.

If switch costs are caused by trial-to-trial comparisons, administering an initial training phase should have no consequences on the behaviour of Rules-Ignorant participants. Likewise, if training leads to increased task awareness, the specifics of the trial-to-trial sequence should not influence performance (nor lead to a change in the strategy developed during the training phase).

Methods

Subjects

A total of 106 Psychology undergraduate students completed this experiment.

Procedure

The apparatus and stimulus material is described in Chapter 2. 56 participants went through the training phase outlined in Section 2.3 before entering the task-switching test phase (Training condition); the other 50 participants received no training but proceeded straight to the test phase (No-Training condition).

For 27 participants in the Training and 25 participants in the No-Training condition, the test phase was the same as described in Section 3.2 (henceforth called the Standard design). The test phase was comprised of 22 blocks of 24 trials each, 528 trials in total.

The remaining participants experienced what will henceforth be referred to as the Sequence design. The only difference to the Standard design was that in this condition the sequence of trials was generated in such a way as to produce performance at chance level if responses are based on a strategy following the heuristic "choose the opposite response to the one that was correct in the previous trial when the current stimulus (ignoring the cue) changes from one trial to the next". This heuristic would lead to an average error rate of approximately 33%, mainly because it would produce a correct response in all trials with congruent-to-congruent-stimulus transitions. Removing transitions of

this type would produce an average error rate nearer to 50% if that heuristic was followed consistently. Thus, unlike in the Standard design, in the Sequence design, a congruent stimulus was never repeated on two subsequent trials, and was never followed by the other congruent stimulus. However, an incongruent stimulus could repeat (this happened on 12.5% of all trials) or could be followed by the other incongruent stimulus (on another 12.5% of trials) on the subsequent trial. Details of the exact number of trial-to-trial transitions can be found in Table 3.3.2.

Table 3.3.2. *Sequence design:* Number of transitions from a certain cue-stimulus combination in trial N-1 to a certain combination in trial N. There were a total of 512 transitions. *Key*: cues: a/A - cues indicating one task (red/green); b/B - cues indicating the competing task (blue/yellow); congruent stimuli (requiring the same response in the two tasks): H/L - Horizontal Orientation/Low Spatial Frequency; V/H - Vertical Orientation/High Spatial Frequency; incongruent stimuli (requiring a different response in the two tasks): V/L - Vertical Orientation/Low Spatial Frequency; H/H - Horizontal Orientation/High Spatial Frequency; R1/R2 - the two required responses (left/right).

			Trial N-1															
Cue			a	A	a	A	b	B	b	B	a	A	a	A	b	B	b	B
Stimulus			H/L	H/L	V/H	V/H	H/L	H/L	V/H	V/H	V/L	V/L	H/H	H/H	V/L	V/L	H/H	H/H
		Correct Response	R1	R1	R2	R2	R1	R1	R2	R2	R1	R1	R2	R2	R2	R2	R1	R1
Trial N																		
a	H/L	R1	0	0	0	0	0	0	0	0	4	4	4	4	2	2	2	2
A	H/L	R1	0	0	0	0	0	0	0	0	4	4	4	4	2	2	2	2
a	V/H	R2	0	0	0	0	0	0	0	0	4	4	4	4	2	2	2	2
A	V/H	R2	0	0	0	0	0	0	0	0	4	4	4	4	2	2	2	2
b	H/L	R1	0	0	0	0	0	0	0	0	2	2	2	2	4	4	4	4
B	H/L	R1	0	0	0	0	0	0	0	0	2	2	2	2	4	4	4	4
b	V/H	R2	0	0	0	0	0	0	0	0	2	2	2	2	4	4	4	4
B	V/H	R2	0	0	0	0	0	0	0	0	2	2	2	2	4	4	4	4
a	V/L	R2	4	4	4	4	2	2	2	2	2	2	2	2	2	2	2	2
A	V/L	R2	4	4	4	4	2	2	2	2	2	2	2	2	2	2	2	2
a	H/H	R1	4	4	4	4	2	2	2	2	2	2	2	2	2	2	2	2
A	H/H	R1	4	4	4	4	2	2	2	2	2	2	2	2	2	2	2	2
b	V/L	R1	2	2	2	2	4	4	4	4	2	2	2	2	2	2	2	2
B	V/L	R1	2	2	2	2	4	4	4	4	2	2	2	2	2	2	2	2
b	H/H	R2	2	2	2	2	4	4	4	4	2	2	2	2	2	2	2	2
B	H/H	R2	2	2	2	2	4	4	4	4	2	2	2	2	2	2	2	2

A third of the transitions between congruent and incongruent stimuli, and half of the transitions from one incongruent stimulus to the other incongruent stimulus, were switch trials; half of the remaining trials were task-repeat trials with changing cues, and the other half were cue-repeat trials.

The overall probability of a switch trial was 37.5%. As a result of these adjustments, following the sequential heuristic would produce a correct response in 50% of incongruent-to-incongruent stimulus transitions (12.5% of all trials), and, as before, also in approximately 50% of the transitions from a congruent to an incongruent stimulus and from an incongruent to a congruent stimulus. Participants might detect that congruent stimuli always afford the same response and thus only apply this heuristic to trials with an incongruent stimulus; however, doing so should yield an average accuracy of 50% in those trials.

Participants in the Sequence group completed 16 blocks of 32 trials each. To ensure that participants experienced all possible trial-to-trial transitions, the first trial of each block was a repeat of the last trial in the previous block, but performance in that trial was not included in any further analyses. This procedure resulted in 512 analysable trial-to-trial transitions per participant.

After completing the task-switching phase, all participants filled out an on-screen questionnaire (Appendix A3) to assess their ability to describe the rules that defined a correct response and accordingly classify them as Rules-Ignorant or Rules-Aware subjects. In addition to the open questions used in the questionnaire of the experiment reported in Section 3.2, participants were asked whether their solving strategy included memorising the correct response to the stimulus presented in the immediately preceding trial and basing their current answer on that information. Following the questionnaire, participants were shown a sample trial showing an incongruent stimulus-cue combination and its correct response. They were then presented with the opposite incongruent stimulus combined with a cue signalling the opposite task as the sample trial, and asked to indicate and explain the response they would give (left or right) to this cue-stimulus combination.

Results

Fifty-one participants who were part of the Training condition completed the training and proceeded to the task-switching test phase after a mean of 144 training trials (two participants in the Training/Standard group and three participants in the Training/Sequence group did not reach the pass criterion of the training in 600 training trials and aborted the experiment). Of those who completed the experiment, 16 participants given the Standard and 17 participants given the Sequence design were able to verbalise the rules for both tasks (orientation and spatial frequency) at the end of the experiment. It was assumed that they had relied on these rules to solve the paradigm (the Rules-Aware participants). Eight participants in the Standard and eight participants in the Sequence group claimed that their responses had not been governed by the application of any specific rules (the Rules-Ignorant participants). One participant in each the Sequence group and the Standard group reported having discovered one of the two rules or having made up their own solution strategies. Their data were not included in any further analyses.

A further fifty participants completed the task-switching paradigm without any prior training. Of these, 16 participants in the Standard and 12 participants in the Sequence group were classified as Rules-Aware participants, and five participants in the Standard and eight participants in the Sequence group were categorised as Rules-Ignorant participants. The data of the remaining four participants in the Standard and five participants in the Sequence group were excluded by the same criteria as stated above. In total, 61 participants were classified as Rules-Aware and 29 participants were labelled Rules-Ignorant. It is the latter group who is of particular interest in determining the effects of training and of the trial sequence on task-switching performance.

Table 3.3.3. Results of repeated-measure ANOVAs on error rates of Rules-Aware and Rules-Ignorant participants, using Training (Yes or No) and Design (Sequence or Standard) as between-subjects factors and Trial Type (Cue Repeat, Task Repeat or Task Switch) and Stimulus Congruency (Congruent or Incongruent) as within-subjects factors. Significant p values are highlighted in bold.

	Error Rates			
	F	df	p	η_p^2
Rules-Aware Participants (n=61)				
Training	8.33	1, 57	**.006**	.127
Sequence/Standard Design	0.02	1, 57	.898	<.001
Training * Design	1.51	1, 57	.224	.026
Trial Type	56.39	2, 114	**<.001**	.497
Trial Type * Training	1.50	2, 114	.229	.026
Trial Type * Design	1.26	2, 114	.289	.022
Trial Type * Training * Design	0.56	2, 114	.572	.010
Stimulus Congruency	58.25	1, 57	**<.001**	.505
Congruency * Training	1.85	1, 57	.179	.031
Congruency * Design	23.23	1, 57	**<.001**	.290
Congruency * Training * Design	0.017	1, 57	.897	<.001
Trial Type * Congruency	37.82	2, 114	**<.001**	.399
Trial Type * Congruency * Training	0.54	2, 114	.586	.009
Trial Type * Congruency * Design	2.18	2, 114	.118	.037
Trial Type * Congruency * Training * Design	0.72	2, 114	.491	.012
Rules-Ignorant Participants (n=29)				
Training	16.06	1, 25	**<.001**	.391
Sequence/Standard Design	0.11	1, 25	.749	.004
Training * Design	0.01	1, 25	.914	<.001
Trial Type	21.76	2, 50	**<.001**	.465
Trial Type * Training	1.39	2, 50	.259	.053
Trial Type * Design	.679	2, 50	.512	.026
Trial Type * Training * Design	0.08	2, 50	.927	.003
Stimulus Congruency	32.89	1, 25	**<.001**	.568
Congruency * Training	5.98	1, 25	**.022**	.193
Congruency * Design	2.613	1, 25	.119	.095
Congruency * Training * Design	1.09	1, 25	.307	.042
Trial Type * Congruency	14.66	2, 50	**<.001**	.370
Trial Type * Congruency * Training	4.33	2, 50	**.018**	.148
Trial Type * Congruency * Design	0.03	2, 50	.969	.001
Trial Type * Congruency * Training * Design	0.90	2, 50	.415	.035

The participants' rule use had a main effect on performance in that Rules-Aware participants showed lower error rates than Rules-Ignorant participants, $F(2,98)=121.93$, $p<.001$, $\eta_p^2=.71$. Rule use also significantly influenced the expression of the two task-switching effects of interest and their interaction, all $p<.001$. Therefore, all analyses were carried out separately for Rules-Aware and Rules-Ignorant participants. The same trial-exclusion criteria as reported in Section 3.1 were applied in this experiment. For each group, a repeated-measures ANOVA using Trial Type (Cue Repeat, Task Repeat or Task Switch) and Stimulus Congruency (Congruent or Incongruent) as within-subjects factors and Design (Standard or Sequence) and Training (Yes or No) as a between-subjects factor was conducted. Where applicable, significance levels were subjected to Huynh-Feldt correction. The results of these analyses are summarised in Table 3.3.3.

The following analyses included data from all task-switching blocks. However, those participants who had not received any training were still unfamiliar with the stimuli and procedure at the start of the experiment, and it was possible that this influenced the magnitude of task-switching effects. To allow for this possibility, the analyses were repeated excluding the first half of blocks; the task-switching effects reported below were present in both sets of analyses.

Rules-Aware participants in the Training/Sequence group performed better than those in the two No-Training groups, Design-by-Training interaction: $F(3,57)=2.91$, $p=.042$, $\eta_p^2=.13$ (Bonferroni post-hoc comparisons: Training/Sequence vs. No-Training groups: both $p\leq.046$; Training/Standard vs. No-Training/Sequence: $p=.059$; all other $p\geq.21$). Performance was better than expected by chance in all four experimental groups (overall errors in the Training/Sequence group: 8.8%, $t(16)=26.92$, adjusted $p.<008$, $\eta_p^2=.98$; Training/Standard: 10.6%, $t(15)=27.34$, adjusted $p<.008$, $\eta_p^2=.98$; No-Training/Sequence: 15.6%, $t(11)=15.02$, adjusted $p<.008$, $\eta_p^2=.96$; No-Training/Standard: 13.6%, $t(15)=20.31$, adjusted $p<.008$, $\eta_p^2=.97$).

Similarly, Rules-Ignorant participants who had received training performed better overall than those in the two No-Training groups, $F(3,25)=5.49$, $p=.005$, $\eta_p^2=.40$ (Bonferroni post-hoc comparisons: Training groups vs. No-Training groups: all $p\leq.036$; No-Training/Sequence vs. No-Training/Standard: $p=.84$; Training/Sequence vs. Training/Standard: $p=.52$). Performance was better than

chance in the two Training groups (Training/Sequence: 36.6%, $t(7)=6.31$, adjusted $p<.008$, $\eta_p^2=.85$; Training/Standard: 34.6%, $t(7)=7.37$, adjusted $p<.008$, $\eta_p^2=.89$), but not in the No-Training groups (No-Training/Sequence: 45.1%, $t(7)=3.07$, adjusted $p=.14$, $\eta_p^2=.57$; No-Training/Standard: 44.4%, $t(4)=1.41$, adjusted $p=1.0$, $\eta_p^2=.33$).

Overall, receiving training improved performance both for participants who had inferred the rules and those who had not.

As before, Rules-Aware participants expressed significant switch costs (errors in cue-repeat trials: 9.4%, task-repeat trials: 10.8%, task-switch trials: 15.2%) and congruency effects (errors in response to congruent stimuli: 9.3%, incongruent stimuli: 14.3%). The factors Trial Type and Stimulus Congruency interacted significantly; switch costs were increased when responding to incongruent stimuli compared to congruent stimuli: the difference in errors between task-repeat (cue-repeat) and task-switch trials, i.e., switch costs, for incongruent stimuli was 6.9%, $p<.001$ (9.0%, $p<.001$), for congruent stimuli it was 2.0%, $p=.011$ (2.6%, $p=.002$). Task-repeat and cue-repeat trials yielded comparable error rates when congruent stimuli were presented (difference: 0.6%, $p=.96$), but Rules-Aware participants made fewer errors when an incongruent stimulus was accompanied by a cue repeat rather than merely a task repeat (difference: 2.1%, $p=.007$).

Rules-Aware participants who had been trained on both tasks individually before the start of the task-switching test generally performed better than those who had not received any training (9.3% vs. 14.3% errors), but the training did not significantly affect the magnitude of switch costs or congruency effects. There was no significant main effect of the Design; however, the specific sequence of trials that participants experienced affected the size of the congruency effect: the effect was smaller in the Sequence group compared to the Standard group (1.8% vs. 8.1%). Bonferroni post-hoc comparisons revealed that the effect of stimulus congruency was not significantly different from zero in the No-Training/Sequence condition (mean congruency effect in errors: -0.9%, $p=.487$; all other comparisons: mean congruency effect above 2.8%, $p\leq.008$).

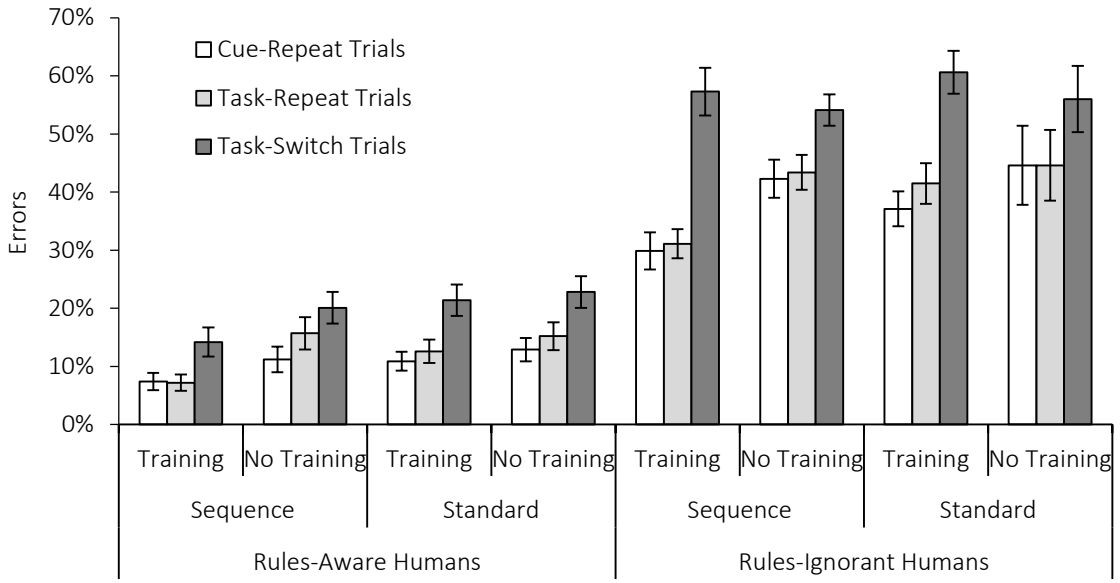

Figure 3.3.1. Error rates when responding to incongruent stimuli on Cue-Repeat, Task-Repeat and Task-Switch trials, for participants who were unaware of any underlying rules (Rules-Ignorant) and participants who inferred the rules (Rules-Aware) under the Sequence and Standard design and had received training or had not received training prior to the test. Error bars represent standard errors.

Rules-Ignorant participants expressed both switch costs (errors in cue-repeat trials: 35.4%, task-repeat trials: 35.7%, task-switch trials: 45.3%) and congruency effects (errors responding to congruent stimuli: 32.4%, incongruent stimuli: 45.2%) in their performance. However, switch costs were only present when responding to incongruent stimuli, but absent in responses to congruent stimuli; the difference in errors between task-repeat (cue-repeat) and task-switch trials for incongruent stimuli was 16.8%, $p<.001$ (18.5%, $p<.001$), for congruent stimuli it was 2.0%, $p=.763$ (2.2%, $p=1.0$). Task-repeat and cue-repeat trials yielded comparable error rates for both incongruent (difference: 1.7%, $p=1.0$) and congruent stimuli (difference: 1.0%, $p=1.0$). The interaction effect was further enhanced for participants who had received training (switch costs on trials with congruent vs. incongruent stimuli: -1.2% vs. 22.6%) compared to those who had not (5.7% vs. 11.1%).

For Rules-Ignorant participants, receiving training positively impacted performance (Training group: 33.8% errors overall, No-Training group: 43.8%). While added training did not affect the size of switch costs, those participants who had received training showed a numerically larger congruency effect (congruency effect for Training group: 18.2%, No-Training group: 7.3%).

Bonferroni post-hoc comparisons revealed that stimulus congruency significantly affected performance only in those groups that had received training (congruency effect in the Training/Sequence group: 12.3%, p=.010; Training/Standard group: 24.1%, p=.002); in the two No-Training groups, the effect was not significantly different from zero (No-Training/Sequence: 6.0%, p=.103; No-Training/Standard: 8.6%, p=.228). The Design did not have any effect on overall performance or the magnitude of switch costs or congruency effects for Rules-Ignorant participants.

Since switch costs were most pronounced in response to incongruent trials, Figure 3.3.1 illustrates the magnitude of errors in each trial type in response to incongruent stimuli only. Bonferroni post-hoc comparisons were used to assess whether these error rates differed significantly between trial types in each of the four experimental groups. For Rules-Aware participants, the difference between task-switch and task-repeat (cue-repeat) trials was significant in all four groups; Training/Standard: mean difference: 8.7%, p<.001 (10.5%, p<.001); No-Training/Standard: 7.6%, p<.001 (9.9%, p<.001); Training/Sequence: 7.0%, p=.002 (6.8%, p<.001); No-Training/Sequence: 4.3%, p=.035 (8.9%, p<.001). Performance of Rules-Ignorant participants when responding to incongruent stimuli on task-repeat (cue-repeat) trials was reliably different from their performance on task-switch trials in the two Training groups, but did not reach significance for either of the No-Training groups; Training/Sequence: 26.1%, p=.001 (27.4%, p=.001); Training/Standard: 19.1%, p=.014 (23.5%, p=.001); No-Training/Sequence: 10.7%, p=.14 (11.9%, p=.24); No-Training/Standard: 11.4%, p=1.0 (11.4%, p=1.0). The effects of the experimental condition on the expression of switch costs in incongruent trials differed significantly between Rules-Aware and Rules-Ignorant participants, Group-by-Condition-by-Trial-Type interaction: $F(6,164)=2.63$, p=.018, η_p^2=.09.

Rules-Ignorant participants reportedly applied different strategies to generate the most correct responses. Four strategies were extracted from the post-test questionnaire and defined as follows:

- followed the sequential heuristic described above;

- thought that sometimes the stimuli had to be classified based on their spatial frequency and sometimes based on their orientation, but that the relevant rule changed frequently;
- tried to memorise all stimuli and their correct responses;
- thought there was no pattern between any stimulus and the correct response.

There was no significant prevalence of any one specific solving strategy in any of the four experimental groups, $\chi^2(9)=15.6$, $p=.075$, although, as can be seen in Figure 3.3.2, none of the participants in the No-Training/Standard condition used the sequential heuristic. Solving strategies based on a rule of some sort ("followed sequential heuristic" and "thought that different rules applied which changed frequently" combined) were more common than chance would allow in the Training groups, while other approaches ("tried to memorise all stimuli" and "thought there was no pattern at all" combined) were more prevalent in the two No-Training groups, $\chi^2(3)=10.2$, $p=.017$.

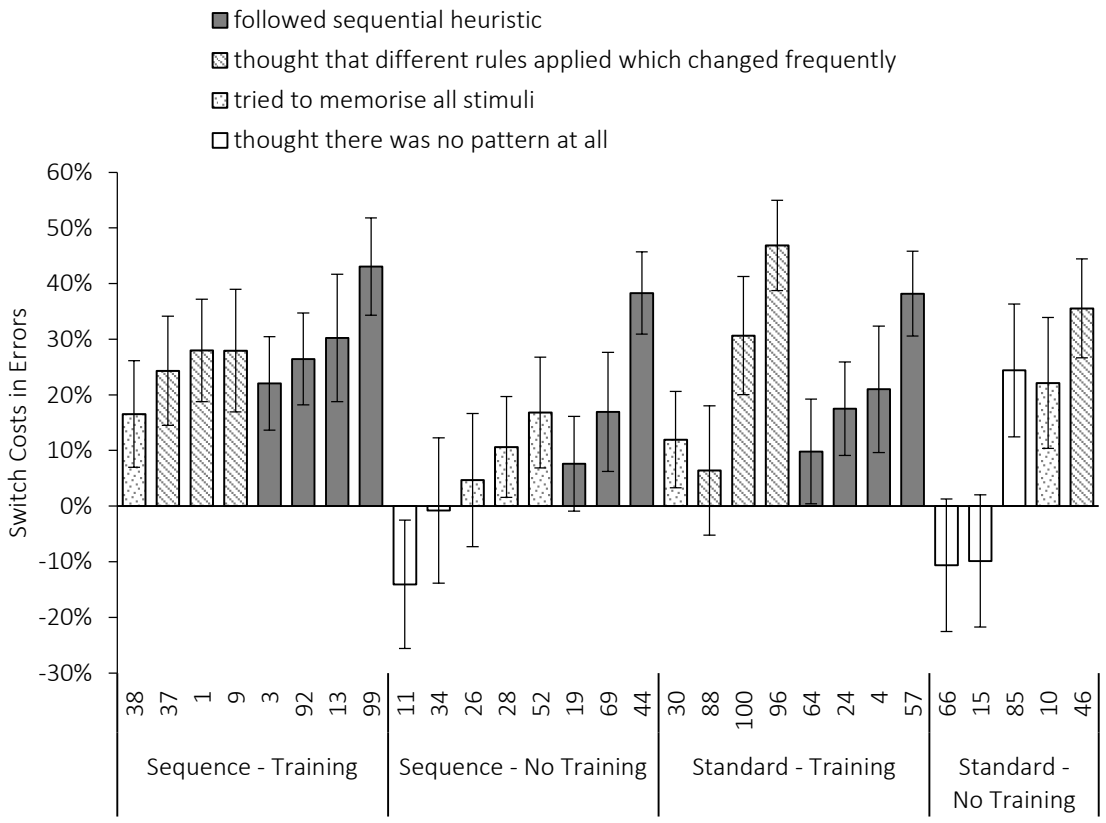

Figure 3.3.2. Switch costs in error rates responding to incongruent stimuli of Rules-Ignorant participants who reportedly had followed a sequential heuristic as described in the text or had developed a different solving strategy. Numbers on the x-axis are participant ID numbers. Error bars represent standard errors.

Overall error rates differed significantly between strategies, $F(3,28)=6.07$, $p=.003$, $\eta_p^2=.42$. Post-hoc tests showed that error rates were comparable (all $p \geq .61$) for those participants who had followed the sequential rule (mean error rate: 38.8%; comparison to 50% chance performance: $t(10)=5.59$, adjusted $p<.004$, $\eta_p^2=.76$; mean error rates for Sequence condition: 40.0%, $N=7$, Standard condition: 36.8%, $N=4$; difference between Sequence and Standard: $U=10.5$, $p=.53$), those who thought that the relevant rule changed frequently (mean error rate: 34.3%; comparison to 50% chance performance: $t(6)=8.82$, adjusted $p<.004$, $\eta_p^2=.93$; Sequence: 34.3%, $N=3$, Standard: 34.3%, $N=4$; difference between Sequence and Standard: $U=4.0$, $p=.63$) and those participants who had tried to memorise all stimuli (mean error rate: 40.0%; comparison to 50% chance performance: $t(5)=3.10$, adjusted $p=.11$, $\eta_p^2=.66$; Sequence: 44.3%, $N=4$, Standard: 31.5%, $N=2$; difference between Sequence and Standard: $U=0.0$, $p=.13$). Those participants who had assumed that there was no pattern (mean error rate: 49.2%; comparison to 50% chance performance: $t(4)=0.67$, adjusted $p=1.0$, $\eta_p^2=.10$; Sequence: 47.0%, $N=2$, Standard: 50.7%, $N=3$; difference between Sequence and Standard: $U=0.0$, $p=.20$) differed significantly in their overall error rate from the participants in the first two groups, both $p \leq .023$, but not from those participants who had tried to memorise the stimuli, $p=.11$.

Additionally, the error rate when responding to incongruent stimuli were of particular interest in determining whether the Sequence manipulation affected the participants' success when employing a sequential heuristic. Errors in trials with incongruent stimuli did not differ significantly between the Sequence ($M=44.4\%$, $N=7$; comparison to 50% chance performance: $t(6)=2.34$, adjusted $p=.116$) and Standard condition ($M=50.3\%$, $N=4$; comparison to 50% chance performance: $t(3)=0.09$, $p=.94$), $U=6.5$, $p=.16$.

The magnitude of congruency effects differed only marginally between the different solving strategies, $F(3,25)=2.73$, $p=.065$, $\eta_p^2=.25$, and the interaction between switch costs and stimulus congruency differed significantly between the four strategies, $F(6,50)=4.06$, $p=.002$, $\eta_p^2=.33$. Both effects were significant (in that performance was better in response to congruent than to incongruent stimuli, and switch costs were more pronounced when responding to incongruent stimuli) for those participants who had used the sequential

heuristic, both $p \leq .007$, and those who assumed that the rules changed frequently, both $p = .001$. Participants who had tried to memorise the stimulus-response contingencies were significantly affected by stimulus congruency, $p = .024$, but the magnitude of switch costs did not differ significantly between congruent and incongruent stimuli, $p = .087$. Participants who had found no pattern did not show a significant congruency effect, $p = .98$, nor did stimulus congruency affect the magnitude of switch costs, $p = .72$.

Figure 3.3.2 illustrates the magnitude of switch costs in response to incongruent trials for each Rules-Ignorant participant, and the specific strategy that that participant reportedly applied to generate the most correct responses. Switch costs among the four solving strategies differed in size, Kruskal-Wallis $\chi^2(3) = 11.5$, $p = .009$. Mann-Whitney post-hoc comparisons revealed that those participants who reportedly thought that there had not been any pattern linking any stimuli to a certain response showed lower switch costs than participants who had applied a sequential heuristic, $U = 15.2$, $N_1 = 5$, $N_2 = 11$, adjusted $p = .014$, and to some degree than participants who had assumed that the rules for responding changed frequently, $U = 11.2$, $N_1 = 5$, $N_2 = 7$, adjusted $p = .087$.

As in Section 3.2, the effect of stimulus repetition on performance was analysed via 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-subjects factors, and Solving Strategy (applied the two task rules, followed sequential heuristic, thought that different rules applied which changed frequently, tried to memorise all stimuli, thought there was no pattern) as between-subjects factor. Where applicable, significance levels were subjected to Huynh-Feldt correction.
As previously found, there was a main effect of Trial Type, $F(2,170) = 130.29$, $p < .001$, $\eta_p^2 = .61$, and of Stimulus Repeat, $F(1,85) = 38.31$, $p < .001$, $\eta_p^2 = .31$, and a significant Stimulus-Repeat-by-Trial-Type interaction, $F(2,170) = 12.08$, $p \leq .001$, $\eta_p^2 = .12$. The Solving Strategy of participants also had a main effect on performance, $F(4,85) = 66.94$, $p < .001$, $\eta_p^2 = .76$, and interacted significantly with the factors Trial Type, $F(8,170) = 27.54$, $p < .001$, $\eta_p^2 = .56$, and Stimulus Repeat, $F(4,85) = 5.42$, $p = .001$, $\eta_p^2 = .20$. The interaction effect between Trial Type and

Stimulus Repeat also differed significantly depending on the participants' strategy, $F(8,170)=2.87$, $p=.006$, $\eta_p^2=.12$; as shown in Figure 3.3.3, participants who had not detected a pattern were differently affected by that interaction than Rules-Aware participants, $p=.002$, and those who believed the rules changed frequently, $p=.035$. All other group comparisons were nonsignificant, all $p \geq .26$.
When considering the patterns for each solving strategy individually, those participants who had not noticed any pattern expressed no significant switch costs, $F(2,8)=0.18$, $p=.82$, but all other participants did, all $p \leq .009$. Further, Stimulus Repeat did not significantly affect the performance of those participants who believed that the rules for classification changed frequently, $F(1,6)=0.73$, $p=.42$; the effect was marginally significant for participants who had found no pattern, $F(1,4)=7.03$, $p=.057$, and for those who tried to memorise the contingencies, $F(1,5)=5.30$, $p=.07$, and significant for participants who were Rules-Aware, $F(1,60)=4.77$, $p=.033$, $\eta_p^2=.07$, and those who reported following the sequential heuristic, $F(1,10)=11.95$, $p=.006$, $\eta_p^2=.54$.

The interaction between Trial Type and Stimulus Repeat was not significant for any strategy, all $p \geq .27$. This result is in contrast to the strong interaction effect reported in Section 3.2, which suggested a universal benefit of response repetitions; the participants in the current experiment mainly experienced a benefit of response repetitions in task-repeat trials, but not in task-switch trials. Interestingly, despite the nonsignificant interaction effect, Figure 3.3.3 suggests that participants that had not noticed any pattern showed performance benefits of a task switch in trials in which the stimulus changed (that is, they performed better in task-switch trials than in task-repeat or cue-repeat trials). The other four groups (applied the two task rules, followed sequential heuristic, thought that different rules applied which changed frequently, tried to memorise all stimuli) experienced switch costs in trials in which the same incongruent stimulus was repeated and also in trials in which the incongruent stimulus changed.

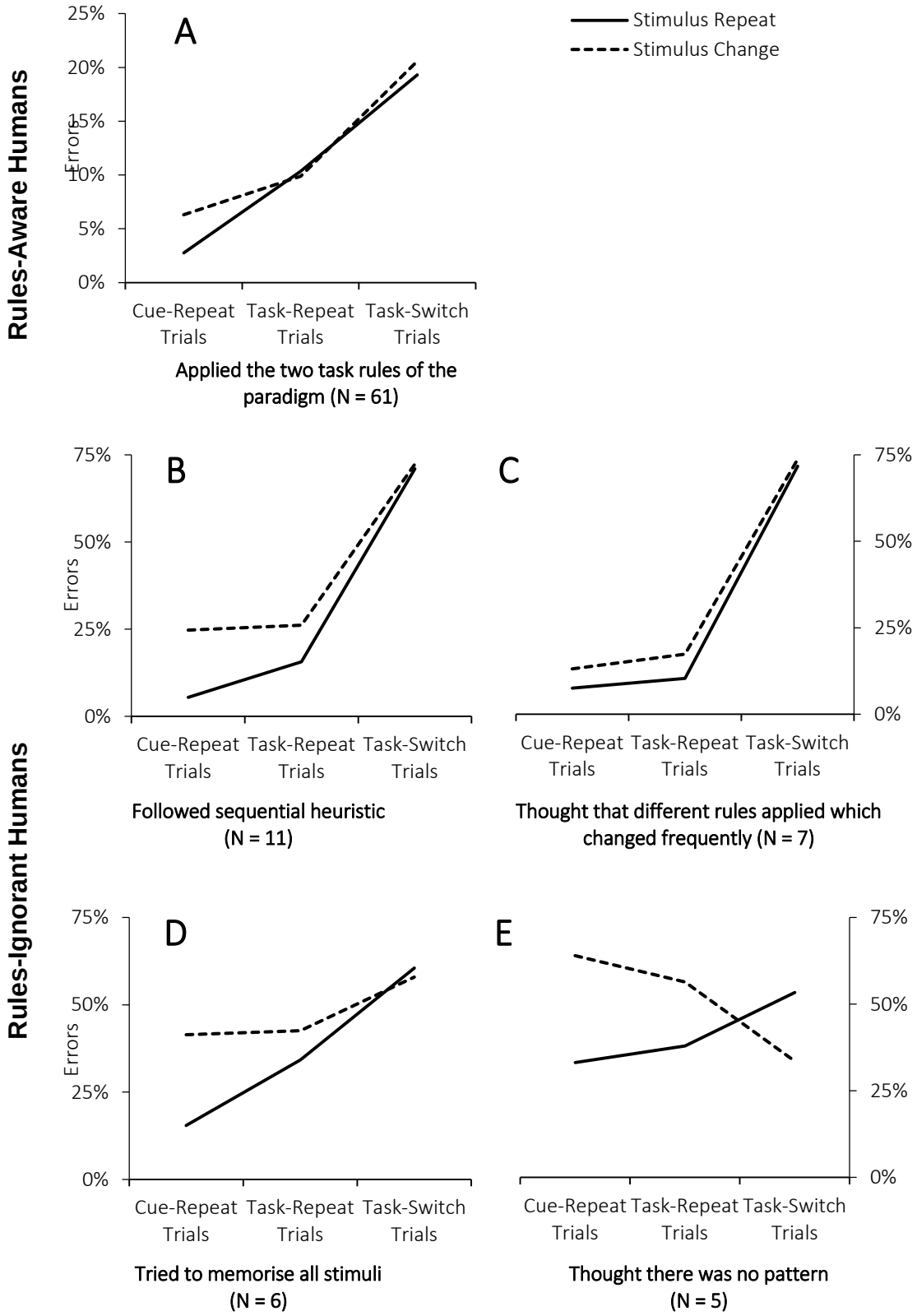

Figure 3.3.3. Error rates in trials in which an incongruent stimulus is presented and is the same as in the immediately preceding trial (Stimulus Repeat) or follows a trial in which the other incongruent stimulus appeared (Stimulus Change), depending on Trial Type and split by solving strategy. Note the different scale for Rules-Aware participants.

Discussion

In the experiment reported in this section, I investigated some potential causes for switch costs in the task-switching performance of Rules-Ignorant participants. First, Rules-Ignorant participants might have solved the test by comparing the stimulus of a given trial to the one that was presented in the previous trial, and then either repeated or changed the response that was required on that previous trial depending on the visual similarity of the two subsequent stimuli. Such a heuristic should be less successful under the Sequence design, and any Rules-Ignorant participants in that condition who employed this heuristic would be expected to perform at chance level, at least in response to trials with incongruent stimuli (irrespective of whether or not they had received any task training prior to the test phase). This was indeed the case: the participants in the Sequence condition (four of eight in the Training/Sequence group, three of eight in the No-Training/Sequence group) who mentioned in the post-test questionnaire and when explaining their response to the post-test probe that they would choose the opposite response to the one that was correct for the previous stimulus when the current stimulus looked very dissimilar performed at chance level in response to incongruent stimuli. However, so did the participants reporting this strategy under the Standard condition (four of eight in the Training/Standard group, none of five in the No-Training/Standard group; see Figure 3.3.2), indicating that a sequential heuristic did not successfully generate a correct response to incongruent stimuli in the Standard condition, either.

Furthermore, those eleven participants showed observable switch costs in their performance. But they were not alone: other Rules-Ignorant participants, who had used a different strategy to guess the correct response, also expressed reliable switch costs in their data. In fact, when faced with incongruent stimuli, all strategies that were based on any kind of systematic approach benefitted performance mainly in task-repeat trials, but impaired performance in task-switch trials (see Figure 3.3.3). Interestingly, the emergence of switch costs likely had different causes depending on the strategy that participants employed. The occurrence of switch costs in the Rules-Ignorant participants who employed a sequential heuristic is explained in detail in Section 3.2. As seen in Figure 3.3.3 Panel B, this strategy would benefit performance more in

task-repeat and cue-repeat trials in which the stimulus repeats than in task-repeat trials in which the stimulus changes, because the paradigm included not only stimulus changes from an incongruent stimulus to the other incongruent stimulus (which afforded a response change on task-repeat trials), but also changes from an incongruent to a congruent stimulus (and vice versa), which might afford a response repetition; thus, stimulus changes were somewhat more ambiguous than stimulus repetitions (which always afforded a response repetition on task-repeat trials).

For the seven participants who had suspected that several rules were at play that changed frequently, the explanation for why switch costs occurred is equally straightforward, if it can be assumed that the participants had a notion of what these changing rules were (for example, a participant might have noticed that line orientation or spatial frequency determined the correct response on some trials, but remained unable to predict when each feature was relevant). After probing which rule determined the correct response in one trial, this rule is applied to all following trials, until a trial occurs in which applying that rule no longer leads to the correct response. Consequently, trials in which the same rule as in the trial before applies (task-repeat and cue-repeat trials) will be answered correctly, whereas trials in which the rule changes from the one that was relevant in the previous trial (task-switch trials) will elicit a wrong response, leading to large switch costs. This strategy should be largely insensitive to stimulus repetitions, and the pattern shown in Figure 3.3.3 Panel C could give an indication that this might be the case (although the pattern does not differ significantly from those in Figure 3.3.3 Panels A, B and D).

Even the six participants who had attempted to memorise all presented cue-stimulus-response combinations experienced small but noticeable switch costs in their performance (see Figure 3.3.3 Panel D). The behaviour of these participants might be the most interesting; it is discussed in more detail in Section 3.4.

In fact, the only participants who were entirely unaffected by a task switch (and even somewhat showed a switch benefit) were the five participants who reported that they had not been able to find any pattern that determined a correct response but who instead thought that the required response to a given stimulus changed randomly (see Figure 3.3.3 Panel E). If these participants thought that everything was random, it can be assumed that they also

responded randomly - as evident by their overall performance being not better than chance. Interestingly, their pattern of behaviour is not dissimilar to the pattern of pigeons (shown in Figure 3.2.2). Like pigeons, the participants who had found no pattern showed improved performance in stimulus-repeat trials that were accompanied by a response repetition (i.e., cue-repeat and task-repeat trials), but performed worse when a stimulus repetition incurred a change in the required response (i.e., task-switch trials). That is, participants who saw no pattern greatly benefitted from a response repetition on all trials. However, unlike the highly accurate pigeons, their performance was well above 50%-chance level in trials in which the response changed, and the participants were not affected by stimulus congruency. The possible approach that might have resulted in this pattern of performance is considered further in Section 3.4.

All the other Rules-Ignorant participants benefitted from a response repetition only in task-repeat and cue-repeat trials. Rules-Aware humans even showed a small impairment to performance when the response repeated in task-switch trials (see Figure 3.3.3 Panel A). As mentioned in Section 3.2, this response-repetition effect (a benefit of response repetitions in task-repeat trials but a cost in task-switch trials) is often found in human task switching (e.g., Rogers & Monsell, 1995; Kleinsorge, 1999; Schuch & Koch, 2004; Hübner & Druey, 2006). It is 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 will generalise to response selection, and in effect facilitate response alteration rather than response repetition. The fact that no such costs were found in the data of Rules-Ignorant participants seems to confirm this hypothesis.

It has to be noted that the effect was very small (and statistically not reliable) in the Rules-Aware participants in this experiment, and the Rules-Aware people in the experiment in Section 3.2 did in fact show a benefit to performance when repeating a response in task-switch trials. However, this might be a result of including the data of all trials into the analysis; the effect would only emerge once participants had inferred the rules of the two competing tasks. Indeed, in the analysis that included only the last half of the experiment, the effect was highly visible in the performance of Rules-Aware participants in the current experiment, and it also emerged in the performance of participants towards the

end of the experiment in Section 3.2, so it can be assumed that participants in both experiments inferred the task rules some time after the beginning of the experiment and, once they were able to consistently apply the two rules in each trial, were affected by the phenomena that accompany the application of task-sets.

Another interesting point is that the majority of Rules-Ignorant participants who attempted to memorise the cue-stimulus-response contingencies, or were convinced that there simply were no discernible patterns, had received no training (see Figure 3.3.2), while almost all participants who had received training developed a heuristic of some sort. This connection between training and the development of heuristics suggests that experiencing the entire set of cue-stimulus-response combinations of one task at once, and separated from the competing task, can provide an opportunity for participants to search for a general rule.

For example, it is plausible that the training that all participants in Sections 3.1 and 3.2 (and the Training groups in this section) had received prior to engaging in the task-switching studies led to an initial consideration of the underlying task rules, but because participants failed to detect a reliable predictor of when each task applied, they dismissed the relevance of these rules in the test phase. It might be that participants, despite reaching a certain level of task awareness during the training of each task, failed to incorporate the task cues as an informative part of the stimulus. Without the information from the cue, task changes in the later test phase appeared to occur at random, and might lead a large number of participants to suspect that "different rules applied that changed frequently". Consequently, even though those participants might have been unable to infer what caused a change in the currently relevant stimulus-response mappings in a task-switch trial, as explained above, they were able to react to the change and choose the correct response on subsequent task-repeat trials. Thus, it might be more accurate to label those participants not as "rules-ignorant" but as "cues-ignorant".

The training phase could also facilitate the development of the sequential heuristic. Provided that participants noticed that only a single dimension determined the correct response in the training phase of each task, applying the heuristic to the correct dimensions in each training block would result in

accurate performance without the need to memorise the exact stimulus-response contingencies (e.g., during the training of the orientation discrimination, participants could have learned that the correct response location changed if the stimulus changed from a vertical orientation to a horizontal orientation). As long as the participants attended to the relevant dimension in each training block, the sequential heuristic would be successful. In the subsequent task-switching phase, the currently relevant dimension became unpredictable, but the participants might have nonetheless continued to apply the heuristic, potentially regularly changing the dimension to which they paid attention. It is possible that at least part of those participants who reported that "the rules changed frequently" employed this strategy, which would explain why they did not report the task rules (e.g., horizontal - left response, vertical - right response).

In summary, altering the sequence of trial-to-trial transitions did not prevent participants from following a sequential heuristic of “repeating the response that was correct in the previous stimulus if the current stimulus looked similar to the previous one, or changing the response if otherwise”. As before, participants who had adopted this heuristic suffered considerable switch costs, because this strategy benefits performance in task-repeat trials, in which the repetition of an incongruent stimulus is accompanied by a response repetition, but impairs performance in task-switch trials, in which the repetition of an incongruent stimulus affords a response change (and vice versa). Other Rules-Ignorant participants reportedly noticed that different tasks were at play but failed to predict which of these tasks would be relevant in a given trial. It is likely that this level of task awareness without cue awareness was mediated by receiving task training prior to the task-switching test. These participants also suffered measurable switch costs in response to incongruent stimuli, arguably because they were able to use the feedback from a given trial to infer which rule had been relevant in that trial, and applied that task rule in all subsequent task-repeat trials and the next task-switch trial. Then, the (incorrectly answered) task-switch trials provided the necessary information that the rule was no longer successful and enabled the participants to change to the other deduced rule in the subsequent trial. Participants who had not noticed any correspondence between stimuli and required response showed performance at chance level

and an absence of switch costs. They also, like the pigeons, benefitted greatly from a response repetition; therefore, their likely strategy is examined further in Section 3.4. Finally, some participants claimed that they had tried to memorise the experienced cue-stimulus-response contingencies - thus seemingly followed an associative approach - and suffered noticeable switch costs in response to incongruent stimuli. The potential mechanisms that may have caused these participants to suffer switch costs when pigeons, which also solved the paradigm associatively, did not are discussed in Section 3.4.

3.4 Discussion - Associative Processes in a Task-Switching Paradigm

The main question that is addressed in this chapter 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 are eliminated when responding to response-congruent stimuli (Dreisbach et al., 2006, 2007; Dreisbach, 2012). Indeed, in Sections 3.1 and 3.2, pigeons did not show any switch costs when responding to such congruent stimuli, and human participants showed strongly reduced or absent switch costs in this case in all three experiments in Sections 3.1, 3.2 and 3.3. Since a congruent stimulus signals the required response unambiguously, no information about the currently relevant task is required to perform accurately - therefore, congruent stimuli should predominantly elicit stimulus-response learning rather than the costly retrieval and reconfiguration of task sets.

More interestingly though, Forrest (2012; Forrest et al., 2014) noticed that humans consistently suffered from switch costs when responding to response-incongruent stimuli, even when they were informed about stimulus-response contingencies instead of task rules. The human participants in the experiments in Chapter 3.1, 3.2 and 3.3 also showed reliable switch costs in response to incongruent stimuli to about the same magnitude as reported by Forrest, regardless of whether or not they had been aware of the task rules. Simulations in associative computational models equally predict small but reliable switch costs under pure associative-learning conditions, which 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 emerge as a product of the automatic retrieval of cue-stimulus-response associations.

Unfortunately, research on the task-switching abilities of animals has been equivocal with respect to this assumption - none of the several independent

studies on rhesus macaques could convincingly demonstrate switch costs in the monkeys' performance (Stoet & Snyder, 2003a, 2003b, 2008, 2009; Avdagic et al., 2014) - and the experiments with pigeons in this chapter and by Castro and Wasserman (2016) found no evidence that associative processes may lead to switch costs in response to incongruent stimuli.

Therefore, an alternative explanation may be required for the occurrence of switch costs despite an absence of task sets in human performance. One possibility is of course 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 behaved entirely associatively and thus lacked switch costs, any switch costs that were present for humans indicate that the performance of those participants was governed by executive-control processes, or at least different processes to those used by the pigeons, even when they failed to verbalise the task rules.

In the case of the pigeons, there is some evidence that this assumption is true: solving the paradigm associatively does not have to incur switch costs. And there is unambiguous evidence that the behaviour of pigeons was indeed governed by associative processes: in every experiment in this chapter, the 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 shows that the pigeons' behaviour was controlled by specific stimulus features, and that interference between the competing cue-stimulus-response contingencies did affect their performance more than abstract task-sets. Further evidence for this fact is the clear benefit of response repetitions for pigeons found in Section 3.2: having to repeat the same response that was correct in the previous trial facilitated the performance of pigeons much more than any other aspect of a given trial. Response-repetition effects have also been shown by task-switching humans, although it affected their performance to a far lesser degree than switch costs. In Section 3.3, participants only benefitted from repeating the

previously correct response on task-repeat trials, but on task-switch trials, having to repeat the previous response did not help - in fact, it often incurs a cost to humans (Kleinsorge, 1999; Kleinsorge & Heuer, 1999; Mayr & Bryck, 2005; Hübner & Druey, 2006). As mentioned in Section 3.2, the enormous benefit for pigeons most likely stems from associative processes (such as response priming) and the integration of stimulus location as a feature of the perceived cue-stimulus compound. In contrast, the often observed costs of response repetitions in task-switch trials for humans are most logically explained by the influence of task sets (e.g., Kleinsorge, 1999): a change in a relevant task dimension that requires a recoding operation will generalise to response selection, and in effect facilitate response alteration rather than response repetition.

As for humans, the results of Section 3.3 might be seen as evidence that humans suffer switch costs predominantly as a result of executive-control processes and the systematic application of rules or heuristics. Only those Rules-Ignorant participants who had been oblivious to any pattern were unaffected by a switch in tasks, whereas all those who had assumed some kind of connection between the stimuli and the required response showed persistent switch costs. As stated in Section 3.3, participants reported a multitude of rule-based strategies, which affected performance in different ways, but each of them selectively impaired performance in task-switch trials and thus created "switch costs" for those participants, despite an absence of task sets. However, if the switch costs in human participants are always due to executive control, why did those participants who reported that they had tried to memorise the individual stimulus-response associations also experience significant switch costs? What's more, computational-modelling accounts (Forrest, 2012; Forrest et al., 2014) also confirm the possibility of switch costs emerging under associative-learning conditions - so might there be some associative component that leads to switch costs after all?

In order to address this question, it is worth looking back at the likely cause for an absence of switch costs in pigeons: in Section 3.2, I argue that the mechanism that Forrest (2012) held responsible for the presence of switch costs in her associative models might not apply to pigeons. Forrest argues that

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. But the data of Section 3.2 indicate that pigeons might 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, making each cue-stimulus pairing a unique stimulus to the pigeon's eye. Thus, in a way, even Forrest's associative algorithms obey a task structure in that the cues are regarded as providing separable information from the stimuli, whereas to the pigeons, cues and stimuli may be indivisible elements of the same image.
Keeping in mind the response-repetition effects on the pigeons' performance, I postulate in Section 3.2 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 side of the centre of the screen. A cue-stimulus compound in one location might then become appetitive in that approaching (and pecking) it is followed by a reward, whereas the same compound in the opposite location might become aversive (or at best neutral) because approaching it is not rewarded. This assumption can most elegantly be summarised as follows: the pigeons employed Pavlovian processes to learn the task-switching paradigm, and the trial-to-trial sequential effects brought about by the application of these processes resulted in an absence of switch costs.

This idea can be verified by applying a simple, yet well validated model of conditioning, specifically, that due to Pearce (1987), to perform a perturbation analysis of the sequential effects that would be expected under the model. In Pearce's model, pigeons (and other animals) learn by associating configurations of stimuli with outcomes, and these associations then generalise to other configurations that share elements with the trained configuration. Pearce gives a simple rule for generalisation, which is:

Equation 1. G(generalization) = NS/TA x NS/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, generalisation 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*.

Since the effects of interest are sequential effects, i.e., the influence of trial N-1 on performance for trial N, assayed after the problem has been learned to a considerable extent, the learning rule specified by Pearce was adapted to accommodate the assumption that all incongruent stimuli are at approximately the same level of associative strength at the beginning of a trial, so that increments in this strength as a result of a trial will be approximately equal. Congruent stimuli are not considered in the analysis; as observed earlier in Chapter 3, performance is typically at or near asymptotic levels for congruent stimuli, making any increment in associative strength very small for those stimuli. Thus, the focus is on incongruent stimuli, for which it can be assumed that the increment in associative strength is small but non-negligible.

To illustrate how Pearce's model estimates performance, it will be assumed that the task requires subjects to learn the correct response to a configuration that includes a cue, a stimulus with different visual features, and a location. The task-switching paradigm developed in Section 2.3 makes use of four cues, *A*, *a*, *B* and *b*: cues *A* and *a* denote one task and *B* and *b* the other. The paradigm also includes two incongruent stimuli that are each made up of two visual dimensions, one with the values *W* and *w*, the other with the values *X* and *x*. The incongruent stimuli differ from each other in both stimulus dimensions; therefore, the two stimulus configurations that are considered are *WX* and *wx* (for example, *WX* might be a stimulus with a horizontal orientation and a low spatial frequency and *wx* would be a stimulus with a vertical orientation and a high spatial frequency). The spatial location of a stimulus is denoted by *L* and *R*, where *L* denotes the left stimulus location and *R* denotes the location on the right-hand side. All these elements are, for simplicity, assumed to have equal salience.

In a Pavlovian setting, one might assume that the pigeons learn to approach the correct cue-stimulus-location configuration - say *AWXL* - and avoid the wrong configuration - which in this case would be *AWXR*. The two configurations occur together in a given trial, but only one of them, *AWXL*, is the correct choice, which will be represented as *AWXL+*. As this combination becomes more strongly associated with reward, its associative strength with reward would increase from its current value *V* to *V+∂*, where *∂* is the small increment to associative strength that occurred on that trial. According to Pearce's (1987) model, this increment to associative strength will generalise to other cue-stimulus configurations that share features with *AWXL*; following Equation 1, the effective increment to the other configuration in this trial, *AWXR* (sharing 3 of a total of 4 elements with *AWXL*), will be 3/4 x 3/4 x *∂* = 9/16 x *∂*. If the next trial is a repeat of the one that has just occurred, the pigeon's improvement in performance in that trial as a result of this increment can be estimated. The increase in associative strength for the correct stimulus configuration *AWXL* is *∂*, the increase for the incorrect stimulus *AWXR* is 9*∂*/16, resulting in a net gain in performance of 7*∂*/16 in the following cue-and-stimulus-repeat trial. Table 3.4.1 shows this calculation, and the net gain for the other possible trial-to-trial transitions that begin with *AWXL+* on trial *N-1*.

Table 3.4.1. Perturbation analysis of a Pavlovian account of task-switching based on Pearce (1987). Please refer to the text for details on how to calculate the difference values in the last column. ***Key:*** *A, a, B* - task cues; *WX, wx* - incongruent stimuli; *L, R* - response locations.
This table appeared in Meier et al. (2016b).

	Previous configuration	Correct choice in current trial	Incorrect choice in current trial	Difference (correct-incorrect)
Cue Repeat + Stimulus Repeat	AWXL+	AWXL	AWXR	7*∂*/16
Task Repeat + Stimulus Repeat	AWXL+	aWXL	aWXR	5*∂*/16
Task Switch + Stimulus Repeat	AWXL+	BWXR	BWXL	-5*∂*/16
Cue Repeat + Stimulus Change	AWXL+	AwxR	AwxL	-3*∂*/16
Task Repeat + Stimulus Change	AWXL+	awxR	awxL	-*∂*/16
Task Switch + Stimulus Change	AWXL+	BwxL	BwxR	*∂*/16

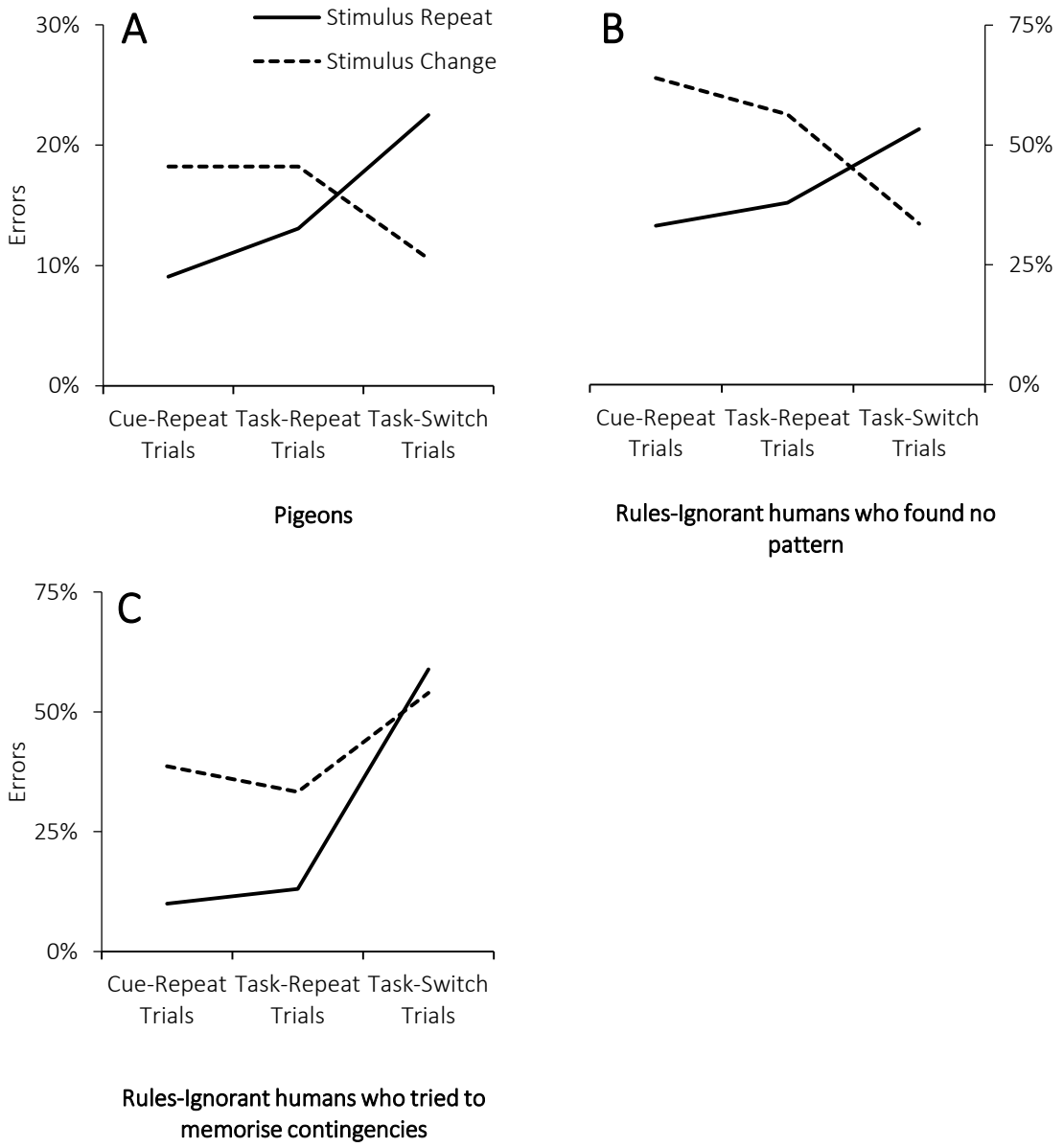

Figure 3.4.1. Error rates in trials in which an incongruent stimulus is presented and is the same as in the immediately preceding trial (Stimulus Repeat) or follows a trial in which the other incongruent stimulus appeared (Stimulus Change), depending on Trial Type, *A*) for pigeons taking part in the experiment in Section 3.2 (this graph is identical to Figure 3.2.2), *B*) for those Rules-Ignorant participants taking part in the experiment in Section 3.3 who reportedly had found no pattern between the stimuli and the correct response, and *C*) for the last half of trials for those Rules-Ignorant participants in the experiment in Section 3.3 who reportedly tried to memorise the cue-stimulus contingencies. Note the different scale for pigeons.

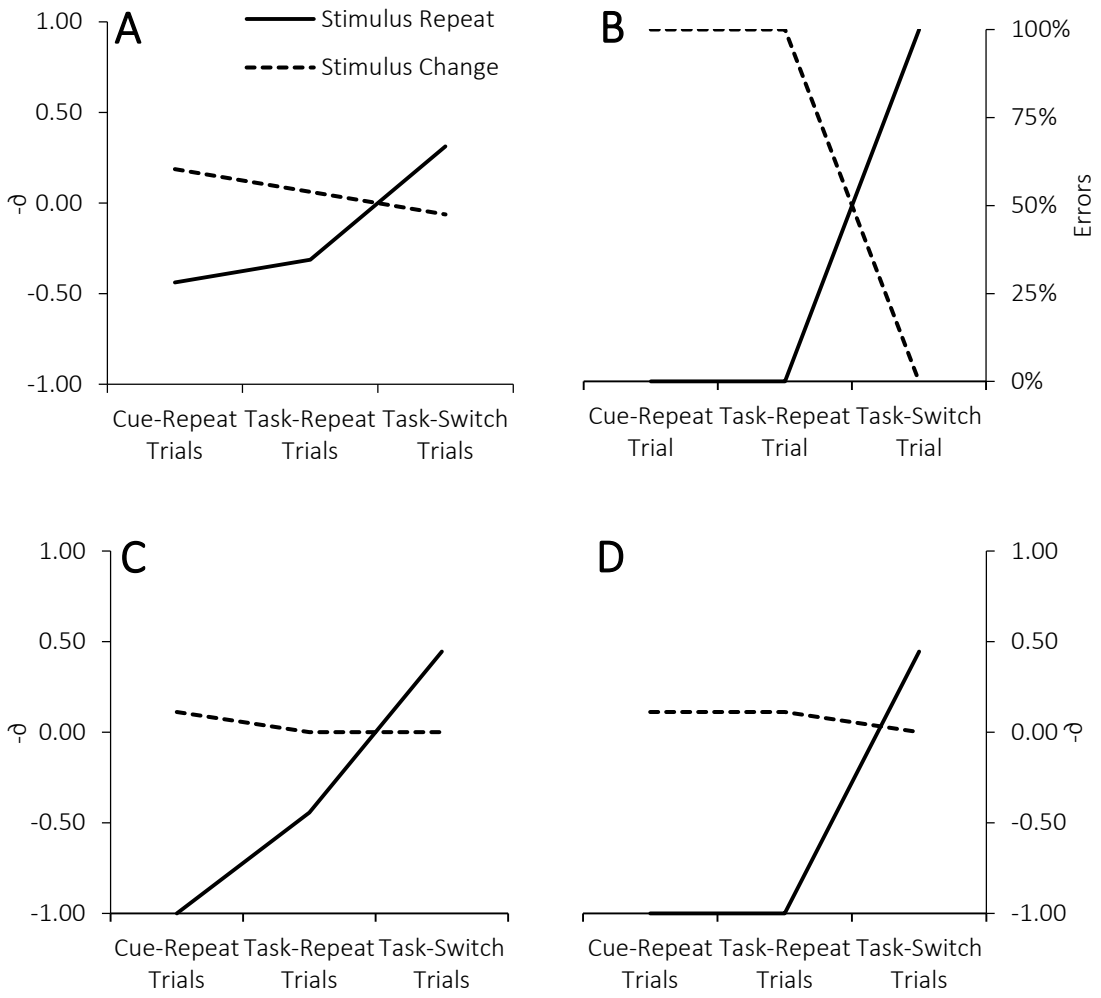

Figure 3.4.2. *A)* Plot of the perturbation analysis of a Pavlovian account of task-switching (AWXL+). The dependent variable is the negative of the difference score reported in Table 3.4.1. *B*) Error rates as predicted by a "win-stay/lose-shift" strategy, by which the response that was correct on the previous trial is repeated until the feedback changes. *C)* Perturbation analysis of an instrumental account of task-switching (AWX→L). The dependent variable is the negative of the difference score reported in Table 3.4.2. *D)* Perturbation analysis of an instrumental account of task-switching that assumes cue equivalence. For all graphs, higher scores mean more errors.

The calculations in Table 3.4.1 can be illustrated in a graph equivalent to Figure 3.2.2 (this figure is replicated in Figure 3.4.1 Panel A for easier accessibility), which has been done in Figure 3.4.2 Panel A. To simulate error rates, this figure shows the negative of the values in the final column of Table 3.4.1, because a positive value in the table equates to fewer errors on that trial. The graph in Figure 3.4.2 Panel A does not look unlike the pattern expressed by pigeons in Figure 3.4.1 Panel A.

In summary, by incorporating the findings of Section 3.2 into Pearce's (1987) model of stimulus categorisation, it becomes evident that the absence of switch costs in the pigeons' task-switching performance occurred because the pigeons acquired the paradigm via Pavlovian processes, and incorporated the cue and the stimulus dimensions (including the stimulus location) into one indivisible cue-stimulus compound, a possibility that is confirmed by previously research that found that pigeons might not readily analyse the separate features of a stimulus (Lea et al., 2009; Wills et al., 2009). These processes produce observable effects of the previous trial on the pigeons' performance on the next trial (as evident by a pronounced response-repetition effect) but no costs to performance when switching from one task to another.

As noted in Section 3.3, the performance of Rules-Ignorant participants who had found no pattern to responding showed some striking similarities to that of the pigeons. For easier comparability, the figure showing the performance of those participants is replicated in Figure 3.4.1 Panel B. Like the pigeons, those participants were mainly influenced by a response repetition, responding with greater accuracy to trials that afford a repetition of the previously correct response, and with accuracy at or above 50% chance level in trials affording a response change; and they showed no consistent switch costs. However, those participants did not show a congruency effect, and showed the highest error rates in Cue-Repeat/Stimulus-Change trials, and not, like the pigeons (and as predicted by the perturbation analysis above), in Task-Switch/Stimulus-Repeat trials. Overall, the pattern in their performance suggests that the main factor that influenced their response was whether the correct response of the previous trial was repeated or not. The Rules-Ignorant participants who had not found any pattern might have chosen to repeat any response that was indicated as correct on the previous trial, irrespective of the attributes of the current cue or stimulus, and to change to the other response location if the one chosen on the previous trial had been marked incorrect. The consistent application of such a 'win-stay/lose-shift' strategy, illustrated in Figure 3.4.2 Panel B, would result in perfect performance on Cue-Repeat and Task-Repeat trials with a stimulus repetition and in Task-Switch trials with a stimulus change, whereas the other three trial types would always be answered incorrectly. As seen in Figure 3.4.1 Panel B, the performance of the participants did not show such extremes, and

these participants also never acknowledged using this strategy but instead assumed that the correct response was chosen at random in each trial. For pigeons, it has been shown that, when the exact response requirements are unpredictable, there is a bias to perform the response that had been given more recently (and led to a reward) than to perform the response that had been given less recently (e.g., Stubbs et al., 1987; Schneider & Davison, 2005; Schneider, 2008). Humans might also have a bias to do so (cf. Bendig, 1951; Senders, 1953; Wiegersma, 1982), and the participants might have implicitly preferred the previously correct response despite assuming randomness.

Of particular interest are also those Rules-Ignorant participants in the experiment in Section 3.3 who attempted to memorise the stimulus-response contingencies of the task-switching paradigm, and who might most closely resemble those participants in Forrest (2012) who were instructed in the cue-stimulus-response contingencies of the paradigm. Switch costs reliably occurred in the performance of all of those participants, and, beyond that, in the simulations using an associative learning algorithm used by Forrest (2012). It can be assumed that the participants were learning to associate the combination of the cue and the stimulus dimensions with making a left or right response, and did not (like the pigeons) encode the response location as part of the stimulus compound. Conceptually, this makes the paradigm an instrumental-conditioning task, and the perturbation analysis based on Pearce's (1987) model of stimulus categorisation can be adapted to allow inferences about the occurrence of switch costs in this case. As before, there are two cues per task, *A*, *a*, *B* and *b*, the two incongruent stimuli *WX* and *wx*, and the response locations *L* and *R*. The functional relationship between the cue, the stimulus dimensions and the correct response shall be illustrated as *AWX*→*L*, to indicate that the combination of cue *A* and stimulus *WX* evokes a response of clicking the left response location *L*. According to Equation 1, the association of *AWX*→*L* would generalise to the cue-stimulus configurations in subsequent trials: for example, if the trial following *AWX* is a cue-repeat and stimulus-repeat trial (sharing all elements with the previous trial), the model predicts an increase in the association of *AWX* with *L* of 3/3 x 3/3 x ∂ = 9∂/9 = ∂. Conversely, if the trial following *AWX* incurs a repetition of the cue but a change of stimulus, namely *Awx* (sharing one of three elements with *AWX*), the estimated increase

in the association of *Awx→L* would be 1/3 x 1/3 x *∂* = *∂*/9. Since the correct response to *Awx* is *R*, the net gain in performance for that trial would be negative, i.e., *-∂/9.* These calculations, and the net gain for the other trial-to-trial transitions following *AWX→L* in trial *N-1*, are reported in Table 3.4.2. The model's predictions for performance are illustrated in Figure 3.4.2 Panel C.

Table 3.4.2. Perturbation analysis of an instrumental account of task-switching based on Pearce (1987). Please refer to the text for details on how to calculate the increment values. *A, a, B* - cues; *WX, wx* - stimuli; *L, R* - response locations.

	Previous configuration and its correct response	Current configuration	Correct response to current configuration	Increment in difference between correct and incorrect choice
Cue Repeat + Stimulus Repeat	AWX→L	AWX	L	*∂*
Task Repeat + Stimulus Repeat	AWX→L	aWX	L	4*∂*/9
Task Switch + Stimulus Repeat	AWX→L	BWX	R	-4*∂*/9
Cue Repeat + Stimulus Change	AWX→L	Awx	R	-*∂*/9
Task Repeat + Stimulus Change	AWX→L	awx	R	0
Task Switch + Stimulus Change	AWX→L	Bwx	L	0

It is possible to work out the expected switch costs for each model by subtracting the average of cue-repeat and task-repeat trials from the average of task-switch trials. For the model assuming Pavlovian conditioning and responding to a cue-stimulus compound *AWXL*, the difference (the "switch costs") is predicted to be 0.25*∂*. Given that *∂* is itself a small increment, and this is multiplied by a factor considerably less than 1, the switch costs in the pigeon data are expected to be small to negligible, even though there are measurable sequential effects in both the observed data and the model. The estimated switch costs for an instrumental account associating *AWX→L* comes to 0.55*∂*,

which is more than twice the estimate for the pigeons. Thus, an important clue in trying to explain the differential expression of switch costs may well lie in the fact that pigeons solve task-switching problems using Pavlovian processes and humans instead solve them instrumentally when they are unable to infer any task rules or heuristics.

Following Forrest's (2012) argument, a large proportion of the "switch costs" in the performance of associatively learning participants may be attributed to the formation of a conceptual equivalence between the two cues that signalled the same task. That is, with repeated activation of the same stimulus-response link in the presence of either cue *A* or cue *a*, it is thought that both cues can come to activate the same mental representation of that stimulus-response link, which in turn would facilitate the retrieval of that stimulus-response link in subsequent trials of the same task. If a total equivalence is achieved, cues *A* and *a* should retrieve the stimulus-response associations that are connected to either cue to the same degree. Performance in such a case can be estimated by assuming that there are only two types of cues in the task-switching paradigm: those signalling task *A* and those signalling task *B*. This has the effect that task-repeat trials take on the values of cue-repeat trials (for trials with both a stimulus repeat and a stimulus change), which, as illustrated in Figure 3.4.2 Panel D, leads to an increase in the difference between task-repeat trials and task-switch trials.

Finally, it is now possible to compare the models in Figure 3.4.2 Panel C and D to the data observed for Rules-Ignorant humans who reportedly memorised the contingencies of the paradigm, which was illustrated in Figure 3.3.3 Panel D. The pattern in that figure does not seem to indicate an equivalence of task cues. However, that pattern changed in the latter half of the experiment. As reported in Section 3.3, all analyses were carried out including all test blocks and again for the last half of blocks to account for the fact that those participants who had not had a training phase had to get acquainted with the paradigm and its contingencies in the earlier blocks of the actual experiment. Figure 3.4.1 Panel C shows the pattern of responding towards a stimulus repeat and stimulus change that emerged in the last half of the experiment for the participants who memorised the cue-stimulus-response contingencies. And indeed, towards the end of the experiment, these participants appeared to treat

the two cues that signalled the same task rather equally, as evident by the very similar performance in cue-repeat and task-repeat trials, both when the incongruent stimulus changed and (although to a lesser degree) when it repeated. Arguably, cue equivalence would facilitate performance more in task-repeat trials in which the stimulus also repeats, since the perceptual similarity of the two subsequent trials is greater than when the stimulus changes. Thus, the observed performance of those participants who memorised the contingencies of the paradigm seems to match the modelled results shown in Figure 3.4.2 Panel D, which incorporate the possibility of task-cue equivalence - but with one obvious, important difference.

The model estimates that "switch costs" should only occur in trials in which the stimulus repeats, whereas performance in stimulus-change trials should at best be equal in task-repeat and task-switch trials. In fact, the perturbation analysis according to Pearce's (1987) model, illustrated in Figure 3.4.2 Panel D, estimates that the acquisition of full cue equivalence would actually produce (small) negative switch costs in stimulus-change trials. This prediction goes very much against the argument of Forrest (2012, Forrest et al., 2014) - to reiterate, she hypothesised that the closer associative proximity of cues signalling the same task would facilitate performance in trials in which these two cues occur consecutively, compared to a sequence of trials in which cues of the two opposing tasks are presented, regardless of whether the same or a different stimulus is presented in subsequent trials. And this is also where the observed data from the contingencies-learning participants differ from the estimated performance in Pearce's model: as seen in Figure 3.4.1 Panel C, participants showed persistent switch costs both in trials in which the incongruent stimulus repeated and in those trials in which it changed, very much in line with Forrest's assumptions.

This finding is intriguing, as it may hint at just how prevalent the human tendency to apply rules (e.g., Maddox & Ashby, 2004; Maddox & Ing, 2005; Smith et al., 2010) might be. Consider the assumptions of Pearce's model about performance in task-switch/stimulus-change trials: following from the perturbation analysis in Table 3.4.2, generalisation from experiencing the configuration AWX affording the response L is estimated to lead to an increment in associative strength between the subsequent configuration Bwx and its correct response L of zero. That is, the configuration AWX→L should not affect

the associative strength of Bwx→L, because the two cue-stimulus compounds share no elements with each other. But undeniably, the Rules-ignorant participants memorising contingencies were affected by the previous trial, as the higher error rates in Task-Switch/Stimulus-Change trials confirm. The apparent lack of associative content that is predicted by Pearce's model might in fact have prompted participants to search for alternative information that could be gathered from comparing the two cue-stimulus configurations of both trials - previous research suggests that, even when learning shaped entirely by contingencies would improve performance, human behaviour might be biased to be controlled by rules (Galizio, 1979; Hayes, 1989; Maddox & Ing, 2005; Doll et al., 2009). For example, they might have returned to testing the hypothesis that only stimuli that share a common visual element demand the same response. Importantly, the data provide evidence that, as Hayes et al. (1986) suggested, human performance can be shaped by an interaction between contingency-shaped and rule-governed behaviour - especially when the rules originally governing behaviour are unreliable or incomplete, as would be the case here.

In conclusion, the lack of any detectable switch costs in pigeons in the experiments in this chapter are most accurately estimated by a Pavlovian-conditioning model that assumes that subjects respond to appetitive and aversive cue-stimulus-location compounds. Conversely, the switch costs that affected the performance of those participants who learned the stimulus-response contingencies may plausibly be attributed to an interplay between an instrumental approach (and, as hypothesised by Forrest, 2012, the establishment of an associative equivalence between the cues that signal the same task, which further elevated the difference in performance in task-repeat and task-switch trials) and continued hypothesis testing. Importantly, the rule-based approach can explain switch costs in response to stimuli that share no perceptual features with the stimulus on the previous trial, whilst instrumental conditioning may contribute greatly to the switch costs in response to stimulus-repetition trials. Thus, it appears that switch costs can occur under associative conditions.

The final question that remains to be answered is: how can the switch costs due to executive control and the "switch costs" caused by associative processes be distinguished? Monsell (2003) postulated that switch costs reflect the executive processes that govern the application of the relevant task set. Dreisbach (2012) added that the switch costs caused by executive-control processes allow subjects to improve performance, by shielding their responses from interference from the competing task set. Thus, switch costs that occur at the level of the task structure but are independent of any perceptual stimulus elements (e.g., switch costs in response to response-congruent stimuli, see Section 3.1; response-repetition costs in task-switch trials, see Section 3.3) can be attributed to executive control; they exist to ensure correct response selection and the inhibition of inappropriate responses. Indeed, those effects were only confirmed for Rules-Aware participants, but did not affect the performance of Rules-Ignorant participants or pigeons. Conversely, trial-to-trial effects that are based on perceptible stimulus features (e.g., stimulus-repetition and response-repetition benefits in task-repeat trials, see Section 3.2) are due to associative processes; those effects were visible (though in different guises) in the performance of pigeons and humans responding on the basis of cue-stimulus-response contingencies, but did not affect the performance of rules-using participants.

CHAPTER 4: ARE ASSOCIATIVE PROCESSES SUFFICIENT TO INHIBIT A RESPONSE IN A RESPONSE-INHIBITION PARADIGM?

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Chapter 3 concluded with the postulation that switch costs might be an expression of executive-control processes involved in ensuring correct response selection and the inhibition of inappropriate responses (cf. Dreisbach, 2012). Reversing this logic, can it be assumed that the mechanisms of response selection and inhibition require executive control, i.e., are only those individuals capable of executive control able to inhibit a prevalent response, or "control an impulse"? The literature on inhibitory control seems to agree that it is indeed executive control that governs the inhibition of prevalent responses (Verbruggen & Logan, 2009a, 2015; Elchlepp et al., 2016; Verbruggen & McLaren, in preparation). However, as described in detail in Section 1.2, response inhibition in Stop-Signal paradigms, in which subjects perform a simple, speeded response towards a stimulus, but are sometimes, by the appearance of a stop signal, instructed to withhold that response, might be (at least in part) governed by associative mechanisms (cf. van Gaal et al., 2009).

As laid out in Section 1.2, the mechanisms of response inhibition in Stop-Signal paradigms are adequately described by the independent horse-race model (Verbruggen & Logan, 2009b), which makes no statement about the involvement of executive control in response inhibition. In fact, the assumption that the two processes of response initiation and inhibition are triggered automatically by the appearance of the relevant stimulus or signal implies that associative processes might be involved (Verbruggen & Logan, 2008b, 2009a; Verbruggen et al., 2014; Best et al., 2016).

Therefore, the influence of executive control on response inhibition might not be present at the trial level. As previously shown for task-switching performance in Chapter 3, the effect of executive-control processes might primarily be observed at the task level, in trial-to-trial effects reflecting a change in the activation of a

specific task goal (e.g., the goal to execute or inhibit a response), whereas effects that relate to stimulus-specific aspects might most readily be attributable to associative processes (cf. Section 1.2). It is thus necessary to examine such effects in the performance of pigeons and humans; in particular, I assessed the occurrence of post-signal response-slowing and the extent to which the subjects utilised information about the likelihood of having to inhibit a response.

Although the Stop-Signal paradigm is the most prominent response-inhibition paradigm, it is also worth considering the Change-Signal paradigm, in which the occurrence of the signal indicates that an alternative response has to be executed instead of the usual Go response. The Stop-Signal and Change-Signal tasks can use the same stimuli and very similar procedures, so it seems logical to assume that they both involve the same inhibition mechanisms. Alternatively, as stated in Section 1.2, it can be argued that Change-Signal tasks, which require the selective stopping of one response and the selection of an alternative response, afford a more cognitively demanding inhibition mechanism and a higher level of behavioural control than merely stopping an action, possibly comparable to the mechanisms involved in task-set reconfigurations during task-switching (cf. Monsell, 2003). However, since pigeons succeeded in the task-switching paradigm reported in Chapter 3, I assumed that, if response inhibition did not rely on executive processes, pigeons would be able to acquire a Change-Signal task to the same level as a Stop-Signal task. In fact, there is the interesting possibility that pigeons in particular might perform better if they are given the option to execute an action instead of having to withhold a response. As detailed in Section 1.2, Change-Signal tasks might in fact be accomplished without inhibitory control, whereas Stop-Signal tasks might require a mechanism to suppress inappropriate responses.

These considerations have an important implication for the success of any comparative response-inhibition paradigm, for example if pigeons acquire a Change-Signal paradigm easily but fail in a Stop-Signal paradigm (or vice versa). Therefore, it is essential to establish whether pigeons can learn to inhibit a prepared response both in a Stop-Signal task, in which the occurrence of a signal indicates the requirement to inhibit any response, and also in a Change-Signal task, in which the appearance of a signal affords the execution of an

alternative response instead of the one that was initially prepared. I took this issue into account in the pilot work described in Section 4.1, in order to develop a response-inhibition paradigm that can adequately assess the performance of different species, the methods of which are reported in Section 4.2.

Using the response-inhibition paradigm established in Sections 4.1 and 4.2, the experiments reported in the subsequent sections were carried out to answer the following questions: firstly, do the predictions made by the independent horse-race model of response inhibition (see Section 1.3) apply to performance that is governed purely by associative processes? And are there marked differences in the performance of associative pigeons and humans, who would be assumed to rely on executive processes to perform response inhibition? These questions are addressed in Section 4.3. Secondly, do pigeons (and humans) integrate information about the likelihood that inhibition will be required in an upcoming trial to improve their ability to inhibit a response? This question is addressed in Section 4.4.

4.1 Developing a Comparative Response-Inhibition Paradigm

As mentioned in Section 2.1, developing a paradigm suitable for use with multiple species requires a series of methodological adaptations.

Firstly, considering the potential cognitive mechanisms underlying different response-inhibition paradigms, outlined above, I examined whether pigeons show a difference in the acquisition of a Change-Signal paradigm and a Stop-Signal paradigm, or whether the two paradigms are acquired at a comparable rate, which would speak for the possibility of one common cognitive mechanism governing performance in both paradigms.

Secondly, on a more methodological level, the way in which behaviour is reinforced might influence pigeons' ability to acquire a response-inhibition paradigm. Positive reinforcement would be the preferred method, because reward maintains a stable level of responding towards the stimuli, whereas negative reinforcement might lead to an overall reduction in responding. Change-Signal paradigms do often reward the correct shift from executing a prevalent response to executing an alternative response, but in conventional Stop-Signal paradigms, it is often the case that wrongly responding when inhibition is required is punished, for example by inducing a timeout period between trials. In the pilot work reported in this section, I assessed whether pigeons would acquire either response-inhibition task more easily when they are being rewarded for successful inhibition or when they are being punished for unsuccessful inhibition.

In summary, the experiment reported in this section was carried out to investigate pigeons' general ability to inhibit a response, either by stopping any action or by performing an alternative action. For this purpose, the pigeons completed a simplified version of either a Stop-Signal or a Change-Signal task, in which the signal to either stop a response or change to another response was presented from the beginning of a trial, that is, the pigeons were not first exposed to a stimulus associated with the target Go response before the signal to inhibit appeared in these "Signal" trials. In contrast to trials in which such a stimulus is initially presented, it would be expected that the execution of the Go response would not be prepared in these trials, and performing the correct behaviour (i.e., withholding any response or performing an alternative response)

should be accomplished without the necessity to inhibit an already activated Go response.

Furthermore, the experiment aimed to establish the relative effectiveness of two different reinforcement methods on task acquisition rates - rewarding correct behaviour with food access, or punishing incorrect behaviour by imposing a delay to the start of the next trial.

Methods

Subjects

Ten pigeons took part in this experiment. The pigeons had previously taken part in unrelated studies but were naïve to the stimuli and the procedure of this experiment. Five pigeons were assigned to the Go/Stop group; the other five pigeons were assigned to the Go/Change group.

Procedure

In both tasks, a trial began with the presentation of a circular white start key (75 pixels / 22.5mm in diameter) presented in the centre of a black display to focus attention to the screen. Two pecks at the start key were required to replace it by two circular response keys (each 50 pixels / 15mm in diameter), the centres of which were offset by 50 pixels (15mm) to the left and the right side of the display centre. One of these keys was filled in red or green; the other key was yellow and served, as explained below, as a pecking alternative to the red or green stimulus. The locations of the stimulus and the alternative key (left or right) were randomised across trials.

The colour of the stimulus (green or red) indicated whether the current trial was a Go trial or a Stop or Change trial; for example, a pigeon might have to learn to associate a green stimulus with Go, and a red stimulus with Change. The colour that indicated a Go trial shall henceforth be referred to as the Go stimulus; the colour that indicated a Stop or Change trial will be referred to as Stop or Change signal, respectively. The assignments of colours to trial type were counterbalanced across subjects. Reinforcement contingencies varied for each trial type, as explained below.

Go Training

The pigeons initially received Go-training sessions, each consisting of 64 Go trials. In Go trials, a single peck at the Go stimulus resulted in the deletion of the stimulus display from the screen and the presentation of a white reward key (75 pixels / 22.5mm in diameter), which was centred 100 pixels (30mm) from the lower edge of the screen and 100 pixels (30mm) from the side of the screen that was closest to the Go stimulus. One peck at the reward key led to immediate access to the food magazine mounted below and to the side of that reward key for 2.5 seconds; then the next trial started after an inter-trial interval of 10 seconds. If no pecks at the stimulus were made during the display presentation interval, the trial was terminated and the next trial started. Any pecks at the yellow alternative key in Go trials were ineffective and had no scheduled consequences.

In the first session of the Go training, the response display containing the Go stimulus and alternative key was presented for 20 seconds in each trial. When overall performance in a session reached 85% or above, the presentation time of the stimulus display was decreased in the following session; this was repeated systematically to reduce the presentation time from 20 seconds to 2.5 seconds as the lowest value in the Go/Stop task and, to account for any additional time needed to perform the alternative response, to 4 seconds as the lowest value in the Go/Change task. Pigeons passed the Go training phase by responding to the Go stimulus on at least 80% of trials in three consecutive training sessions with the lowest presentation time.

Go/Stop and Go/Change Task

Once the Go-training criterion was met, pigeons completed twenty Go/Stop or Go/Change sessions. These sessions each consisted of 32 Go trials and 32 Stop or Change trials, presented in random order. Only one peck was required for the presentation of the reward key during the Go training, to facilitate task acquisition; this was still the case for the Go/Change task. It was increased to two pecks for the pigeons in the Go/Stop task, to account for the possibility that presenting any image on screen might have automatically triggered a pecking response (even before the image was sufficiently processed by the pigeon); due to the ballistic nature of the pigeon's peck, once it was initiated, the execution of the peck might not be stoppable but had to be completed. If this was the case,

pigeons might find it difficult to withhold a response altogether in Stop trials, but they might be able to withhold the second peck at the stimulus. If fewer than two pecks were made at the Go stimulus within the stimulus-presentation interval, the trial was terminated and the next trial started after an inter-trial interval of 10 seconds. As before, any pecks at the yellow alternative key were ineffective on Go trials.

For pigeons in the Go/Stop task, the stimulus-presentation interval was 2.5 seconds by default (for three pigeons, this interval was increased to 3 or 4 seconds to ensure that the stimulus was pecked twice within this time); for pigeons in the Go/Change task, the stimulus display was presented for a maximum of 4 seconds by default (for one pigeon, it was increased to 5 seconds to ensure continued responding).

The way in which behaviour was reinforced in Stop and Change trials was varied in two conditions: two pigeons in the Go/Stop task experienced the Reward condition, the other three pigeons in that task entered the Delay condition. Similarly, three pigeons in the Go/Change task experienced the Reward condition, and the other two pigeons completing that task were put into the Delay condition. The procedures of each condition were as follows:

- Go/Stop - Reward:

  Any pecks that were made at the Stop signal during the stimulus presentation interval in Stop trials were counted. If a pigeon made no or only a single peck at the Stop signal within this interval, the reward key was presented and, upon pecking this key once, the pigeon received access to the food magazine for 2.5 seconds, before the next trial began after an inter-trial interval of 10 seconds. If a pigeon made two or more pecks to the Stop signal, the trial terminated after completion of the stimulus presentation interval; the next trial started after the inter-trial interval.

- Go/Stop - Delay:

  If a pigeon made no or only a single peck at the Stop signal during the stimulus presentation interval, the trial terminated after completion of this interval and a new trial started after the inter-trial interval. As soon as the pigeon made a second peck at the Stop signal, it entered a delay period in which the Stop signal remained on screen for four times the duration of

the stimulus presentation interval (i.e., if the pigeon's stimulus presentation interval was 2.5 seconds, the delay period was set to 10 seconds), before the trial was terminated and a new trial started after the inter-trial interval. During this delay period, pecking the Stop signal had no effect.

- Go/Change - Reward:

  A peck at the yellow alternative key resulted in the immediate deletion of the response display and the presentation of the reward key closest to the alternative key, followed by access to the respective food magazine for 2.5 seconds. Any pecks at the Change signal were ineffective; if no pecks at the alternative key were made during the stimulus presentation interval, the trial was terminated and the next trial started after the inter-trial interval.

- Go/Change - Delay:

  If a pigeon made a peck at the Change signal, it entered a delay period in which the Change signal remained on screen for four times the duration of the stimulus presentation interval (i.e., if the pigeon's stimulus presentation interval was 4 seconds, the delay period was set to 16 seconds), before the trial was terminated and a new trial started after an inter-trial interval of 10 seconds. During this delay period, pecking the Change signal had no effect. Alternatively, a peck at the alternative key immediately terminated the trial; if no pecks at either the Change signal or the alternative key were made during the stimulus presentation interval, the trial was terminated and the next trial started after the inter-trial interval.

Data Collection

To assess the pigeons' performance, I collected the percentage of errors that the pigeons made overall and in response to Go trials and Stop or Change trials.

Further, to estimate the pigeons' acquisition of the contingencies in the Stop and Change trials under the different reinforcement conditions, I examined the pecking rates in Stop and Change trials: the number of incorrect pecks at the Go stimulus and the rate of pecking at the alternative key.

For the Go/Stop task, if a pigeon pecked the Go stimulus twice in a Go trial or if pecked the signal in a Stop trial only once or less, that trial was marked as correct. In the Go/Change task, if the first peck was made towards the Go stimulus in Go trials or towards the yellow alternative key in Change trials, that trial was marked as correct. All other responses were coded as incorrect.

I compared average error rates overall, in response to Go trials, and in response to Stop or Change trials, and also the number of pecks made in Stop and Change trials at the Go stimulus and the alternative key, between the four experimental groups in a series of repeated-measures ANOVAs using Sessions (1 to 20) and Trial Type (Go or Stop/Change) as within-subjects factors, and Condition (Go/Stop-Reward, Go/Stop-Delay, Go/Change-Reward, Go/Change-Delay) as between-subjects factor.

Results

Descriptive statistics for each of the variables are summarised in Table 4.1.1.

Overall error rates differed between groups, in that the pigeons in the Go/Change-Delay group produced more errors overall in the twenty test sessions than the pigeons in any of the other three groups, $F(3,6)=18.81$, $p=.002$, $\eta_p^2=.90$, Bonferroni post-hoc comparisons: $p \leq .028$, all comparisons between the other three groups: $p \geq .25$. As shown in Figures 4.1.1 and 4.1.2, this difference was mainly due to an inability of the subjects in the Go/Change-Delay group to perfrom the correct response in Change trials, which the subjects in the other three groups learned reliably over the course of the training, and which was accomplished fastest by the Go/Stop-Delay group. However, the subjects in the Go/Change-Delay group were fastest to learn the correct performance in Go trials, performing consistently at or above 80% accuracy from the first session, while the other three groups only approached this criterion towards the end of the 20 training sessions (see Figure 4.1.1).

To assess whether this difference was task-specific or caused by an innate group difference, I compared the error rates in the first session of the Go/Stop and Go/Change tasks; they did not differ significantly between groups, $F(3,6)=0.32$, $p=.81$, Bonferroni post-hoc comparisons: all $p=1.0$.

As shown in Figure 4.1.1, performance on Go trials differed significantly between the four groups, $F(3,6)=7.42$, $p=.019$, $\eta_p^2=.79$; Bonferroni post-hoc

comparisons revealed that error rates were significantly lower in the Go/Change-Delay than in the Go/Change-Reward condition, p=.021; all other comparisons: p≥.11. The performance in Stop and Change trials also differed significantly between groups (shown in Figure 4.1.2), $F(3,6)=37.35$, $p<.001$, η_p^2=.95; in these trials, performance of the Go/Change-Delay group was significantly worse than that of the other three groups, Bonferroni post-hoc comparisons: p≤.005, all comparisons between the other three groups: p≥.11.

Table 4.1.1. Mean performance and standard errors of the four experimental groups in terms of overall errors, errors in Go trials, errors in Stop/Change trials, and number of incorrect pecks at the Go stimulus and alternative key, for all 20 sessions and for the last half (10 sessions) of the experiment.

		Go/Stop - Reward	Go/Stop - Delay	Go/Change - Reward	Go/Change - Delay
Overall errors	Mean	23.4%	11.1%	19.7%	46.5%
	SD	3.7	3.0	3.0	3.7
last half of experiment	Mean	19.7%	8.7%	15.0%	49.7%
	SD	2.4	1.9	1.9	2.4
Errors in Go trials	Mean	17.8%	20.7%	27.4%	6.0%
	SD	3.6	2.9	2.9	3.6
last half of experiment	Mean	18.6%	17.2%	21.9%	3.9%
	SD	5.3	4.4	4.4	5.3
Errors in Stop/Change trials	Mean	29.0%	1.5%	11.9%	87.0%
	SD	6.6	5.4	5.4	6.6
last half of experiment	Mean	20.9%	0.2%	8.1%	95.4%
	SD	4.4	3.6	3.6	4.4
Number of incorrect pecks at Go stimulus in Stop/Change trials	Mean	0.72	0.07	0.16	0.04
	SD	0.18	0.15	0.15	0.18
last half of experiment	Mean	0.76	0.03	0.03	0.05
	SD	0.21	0.17	0.17	0.21
Number of pecks at alternative key in Stop/Change trials	Mean	4.34	0.26	0.93	0.07
	SD	1.09	0.89	0.89	1.09
last half of experiment	Mean	4.38	0.14	0.95	0.46
	SD	1.16	0.95	0.95	1.16

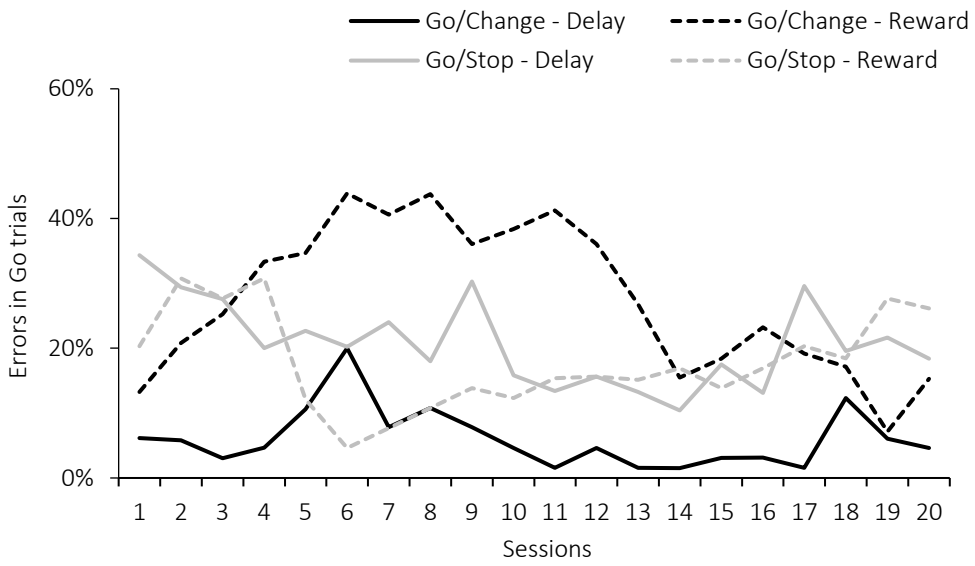

Figure 4.1.1. Error rates in Go trials, depending on experimental condition. An error in a Go trial is defined as, for the Go/Stop task, making fewer than two pecks at the Go stimulus and, for the Go/Change task, pecking the alternative key or not pecking any key.

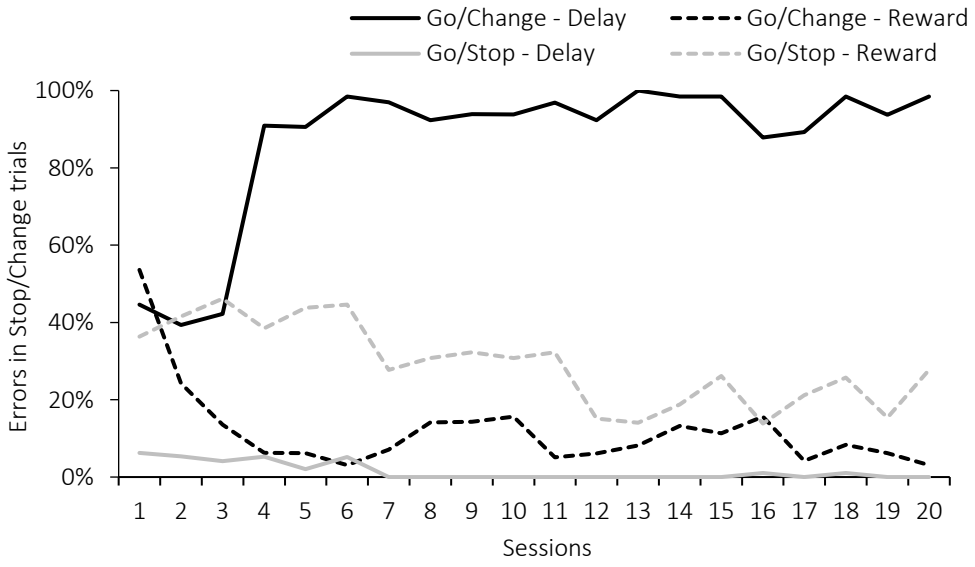

Figure 4.1.2. Error rates in Stop trials (for the pigeons in the Go/Stop task) and Change trials (for the pigeons in the Go/Change task), depending on experimental condition. An error in a Stop trial is defined as making two or more pecks at the Go stimulus, an error in a Change trial is defined as pecking the Go stimulus or not pecking any key.

Despite the differences in error rates, the number of pecks that pigeons made in Stop and Change trials were not significantly different between conditions; neither in the number of incorrect pecks at the Go stimulus, $F(3,6)=3.31$, $p=.099$, nor in the number of pecks at the yellow alternative key, $F(3,6)=3.52$, $p=.089$.

To account for the fact that the pigeons had to learn how to respond to the Stop and Change stimulus in the first few sessions of the task, the analyses were repeated using only the last half of sessions.

Overall errors remained significantly different between groups, $F(3,6)=65.92$, $p<.001$, $\eta_p^2=.97$. This difference was still caused by pigeons in the Go/Change-Delay group performing significantly worse than those in any other group, Bonferroni post-hoc comparisons: relevant $p\leq.001$, comparison between Go/Stop-Delay and Go/Stop-Reward: $p=.068$, other comparisons: $p\geq.37$. The difference between groups in response to Go trials disappeared entirely in the second half of the experiment (see Figure 4.1.1); in the last ten sessions, accuracy levels in Go trials were not significantly different across the four conditions, $F(3,6)=2.43$, $p=.16$. The differences between groups in Stop and Change trials however remained (see Figure 4.1.2), $F(3,6)=106.85$, $p<.001$, $\eta_p^2=.98$; the pigeons in the Go/Change-Delay group performed significantly worse than those in the other three groups, all $p<.001$; the pigeons in the Go/Stop-Reward group performed marginally worse than the pigeons in the Go/Stop-Delay group, $p=.068$; all other comparisons: $p\geq.41$.

Pecking rates in Stop and Change trials did not differ between groups in the second half of the experiment, neither in the number of pecks directed at the Go stimulus, $F(3,6)=3.16$, $p=.11$, nor the pecks directed at the alternative key, $F(3,6)=3.28$, $p=.10$.

Discussion

In this section, I aimed to establish the most efficient method of training pigeons in a response-inhibition paradigm. Specifically, I investigated the following questions: can pigeons acquire either a Stop-Signal task or a Change-Signal task, or might there be a bias towards learning one task more readily than the other? And does the ease of acquisition of either task depend on whether the

pigeons are rewarded for successful response inhibition or punished for a failure of inhibition?

The results paint a clear picture: whilst there is no direct indication that one task is more readily acquired than the other, the ease of acquisition of either task does seem to vary depending on reinforcement method. Pigeons in the Go/Change task, in which they had to perform an alternative action when the Change stimulus was presented, learned to do so much faster (or only) when they were rewarded for making that alternative response than when the incorrect execution of the Go response was punished with a delay period.

For the pigeons in the Go/Stop task, which required the withholding of any response in trials in which the Stop signal was shown, as seen in Figure 4.1.2, being punished for making a wrong response resulted in a somewhat more successful performance in Stop trials in the latter half of the experiment than receiving a reward for correctly withholding any response.

Overall, the Go/Stop-Delay condition seemed to achieve the most stable level of response inhibition. The Go/Change-Reward condition also elicited good levels of response inhibition, as overall accuracy was above the success criterion of 80%. Similar results have previously been found in humans, for example by Guitart-Masip, Huys, Fuentemilla et al. (2012), whose participants were better at learning a particular response when correct behaviour was rewarded, and better at withholding a response when incorrect behaviour was punished. Guitart-Masip et al. (2012) argued that these findings reflect the disruptive influence of Pavlovian processes, by which an individual learns about the affective value of an outcome, on instrumental learning, by which an individual learns a behavioural response based on its consequences. As discussed in Sections 2.2 and 3.4, the behaviour of pigeons might predominantly be determined by Pavlovian processes, which was reflected in the marked influence of the positive or negative affect associated with a particular response key on the pigeons' behaviour.

4.2 Procedures for a Comparative Response-Inhibition Paradigm

In Section 4.1, it was shown that pigeons could succeed in both a Go/Stop and a Go/Change paradigm. The pigeons' performance in the Go/Stop task seemed to be the most stable if the pigeons were punished for failing to inhibit a response. Conversely, the pigeons completing the Go/Change task in Section 4.1 showed a better level of accuracy if they were rewarded for correct response alteration.

Because both tasks have distinct merits in the investigation of response-inhibition processes, in the following sections, the response-inhibition ability of pigeons and humans were assessed in both a Stop-Signal and a Change-Signal task. The tasks that the humans completed were modelled on the tasks used with pigeons. For each task, I administered the reinforcement method that facilitated performance of the pigeons the most in that task; that is, subjects assigned to the Stop-Signal task were punished with a delay to the next trial for failing to inhibit the Go response in trials that afforded it, and subjects performing the Change-Signal task were rewarded for correctly executing the alternative response when signalled to do so. The procedures of the Stop-Signal and the Change-Signal tasks were otherwise identical, except of course for the response requirements to Stop or Change. Figure 4.2.1 illustrates the trial procedure and reinforcement contingencies for the two tasks.

Pigeons

In the full Change-Signal and Stop-Signal tasks (shown in Figure 4.2.1), each trial began with the presentation of a white start key (75 pixels / 22.5mm in diameter) presented in the centre of a black display to focus attention on the screen. Following two pecks at the start key, it was replaced by a smaller circular key (50 pixels / 15mm in diameter) in the display centre that varied in appearance, to serve as a cue (its function is described below). A peck at this cue led to the addition of two circular response keys (each 50 pixels / 15mm in diameter), whose centres were offset by 50 pixels (15mm) to the left and the right side of the centre of the still visible cue. One of these keys was filled in red or green (counterbalanced across subjects). The other key was yellow and

served as a pecking alternative to the red or green stimulus. The locations of the stimulus and the alternative key (left or right) were randomised across trials.

For some pigeons, a green stimulus indicated that the current trial was a Go trial and a red stimulus indicated a Stop or Change trial; for other pigeons, the colour assignment was reversed. Only on some of the Stop/Change trials (see below for the exact ratio), the Stop/Change signal was shown right from the beginning of the trial; on the remaining Stop/Change trials, the trial started with the presentation of the Go stimulus, which was then replaced with the Stop/Change signal after one of three stimulus-onset intervals. This procedure is described in more detail below.

Before performing the full task, pigeons went through several training stages to learn the correct response to each part of the task. During all training sessions, pecking the start key led directly to the presentation of the two response keys; that is, the cue was omitted from the display entirely during training.

Go Training

First, the pigeons received Go-training sessions, each consisting of 64 Go trials. The procedure of the Go training was identical to that reported in Section 4.1.
The presentation time of the stimulus display was decreased as described in Section 4.1 from 20 seconds to 4 (the lowest value in the Change-Signal task) or 2.5 seconds (the lowest possible value in the Stop-Signal task). If performance was below 70% overall in a session, the presentation time was increased by a second for the following session. After an increase, the value was decreased again if the pigeon completed the next two sessions above 85%. Otherwise, training continued at the increased value until the pigeon performed at 80% or above in two consecutive training sessions to pass this training stage. The stimulus presentation interval at which a pigeon passed the Go training was used as the stimulus presentation interval for all following sessions for that pigeon.

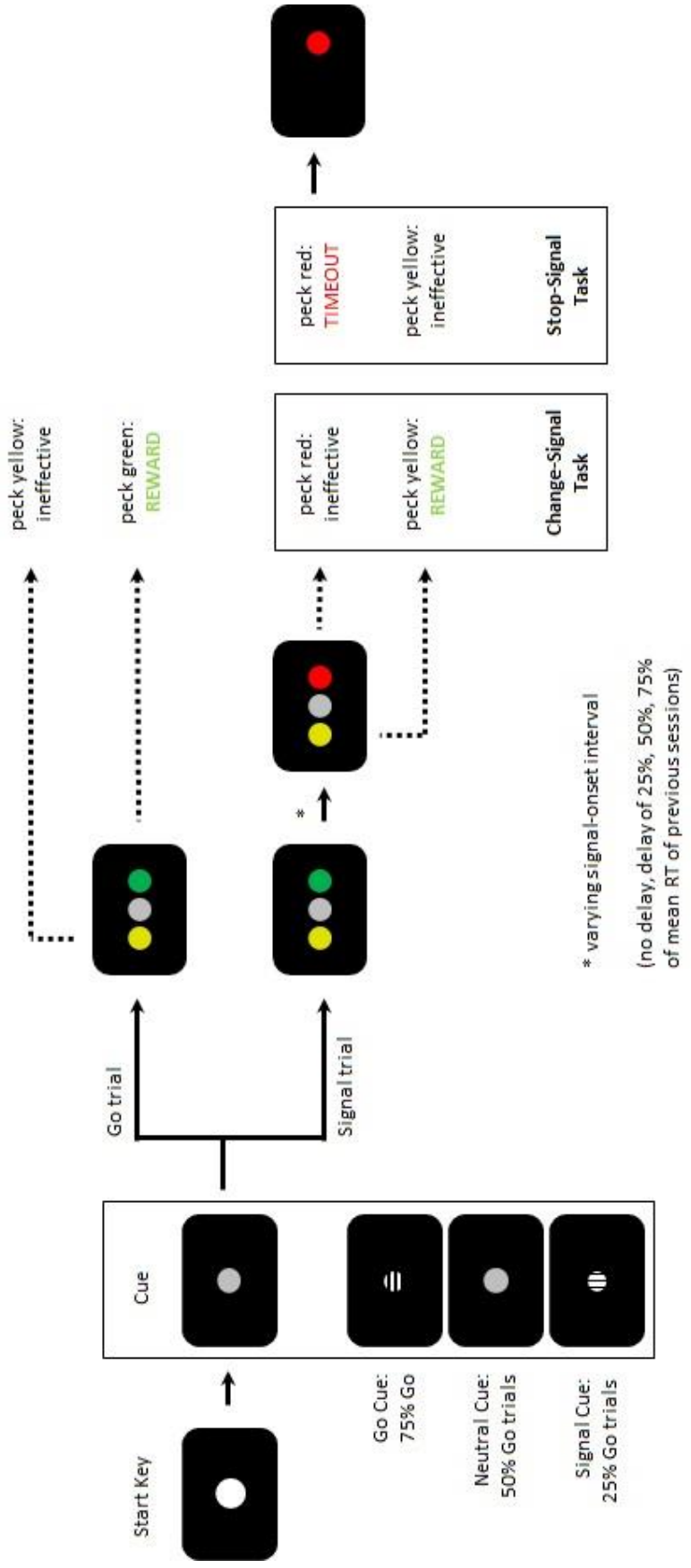

Figure 4.2.1. Procedure of Go and Signal trials and respective reinforcement contingencies in the Change-Signal and Stop-Signal task. *Note:* the Start Key was only presented to pigeons, but not to humans. The colour of the Go stimulus and Signal (green and red) were counterbalanced across subjects.

Go/Stop and Go/Change Training

Once the Go-training pass criterion was met, pigeons completed twenty Go/Stop or Go/Change training sessions, which were identical in procedure to those described in Section 4.1, with the difference that, for both tasks, now, two pecks at the stimulus were required in Go trials to obtain the reward key.

For reasons that will become apparent below, the remaining trials will be referred to as no-delay Stop-Signal and no-delay Change-Signal trials. In these trials, instead of the Go stimulus, the Stop or Change signal was presented; reinforcement contingencies varied between the Stop-Signal and the Change-Signal task.

In the Stop-Signal task, if a pigeon made no or only a single peck at the Stop signal during the stimulus presentation interval, the trial terminated after completion of this interval and a new trial started. If the pigeon made a second peck at the Stop signal, it entered a timeout period in which the signal remained on screen for four times the duration of the stimulus presentation interval (i.e., if the pigeon's stimulus presentation interval was 3 seconds, the delay period was set to 12 seconds), before the trial was terminated and a new trial started after an inter-trial interval of 10 seconds. During this timeout period, pecking the Stop signal had no effect. The six pigeons completing the Stop-Signal task reliably responded to at least 80% of Go trials and withheld a response on at least 80% of no-delay Stop-Signal trials at the end of the twenty training sessions.

In no-delay Change-Signal trials, two pecks at the yellow alternative key resulted in the immediate deletion of the response display and the presentation of the reward key closest to the alternative key, followed by access to the respective food magazine for 2.5 seconds. Any pecks at the Change signal were ineffective for the duration of the display presentation interval; if no pecks at the alternative key were made during this interval, the trial was terminated and the next trial started after an inter-trial interval of 10 seconds. The six pigeons in the Change-Signal task successfully pecked the Go stimulus on at least 80% of Go trials and pecked the alternative key on at least 80% of no-delay Change-Signal trials by the end of the twenty training sessions.

Delayed Signal Training

Upon reaching the pass criterion of the Go/Stop and Go/Change training, pigeons were given ten sessions in which, in addition to Go and no-delay Signal

trials, they also experienced Signal trials in which the appearance of the signal was delayed. In these trials, after pecking the start key, the Go stimulus was initially presented; it was subsequently replaced by the Stop or Change signal after one of three defined intervals (conventionally referred to as stop-signal-onset intervals, or SSOs): they were set to 25%, 50% and 75% of a pigeon's mean response time in the previous session. That is, the absolute values of the SSOs in a given session depended on the pigeon's performance in the previous session; it could thus change from one session to the next. I established this tracking procedure in an effort to estimate the pigeons' ability to withhold a response at different stages of response preparation better than would be possible using arbitrarily chosen, fixed values, which might be too short or too long to necessitate any potential inhibitory control. Each of the three SSOs occurred equally often. The onset of the Stop or Change signal indicated that any pecking response towards the Go stimulus should be withheld. If, in the Stop-Signal task, the Go stimulus was pecked twice before the signal appeared, the pigeon immediately entered the timeout period in which the signal was presented on its own; to calculate the probability of incorrectly responding (and failing at inhibition), such a pre-emptive response was coded as an incorrect response in both the Stop-Signal and the Change-Signal task (even though at the time of making the response the signal had not appeared yet). Similarly, if, in the Change-Signal task, the alternative key was pecked twice before the signal onset, it was coded as a correct response; the second peck led to the immediate presentation of the reward key.

Each of the ten 64-trial Signal-training sessions consisted of 48 Go trials, four no-delay Signal trials, four 25%-delayed Signal trials, four 50%-delayed Signal trials and four 75%-delayed Signal trials; that is, 75% of all trials were Go trials.

Cued Stop-Signal and Change-Signal Task

Following the Delayed Signal training sessions described above, the pigeons completed 30 further Signal sessions in which cues were presented prior to and during the stimulus display, as shown in Figure 4.2.1. The cue predicted the likelihood of the occurrence of a signal on this trial. There were three distinct cues: Cue A indicated that there would be a signal on the current trial with a probability of 25%; it preceded 18 Go trials, three no-delay Signal trials and three delayed Signal trials (each one with a different SSO). Cue B indicated a

50% probability of a signal; it preceded twelve Go trials, six no-delay Signal trials and six delayed Signal trials (two trials of each SSO). Cue C indicated a 75% probability that the current trial would be a Signal trial; it preceded six Go trials, nine no-delay Signal trials and nine delayed Signal trials (three trials of each SSO). For easier discriminability, I shall henceforth refer to Cue A as a Go cue (as it was most likely to be followed by a Go trial), to Cue B as a neutral cue and to Cue C as a Signal cue (as it was most likely to be followed by a Signal trial).

The Go and Signal cues were composed of vertically or horizontally orientated Gaussian grating patterns of high (21 circles per 100 pixels) or low (7 circles per 100 pixels) spatial frequency, 50 pixels (15mm) in diameter. All four possible combinations of horizontal/vertical orientation of the grating and low/high spatial frequency were used and counterbalanced across subjects such that the two cues that indicated either a 25% or a 75% likelihood of a Stop signal on the current trial did not share any identical visual dimensions. For example, if one of the cues was made up of a horizontal grating pattern with a low spatial frequency, the complementary cue was a vertical pattern with a high spatial frequency grating. The neutral cue that indicated a 50% likelihood of an upcoming Signal trial was always uniformly filled with grey. A single peck at a cue led to the addition of the stimulus and alternative key to the display. From here on, the trial procedure matched that of an un-cued Signal trial as described for the Signal-training sessions.

The ratio of Go trials was decreased to 50% of all trials in the cued sessions; this was done to limit the overall duration of a session whilst presenting a sufficient number of Signal trials. Furthermore, to highlight the function of the cues, the number of no-delay Signal trials was increased from ca. 6% of trials in the un-cued Signal-training sessions to 25% of all trials in the cued sessions. Thus, each cued session consisted of 36 Go trials, 18 no-delay Signal trials and 18 delayed Signal trials.

Cue-Probe Sessions

Following the thirty cued Signal sessions, two probe sessions were administered to examine any transfer of response inhibition from the signal to the cues. In these sessions, the same three cues as in the cued Signal sessions were presented, but each cue was followed by 18 Go trials, nine no-delay

Signal trials, and nine delayed Signal trials (three trials of each SOA). That is, all three cues predicted a 50% chance of the occurrence of a signal.

Humans

Human participants completed one block of 72 trials of Signal training as described above for pigeons. This block was followed by 14 blocks of 72 trials of the cued Stop-Signal or Change-Signal task as described above, and then one cue-probe block of 72 trials, also as described above. Each block consisted of 36 Go trials, 18 no-delay Signal trials, six 25%-delayed Signal trials, six 50%-delayed Signal trials and six 75%-delayed Signal trials.
At the start of the experiment, i.e., in the Signal-training block, the signal-onset intervals for the delayed Signal trials were fixed to be 250ms, 500ms and 750ms, respectively. The stimulus-presentation interval was set to two seconds in the Signal-training block; in subsequent blocks, the interval was defined as twice the mean response time of the previous block.

The trial procedure was mainly identical to the procedure used with pigeons, shown in Figure 4.2.1, with the one difference that, in the full Stop-Signal and Change-Signal tasks, the observing key was omitted.
During Signal training, each trial began with the presentation of a white observing key (200 pixels / 60mm in diameter) presented in the centre of a black display. Following a click at the observing key, it was replaced by two circular response keys (each 200 pixels / 60mm in diameter), whose centres were offset by 200 pixels (60mm) to the left and the right side of the display centre. For the cued trials in the subsequent blocks, a cue was presented instead of the observing key; i.e., a trial started with the presentation of one of the three predictive cues (200 pixels / 60mm in diameter). The cue remained visible on screen after being clicked, and the two response keys were added to the display on either side of the cue. One of the response keys was filled in red or green. For some participants, a green stimulus indicated that the current trial was a Go trial and a red stimulus indicated a Stop or Change trial; for other participants, the colour assignment was reversed. The other key was yellow and served as a choice alternative to the red or green stimulus. The locations of the stimulus and the alternative key (left or right) were randomised across trials.

For both the Stop-Signal and the Change-Signal task, in Go trials, a click at the Go stimulus resulted in the deletion of the response display and the presentation of a gold star in the location of the Go stimulus, next to the word “Correct!” presented in white letters in the centre of the display for one second. Then, the next trial started after an inter-trial interval of 100ms. Any clicks on the alternative key were ineffective; if the participant did not click the Go stimulus within the stimulus-presentation interval, the trial ended and the next trial started after the inter-trial interval.

For Signal trials, reinforcement varied between the two tasks. In the Stop-Signal task, any mouse-clicks on the alternative key were ineffective. As for the pigeons, as soon as a participant clicked on the Go stimulus/Stop signal, he or she entered a timeout period in which only the Stop signal remained on screen for three times the stimulus-presentation interval. If no click was made at the stimulus, the trial terminated at the end of the stimulus-presentation interval and the next trial started after an inter-trial interval of 100ms. In the Change-Signal task, any clicks on the stimulus/Stop signal were ineffective. A click on the alternative key resulted in the deletion of the response display and the presentation of a gold star in the location of the alternative key, next to the word “Correct!” presented in white letters in the centre of the display for one second. Then, the next trial started after the inter-trial interval. If the participant did not click the alternative key within the stimulus-presentation interval, the trial ended and next trial started after the inter-trial interval.

At the end of the experiment, participants completed an on-screen questionnaire to assess their approach to the paradigm, and their awareness of the function of the two stimulus colours as either Go or Stop/Change signals and of the function of the predictive cues. The questionnaire is attached as Appendix A4.

Data Collection

To assess whether the predictions made by the independent horse-race model about the duration of Go and Stop processes apply to the performance of pigeons and humans in this paradigm, and to examine the potential influence of cue information on the subjects’ ability to inhibit a response, I recorded error

rates in response to each type of trial. For pigeons, correct responses were defined as follows: for Go trials, pecking the Go stimulus twice in succession (in the Change-Signal task, doing so without previously pecking the alternative key); for Signal trials in the Stop-Signal task, pecking the Go stimulus or Stop signal once or not at all (pecks at the alternative key were irrelevant); for Signal trials in the Change-Signal task, pecking the alternative key twice in succession without previously pecking the Go stimulus. All other responses (including, in the Change-Signal task, making no response) were coded as errors. For humans, correct responses were defined as follows: for Go trials, clicking the Go stimulus; for Stop-Signal trials, not clicking the Go stimulus or Stop signal (clicks at the alternative key were irrelevant); for Change-Signal trials, clicking the alternative key (to allow for comparison to the Stop-Signal task, making no response at all was also considered correct). All other responses were coded as errors. From these measures, it was possible to calculate the probability of responding incorrectly on Signal trials, P(respond), the probability of incorrectly responding on Signal trials after the signal had occurred, P(respond|Signal), and the probability of missing a correct response to the Go stimulus on Go trials, P(miss|Go). These data are conventionally reported in the stop-signal literature and will allow for an accurate comparison of the pattern of performance of pigeons to that of humans. Additionally, I recorded response latencies of the pigeons' first and the second peck, including the identity of the key that was chosen at the first and second peck. For the pigeons in the Change-Signal task, I also recorded the number of pecks at the alternative key and the latencies of the first and second peck at that key. It has to be noted that, although I collected information about the first peck, I focussed the analyses on the second consecutive peck made towards a stimulus, since the first peck might have been of a ballistic nature and might not have been target-specific. For humans, the latencies of clicking a response key and the identity of that key were recorded.

4.3 Are Associative Processes Sufficient to Inhibit or Change a Prepared Response?

In this section, I aimed to verify Verbruggen et al.'s claims (Verbruggen & Logan, 2008b, 2009a; Verbruggen et al., 2014; Best et al., 2016) by assessing whether the predictions made by the independent horse-race model of response inhibition apply to performance that is governed purely by associative processes. More specifically, I investigated whether the model fits the performance of pigeons in the response-inhibition paradigms developed in Section 4.2, which included a Stop-Signal task in which the failure to inhibit the Go response in trials that afforded it was punished with a timeout, and a Change-Signal task in which the correct execution of an alternative response was rewarded, to estimate whether the same or different cognitive processes govern response inhibition in these two tasks. I also accounted for the possibility that executive control mediates goal activation, which might become apparent in sequential effects across trials, by examining the effects of executing or inhibiting a response in one trial on performance in the subsequent trial.

In addition to pigeons, I tested human participants in the same paradigms, to assess whether the Stop-Signal and Change-Signal tasks established in Section 4.2 could elicit the pattern of behaviour in humans that is conventionally observed when completing these response-inhibition tasks.

Subjects

Forty-seven undergraduate Psychology students and twelve pigeons were subjected to the experimental procedure described in Section 4.2. Six pigeons completed the Stop-Signal task, the other six pigeons completed the Change-Signal task. Of the human participants, 30 participants were assigned to the Stop-Signal task, the other 17 participants were in the Change-Signal task. Because trial lengths were adjusted dynamically based on a participant's mean response times, the average trial length increased from one test block to the next for participants who responded very slowly or not at all, to the point that they had not completed the entire experiment before the end of the two hours allocated for the experiment and consequently aborted the task. This affected

15 participants in the Stop-Signal task and one participant in the Change-Signal task. This difference between tasks is not surprising, since the participants in the Stop-Signal task learned that an early response potentially has negative consequences (see Section 3.2 for details) and thus responded more and more slowly; the demand in the Change-Signal task to make a response (either towards the Go stimulus or the alternate key, see Section 3.2 for details) prevented an escalation of response times. The data of those participants was excluded from the analyses reported below, which only includes the data of the 15 participants from the Stop-Signal task and the 16 participants from the Change-Signal task who did complete all test blocks including the probe block. However, the data of the excluded participants that was available at the point at which their session was aborted was compared to the data of those who did complete the experiment. As expected, the participants who were excluded for responding too slowly or not at all showed longer latencies to respond towards the Go stimulus than the included participants, $F(1,32)=25.57$, $p<.001$, $\eta_p^2=.44$, and showed a lower probability of responding to the signal, $F(1,43)=9.28$, $p=.004$, $\eta_p^2=.18$, but they showed no significant differences in their error rates, $F(1,43)=3.05$, $p=.088$.

Results

Pigeons

The pigeons completed the Go training in a mean of 14 sessions. Final stimulus presentation intervals ranged from 2.5 to 4 seconds for pigeons completing the Stop-Signal task and from 4 to 5 seconds for pigeons in the Change-Signal task.

Both error rates and latencies to make two pecks at the stimulus in Go trials, no-delay Signal trials and delayed Signal trials were analysed in repeated-measures ANOVAs using Trial Type (Go, no-delay Signal, 25%-delayed Signal, 50%-delayed Signal, 75%-delayed Signal) as a within-subjects factor and Task (Stop-Signal or Change-Signal) as a between-subjects factor.

Conventionally, the human response-inhibition literature considers the probability of incorrectly responding on Signal trials, P(respond), and the latency to make a response to the Go stimulus on both Go and Signal trials to be the

most informative measures of performance in Stop-Signal and Change-Signal paradigms. In the Stop-Signal task, P(respond) is identical to the pigeons' error rates on Signal trials. For the pigeons in the Change-Signal task, overall error rates additionally included trials in which fewer than two consecutive pecks at either key were made. Hence, in order to facilitate comparison to P(respond) in the Stop-Signal task, trials with such missing responses were recoded as correct in Change-Signal trials (making errors on Change-Signal trials synonymous to the probability of responding to the incorrect key instead of making any other response), those data are also reported in Table 4.3.1. P(respond) includes responses to the Go stimulus before the appearance of the signal; I also recorded the probability of responding to the signal when it had already occurred, P(respond|Signal), so that this could be contrasted with the overall error rates on Signal trials. P(respond|Signal) in Signal trials was examined via a repeated-measures ANOVA using Signal Delay (no delay, 25% delay, 50% delay and 75% delay) as a within-subjects factor and Task (Stop-Signal or Change-Signal) as a between-subjects factor.

For the Change-Signal task, I also recorded the latencies to peck the alternative key, which made it possible to compare the latencies to peck the correct key across trial types, using a repeated-measures ANOVA with Trial Type as a within-subjects factor. Where applicable, the reported results were subject to Huynh-Feldt corrections. Descriptive statistics for all dependent variables are summarised in Table 4.3.1.

The potential influence of the previous trial type (Go or Signal trial) on performance in each measure was examined in repeated-measures ANOVAs using Current Trial Type (Go, no-delay Signal, 25%-delayed Signal, 50%-delayed Signal, 75%-delayed Signal) and Previous Trial Type (Go or Signal) as within-subjects factors, and Task (Stop-Signal or Change-Signal) as between-subjects factor (with the exception of the latencies to peck the correct key, which was analysed for the Change-Signal task only). Only trials following a correct trial were included in these analyses to ensure that response execution and inhibition in the previous trial had been successful.

Table 4.3.1. *Pigeons:* Descriptive statistics of errors, P(respond|Signal), latency to peck the Go stimulus and latency of correct responses (Change-Signal task only) depending on Trial Type.

		Trial Type				
		Go	Signal - no delay	Signal - 25% delayed	Signal - 50% delayed	Signal - 75% delayed
Stop-Signal Task						
Errors	Mean %	16.5	0.2	1.8	12.8	34.8
	Std. Error	5.0	2.7	2.5	2.0	2.5
P(respond|Signal)	Mean	-	0.00	0.02	0.11	0.24
	Std. Error	-	0.00	0.00	0.01	0.05
Latency to peck the Go stimulus	Mean ms	1606	2469	667	821	999
	Std. Error	153	523	96	62	82
	Number of valid trials	5417	12	17	136	378
	% of all trials of this type	83.5	0.6	1.6	12.6	35.0
Change-Signal Task						
Errors	Mean %	30.2	24.7	36.0	49.2	61.3
	Std. Error	5.4	3.9	3.8	2.7	2.6
Errors recoded as P(respond)	Mean %	30.2	1.5	1.8	4.8	12.3
	Std. Error	5.4	0.9	0.9	1.3	2.3
P(respond|Signal)	Mean	-	0.02	0.02	0.05	0.08
	Std. Error	-	0.01	0.01	0.01	0.04
Latency to peck the Go stimulus	Mean ms	2016	1802	538	1115	1131
	Std. Error	105	466	357	146	91
	Number of valid trials	4513	50	20	53	133
	% of all trials of this type	69.9	1.5	1.9	4.9	12.4
Latency of correct response (SSO subtracted)	Mean ms	2015	1997	1896	1812	1673
	Std. Error	104	105	84	62	48
	Number of valid trials	752	406	116	91	69
	% of all trials of this type	69.8	75.4	64.3	50.9	38.6

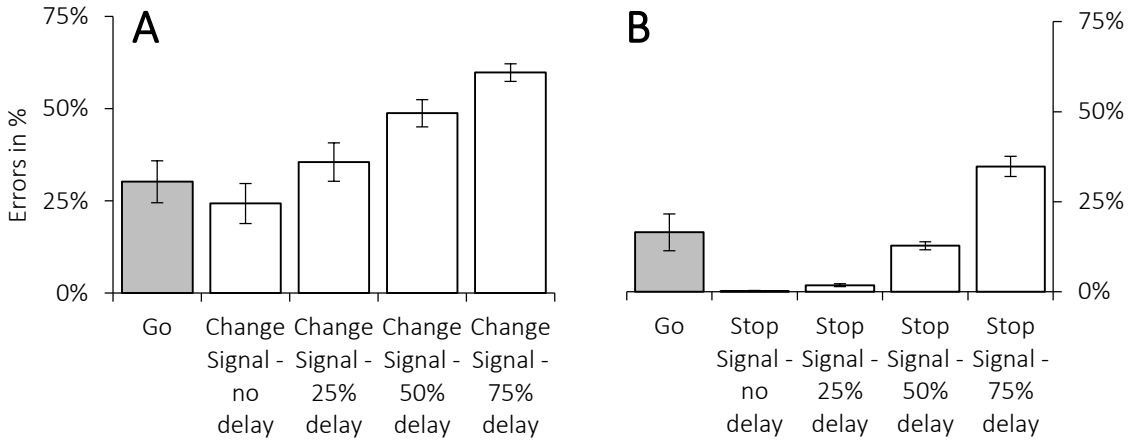

Figure 4.3.1. *Pigeons:* Error rates in % depending on Trial Type in *A)* the Change-Signal task and *B)* the Stop-Signal task. Error bars represent standard errors.

Errors

Error rates are illustrated for each task respectively in Figure 4.3.1. They differed between the Stop-Signal and the Change-Signal tasks, $F(1,10)=38.96$, $p<.001$, $\eta_p^2=.80$, as pigeons in the Change-Signal task made more errors than the pigeons performing the Stop-Signal task. The Trial Type greatly influenced error rates, $F(4,40)=54.66$, $p<.001$, $\eta_p^2=.85$, and the way that error rates depended on Trial Type was significantly affected by the task that pigeons performed, $F(4,40)=5.90$, $p=.009$, $\eta_p^2=.37$.

Post-hoc comparisons revealed that, for the Stop-Signal task, errors on Go trials (i.e., pecking the Go stimulus once or not at all) differed significantly from errors on no-delay Stop-Signal trials (i.e., pecking the Go stimulus twice or more), $p=.026$; for the Change-Signal task, performance was also significantly different between Go trials and no-delay Change-Signal trials, $p=.030$. The uncorrected comparisons are provided here as these give some insight into the pattern present in the data; however, when applying Bonferroni corrections on the basis of all comparisons made in analysing these data, the comparison of Go trials to no-delay Signal trials becomes non-significant for both tasks, both $p\geq.26$.

The mean percentage of errors in Signal trials differed significantly for all uncorrected comparisons between these four trial types in both tasks, all $p\leq.020$.

There was a significant linear trend for both tasks (both $p<.001$; due to the low errors for no-delay and 25%-delayed Stop-Signal trials, there was also a significant quadratic trend in the Stop-Signal task, $p<.001$) in that error rates increased from no-delay Signal trials to 25%-delayed Signal trials to 50%-delayed Signal trials to 75%-delayed Signal trials in both the Stop-Signal task and the Change-Signal task, which is in line with the predictions of the independent horse-race model.

Comparing errors in each Trial Type between the two tasks, error rates in Signal trials differed significantly between the Stop-Signal and the Change-Signal task, all $p\leq.007$; as reported in Table 4.3.1, error rates in response to the signal were higher in the Change-Signal task than in the Stop-Signal task for all four types of Signal trials. Errors on Go trials however, though also somewhat higher in the Change-Signal task, were not significantly different between the two tasks, $p=.10$.

Figure 4.3.6 shows these data in comparison to the human data. The previous trial (Go or Signal) did not significantly affect error rates overall, $F(1,10)=3.93$, $p=.076$, but there was a significant interaction between the previous trial type and the current trial type, $F(4,40)=4.81$, $p=.008$, $\eta_p^2=.33$. The task that the pigeons performed did not influence these results, both interactions: $p\geq.79$. However, the differences were only significant in post-hoc comparisons when no corrections for multiple comparisons were applied; on Go trials, error rates were marginally higher following a Signal trial than following a Go trial (difference: 2.5%, *SE*: 1.1%), $p=.050$. In Signal trials, error rates were somewhat higher following a Go trial than following a Signal trial when the current trial was a 50%-delayed Signal trial (difference: 2.9%, *SE*: 5.1%), $p=.050$, or a 75%-delayed Signal trial (difference: 4.8%, *SE*: 3.6%), $p=.042$; all other comparisons: $p\geq.28$. When Bonferroni-corrections were applied, none of the comparisons were significant, all $p\geq.21$. That is, the pigeons showed a slight tendency to benefit from a repetition in response requirements, but this benefit did not persist in the light of statistical corrections.

P(respond|Signal)

Like overall error rate, the probability of pecking at the signal differed significantly between tasks, $F(1,10)=7.94$, $p=.018$, $\eta_p^2=.44$, although the direction was reversed: pigeons in the Stop-Signal task showed a greater probability of responding after the signal was shown than those in the Change-Signal task, as shown in Figure 4.3.2. Signal Delay had a strong influence on the probability of responding to the signal, $F(3,30)=28.97$, $p<.001$, $\eta_p^2=.74$. The task that pigeons performed influenced the effect of Signal Delay on the likelihood to respond to the signal, $F(3,30)=9.02$, $p=.006$, $\eta_p^2=.47$.

For the pigeons in the Stop-Signal task, uncorrected post-hoc comparisons indicated that P(respond|Signal) differed between all four types of Stop-Signal trials, all $p\leq.035$. A significant linear trend ($p=.003$) confirms that the likelihood of responding to the signal increased from no-delay Stop-Signal trials to 25%-delayed Stop-Signal trials to 50%-delayed Stop-Signal trials to 75%-delayed Stop-Signal trials. However, when applying Bonferroni corrections, P(respond|Signal) did not differ significantly between no-delay Stop-Signal and 25%-delayed Stop-Signal trials, $p=.12$, nor between 50%-delayed and 75%-delayed Stop-Signal trials, $p=.21$; all other $p\leq.045$. In the Change-Signal task, P(respond|Signal) was of a similar magnitude in no-delay Change-Signal and 25%-delayed Change-Signal trials, $p=.70$, and increased significantly from 25%-delayed to 50%-delayed to 75%-delayed Change-Signal trials, all pairwise comparisons: $p\leq.028$. The significant quadratic trend of the data confirms this pattern, $p=.015$. When applying Bonferroni corrections, the difference between 50%-delayed and 75%-delayed Change-Signal trials becomes nonsignificant, $p=.17$, and the difference between no-delay and 75%-delayed Change-Signal trials was marginal, $p=.059$; all other $p\leq.038$. All in all, the patterns for each task largely adhered to the predictions of the independent horse-race model.

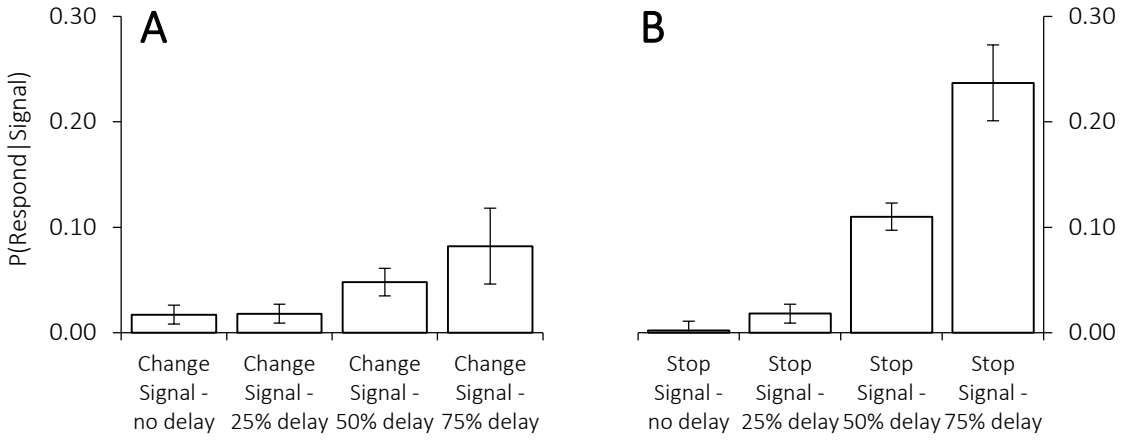

Figure 4.3.2. *Pigeons:* The probability of responding on Signal trials after the signal had occurred, P(Respond|Signal), depending on Trial Type in *A)* the Change-Signal task and *B)* the Stop-Signal task. Error bars represent standard errors.

Figure 4.3.8 shows these data in comparison to the human data. The previous trial (Go or Signal) significantly affected P(respond|Signal), $F(1,10)=6.30$, $p=.031$, $\eta_p^2=.39$, in that the probability of responding to the Signal was greater in trials following a Go trial than in trials following a Signal trial (difference: 0.015, *SE*: 0.006), but there was no significant interaction between the previous trial type and the signal-onset delay of the current trial, $F(3,30)=1.42$, $p=.27$. The task that the pigeons performed did not influence these results, both interactions: $p \geq .42$. This result implies that the pigeons generally showed a greater probability of making an incorrect response if that response was required (and executed) in the previous trial.

Latency to respond

The latencies of the second consecutive peck at the Go stimulus or signal (for the Change-Signal task, without having previously pecked the alternative key) are illustrated in Figure 4.3.3. It has to be noted that only four of the pigeons completing the Stop-Signal task and two pigeons completing the Change-Signal task responded (incorrectly) to the stimulus in at least one trial of each type of Signal trial, and thus produced analysable latencies for every trial type.

For those six pigeons, response latencies did not differ significantly between tasks, $F(1,5)=0.16$, $p=.71$, nor did the task that pigeons performed influence the effect of Trial Type on response times, $F(4,20)=1.83$, $p=.17$. The factor Trial Type did affect latencies significantly, $F(4,20)=10.80$, $p<.001$, $\eta_p^2=.68$.

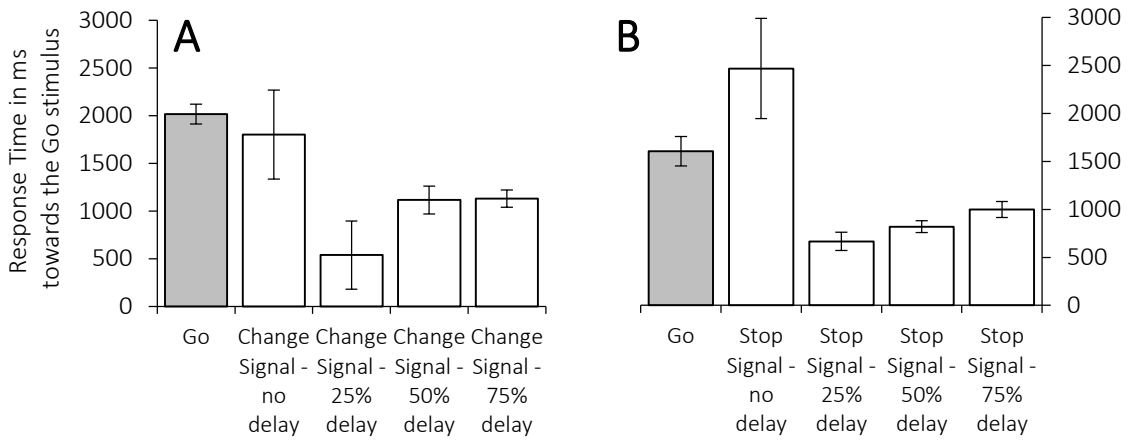

Figure 4.3.3. *Pigeons:* Latencies in ms of the second peck that is made at the Go stimulus, depending on Trial Type, in *A)* the Change-Signal task (given that there have not been any pecks to the alternative key) and *B)* the Stop-Signal task. Error bars represent standard errors.

Post-hoc comparisons between trial types (regardless of task) showed that latencies of correct responses in Go trials and of incorrect responses to the stimulus/signal in no-delay Signal trials were significantly longer than those in the three types of delayed Stop-Signal trials, all $p \leq .023$. The latency to incorrectly peck the stimulus in no-delay trials however did not differ significantly from latencies in Go trials, $p = .38$. Furthermore, the latencies of 75%-delayed Signal trials were significantly longer than those in 50%-delayed Signal trials, $p = .019$. Again, the uncorrected comparisons are provided here to illustrate the pattern present in the data; when applying Bonferroni corrections, only the differences in latencies in Go trials compared to 50%-delayed and 75%-delayed Signal trials stays significant, $p = .002$ and $p = .001$, respectively; all other comparisons: $p \geq .14$. This result is not surprising considering that the number of Signal trials in which the pigeons made an error was very low (it only happened in 799 of the 12932 (6.2%) Signal trials, which resulted in very high variability in the data).

Only two pigeons (one in each task) produced enough data to compare the effects of the previous trial type on response times when the current trial was a Signal trial; therefore, the analysis of sequential effects included Go trials only. Response times in Go trials were not significantly affected by the previous trial type (difference between trials following a Signal trial and following a Go trial: 27ms, *SE*: 24ms), $F(1,10) = 1.58$, $p = .24$. The task that pigeons performed had no

significant influence on this result, $F(1,10)=3.47$, $p=.092$. Figure 4.3.10 shows these data in comparison to the human data.

Latency of correct responses in the Change-Signal task

The data of the Change-Signal task made it possible to assess response latencies to make a correct choice from the moment of the signal onset. For this analysis, I considered only those trials in which both a pigeon's first and second peck were made towards the correct stimulus (Go stimulus on Go trials, alternative stimulus on Change-Signal trials) and occurred after the onset of the Change signal, and subtracted the corresponding SSO of each type of Change-Signal trial from the latency of the second peck. The resulting latencies of the second peck from signal onset are illustrated in Figure 4.3.4. Latencies differed significantly between the five trial types, $F(4,20)=7.40$, $p=.001$, $\eta_p^2=.60$. Uncorrected post-hoc comparisons showed that the latency to peck the correct response key once the signal had appeared in 75%-delayed Change-Signal trials was significantly shorter than the latency to respond correctly in Go trials, $p=.007$, no-delay Change-Signal trials, $p=.012$, and 25%-delayed Change-Signal trials, $p=.025$, and marginally shorter than latencies in 50%-delayed Change-Signal trials, $p=.080$. Further, the difference between making a second peck at the correct key in no-delay Change-Signal trials and in 25%-delayed Change-Signal trials was statistically significant, $p=.008$.

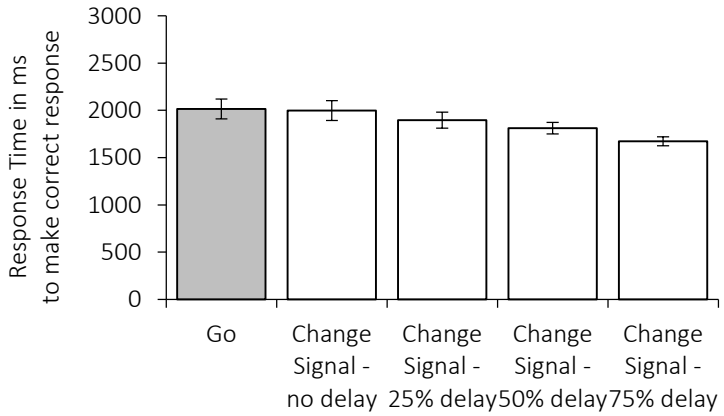

Figure 4.3.4. *Pigeons:* Latencies in ms to make two pecks at the correct key after the signal had occurred in the Change-Signal task. *Note*: in no-delay Signal trials, the signal occurred immediately; in Go trials, no signal occurred, reported are the latencies to respond to the Go stimulus. Error bars represent standard errors.

However, after applying Bonferroni corrections, the latencies to make a correct response did not differ significantly across the five trial types, although the difference between Go trials and 75%-delayed Change-Signal trials and the difference between no-delay and 25%-delayed Change-Signal trials remained marginally significant, p=.065 and p=.081 respectively, all other $p \geq .13$. Nonetheless, there is a significant linear trend in the data, p=.013; latencies decrease across trial types.

The previous trial (Go or Signal) did not significantly affect latencies to peck the correct key, $F(1,5)=1.02$, p=.36, nor was there an interaction between the previous and the current trial type, $F(4,20)=2.27$, p=.15.

Humans

As for pigeons, error rates and latencies to click on the stimulus in Go trials, no-delay Signal trials and delayed Signal trials were analysed in two repeated-measures ANOVAs using Trial Type (Go, no-delay Signal, 25%-delayed Signal, 50%-delayed Signal, 75%-delayed Signal) as a within-subjects factor and Task (Stop-Signal or Change-Signal) as a between-subjects factor. The error rates for Signal trials are identical to P(Respond) for both the Stop-Signal and the Change-Signal task, as only clicks at the Go stimulus were marked incorrect in these trials; all other behaviour (i.e., clicking the alternative key or making no response) were marked as correct. As for the pigeons, I also assessed the probability of responding to the signal when it had already occurred, P(respond|Signal), via a repeated-measures ANOVA, using Signal Delay (no delay, 25% delay, 50% delay and 75% delay) as a within-subjects factor and Task (Stop-Signal or Change-Signal) as a between-subjects factor.

For the Change-Signal task, I additionally compared the latencies to click the correct key across trial types, using a repeated-measures ANOVA with Trial Type as a within-subjects factor. Where applicable, the reported results were subject to Huynh-Feldt corrections. Descriptive statistics for all dependent variables are summarised in Table 4.3.2.

As for the pigeons, the potential influence of the previous trial type (Go or Signal trial) on performance in each measure was examined in repeated-measures ANOVAs using Current Trial Type (Go, no-delay Signal, 25%-delayed Signal, 50%-delayed Signal, 75%-delayed Signal) and Previous Trial Type (Go or

Signal) as within-subjects factors, and Task (Stop-Signal or Change-Signal) as between-subjects factor (with the exception of the latencies to click the correct key, which was analysed for the Change-Signal task only). Only trials following a correct trial were included in these analyses to ensure that response execution and inhibition in the previous trial had been successful.

Table 4.3.2. *Humans:* Descriptive statistics of errors, latency to click the Go stimulus, P(respond|Signal) and latency of correct responses (Change-Signal task only) depending on Trial Type.

		Trial Type				
		Go	Signal - no delay	Signal - 25% delayed	Signal - 50% delayed	Signal - 75% delayed
Stop-Signal Task						
Errors	Mean %	5.7	11.8	46.7	73.5	87.1
	Std. Error	3.0	4.4	3.6	3.2	3.0
P(respond|Signal)	Mean	-	0.13	0.48	0.57	0.55
	Std. Error	-	0.04	0.04	0.05	0.04
Latency to click the stimulus	Mean ms	676	831	538	581	628
	Std. Error	36	95	25	22	27
	Number of valid trials	7119	449	590	925	1096
	% of all trials of this type	94.2	11.9	46.8	73.4	87.0
Change-Signal Task						
Errors	Mean %	16.0	11.3	19.9	47.9	69.9
	Std. Error	5.1	4.4	4.0	4.2	4.1
P(respond|Signal)	Mean	-	0.13	0.21	0.47	0.57
	Std. Error	-	0.04	0.04	0.04	0.05
Latency to click the stimulus	Mean ms	749	754	613	606	658
	Std. Error	52	89	77	42	45
	Number of valid trials	6775	457	268	644	939
	% of all trials of this type	84.0	11.3	19.9	47.9	69.9
Latency of correct response (SSO subtracted)	Mean ms	737	755	691	721	642
	Std. Error	55	43	42	61	43
	Number of valid trials	6775	3511	1030	575	218
	% of all trials of this type	84.0	87.1	76.6	42.8	16.2

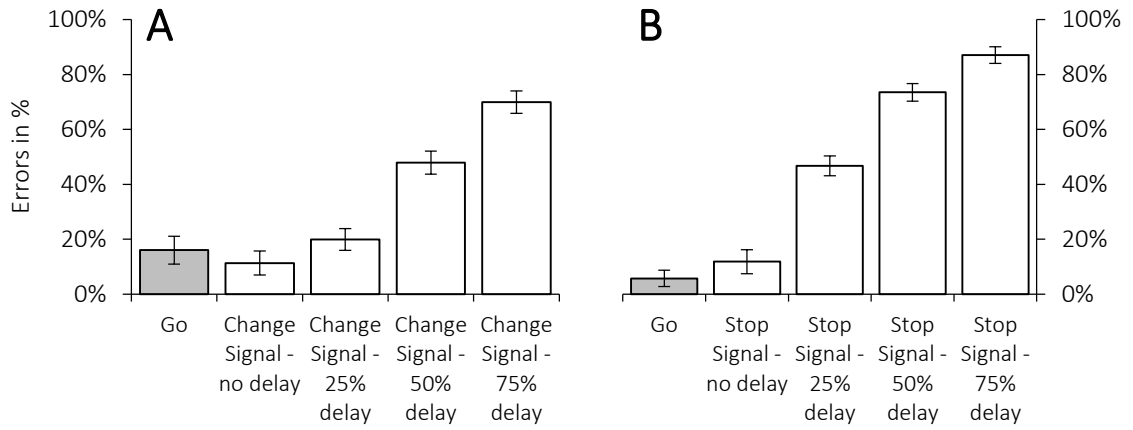

Figure 4.3.5. *Humans:* Error rates in % depending on Trial Type in *A)* the Change-Signal task and *B)* the Stop-Signal task. Error bars represent standard errors.

Errors

Error rates are illustrated for each task respectively in Figures 4.3.5. For both Stop-Signal and Change-Signal trials, error rates are identical to the probability of incorrectly responding to the Go stimulus, P(respond). Errors differed between the Stop-Signal and the Change-Signal tasks, $F(1,29)=18.11$, $p<.001$, $\eta_p^2=.38$, as participants in the Stop-Signal task made more errors overall than those in the Change-Signal task. The Trial Type greatly influenced error rates, $F(4,116)=119.66$, $p<.001$, $\eta_p^2=.81$, and the task that was performed significantly influenced the effect of Signal Delay on error rates, $F(4,116)=8.82$, $p=.001$, $\eta_p^2=.23$.

Bonferroni post-hoc comparisons revealed that, for the Stop-Signal task, errors in Go trials (i.e., not clicking the Go stimulus) did not differ significantly from errors in no-delay Stop-Signal trials (i.e., clicking the Go stimulus), $p=.63$, but did differ from errors in the three delayed Stop-Signal trials, all $p<.001$. Mean error rates in Stop-Signal trials differed significantly for all comparisons between these four trial types, all $p\leq.001$, as errors increased from no-delay Stop-Signal trials to 25%-delayed Stop-Signal trials to 50%-delayed Stop-Signal trials to 75%-delayed Stop-Signal trials.

In the Change-Signal task, performance was significantly different for all comparisons of 50%-delayed and 75%-delayed Signal trials, all $p\leq.003$. Error rates in no-delay Change-Signal trials were not significantly smaller than those

in 25%-delay Change-Signal trials, p=.17, and marginally but non-significantly smaller than those in Go trials, p=.056. Taken together, error rates were of comparable size in no-delay and 25%-delayed Change-Signal trials, but increased to 50%-delayed Change-Signal trials and again to 75%-delayed Change-Signal trials.

Comparing errors in each trial type between the two tasks, error rates in the three delayed types of Signal trials differed significantly between the Stop-Signal and the Change-Signal task, all p≤.002; as reported in Table 4.3.2, error rates in response to the signal were higher in the Stop-Signal task than in the Change-Signal task for those Signal trials. Errors in no-delay Signal trials were of comparable magnitude in the two tasks, p=.94. Errors in Go trials, though somewhat lower in the Stop-Signal task, were also not significantly different between the two tasks, p=.095.

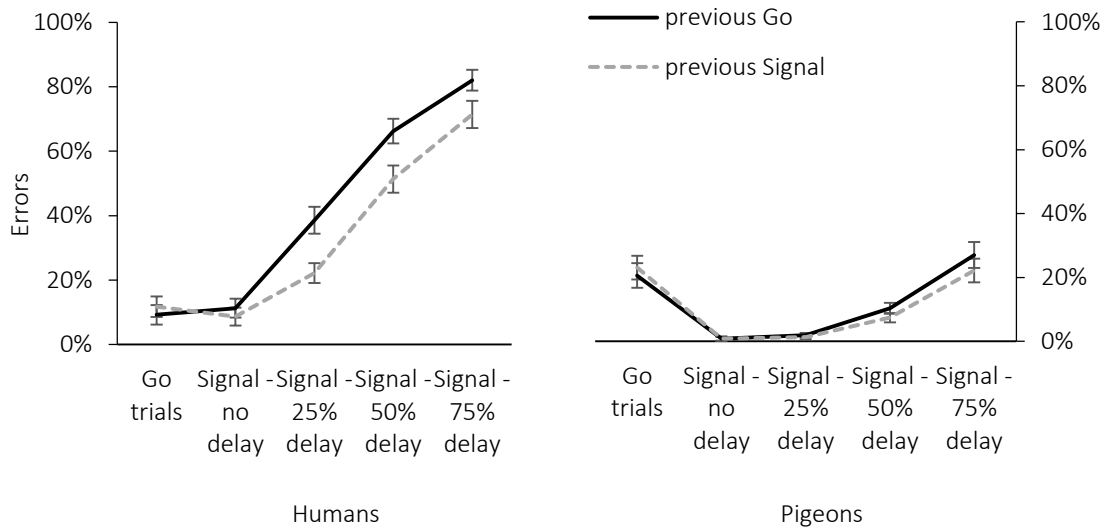

Figure 4.3.6. Error rates in trials following a Go trial and trials following a Signal trial, depending on the current trial type (Go, no-delay Signal, 25%-delayed Signal, 50%-delayed Signal or 75%-delayed Signal trial), for humans and pigeons.

As shown in Figure 4.3.6, the previous trial (Go or Signal) significantly affected error rates, F(1,29)=44.92, p<.001, η_p^2=.61, and there was a significant interaction of the previous trial type with the current trial type, F(4,116)=12.48, p<.001, η_p^2=.30. These results did not differ between the two tasks that were

performed, both interactions: $p \geq .11$. Bonferroni post-hoc comparisons showed that, on Go trials, error rates were significantly higher following a Signal trial than following a Go trial (difference: 2.4%, *SE*: 0.7%), $p = .005$. In Signal trials, error rates were significantly higher following a Go trial than following a Signal trial when the current trial was a 25%-delayed Signal trial (difference: 16.6%, *SE*: 2.5%), *p<.001;* 50%-delayed Signal trial (difference: 14.9%, *SE*: 3.2%), $p = .001$, or a 75%-delayed Signal trial (difference: 10.6%, *SE*: 2.3%), $p = .001$. For no-delay Signal trials, the difference was not-significant (difference: 2.7%, *SE*: 0.9%), $p = .13$.

Comparing across species, humans and pigeons differed significantly in the way the previous trial type affected error rates on the subsequent trial, three-way interaction between previous trial type, current trial type and species: $F(4,156) = 2.96$, $p = .030$, $\eta_p^2 = .07$. Although the same general pattern - in that performance benefitted when the current trial afforded the same response (either response execution or response inhibition) as the previous trial - was somewhat visible in the performance of pigeons, humans showed a greater decrease in error rates following a Signal trial than pigeons when the current trial was a 25%-delayed Signal trial, $p < .001$, or a 50%-delayed Signal trial, $p = .017$ (see Figure 4.3.6).

P(respond|Signal)

The probability of responding to the signal, shown in Figure 4.3.7, differed significantly between tasks, $F(1,29) = 6.47$, $p = .017$, $\eta_p^2 = .18$. Signal Delay had a strong influence on the probability of responding to the signal, $F(3,87) = 50.43$, $p < .001$, $\eta_p^2 = .64$, and the task that was performed significantly influenced the effect of Signal Delay on the likelihood to respond to the signal, $F(3,87) = 5.42$, $p = .003$, $\eta_p^2 = .16$.

For the Stop-Signal task, Bonferroni post-hoc tests indicated that P(respond|Signal) was significantly lower for no-delay Stop-Signal trials than for the other three types of Stop-Signal trials, all $p \leq .001$. All comparisons between the other three trial types were non-significant, all $p \geq .41$.

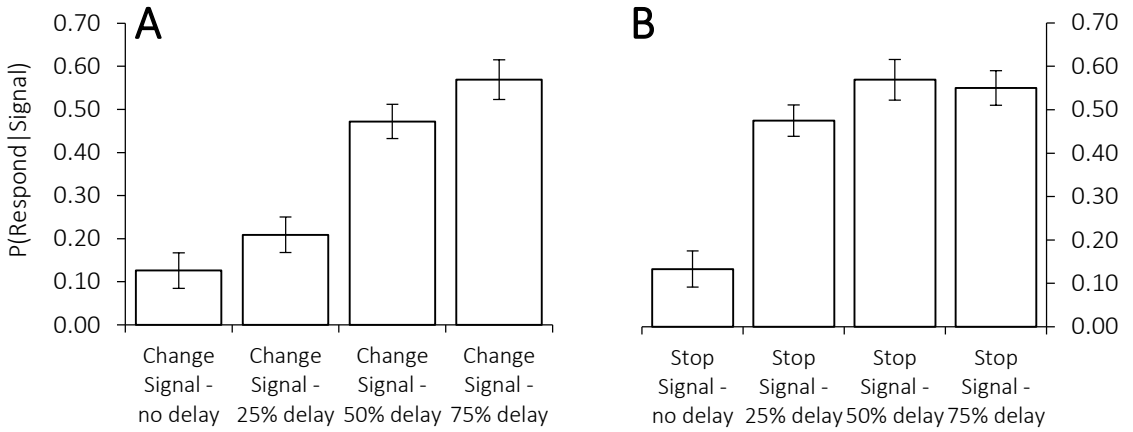

Figure 4.3.7. *Humans:* The probability of responding on Signal trials after the signal had occurred, P(Respond|Signal), depending on Trial Type in *A)* the Change-Signal task and *B)* the Stop-Signal task. Error bars represent standard errors.

In the Change-Signal task, P(respond|Signal) was of a similar magnitude in no-delay Change-Signal and 25%-delayed Change-Signal trials, p=.11, but it was significantly increased in 50%-delayed and 75%-delayed Change-Signal trials, all p≤.001. 50%-delayed and 75%-delayed Change-Signal trials did not differ from each other, p=.31.

As shown in Figure 4.3.8, the previous trial (Go or Signal) significantly affected P(respond|Signal), $F(1,28)=21.79$, $p<.001$, $\eta_p^2=.44$, and there was a significant interaction between the previous trial type and the current trial type, $F(3,84)=3.40$, $p=.027$, $\eta_p^2=.11$. The task that was completed did not affect these results, both interactions: $p\geq.24$. Bonferroni post-hoc comparisons show that the probability of responding to the signal was significantly higher following a Signal trial than following a Go trial when the current trial was a no-delay Signal trial (difference: 0.03, *SE*: 0.01), p=.026, 25%-delayed Signal trial (difference: 0.16, *SE*: 0.03), $p<.001$, or a 50%-delayed Signal trial (difference: 0.13, *SE*: 0.04), p=.003, but not when the current trial was a 75%-delayed Signal trial, p=.091. Humans and pigeons did not differ significantly in the way the previous trial type affected P(respond|Signal) on the current trial, three-way interaction between previous trial type, current trial type and species: $F(3,117)=1.04$, p=.38.

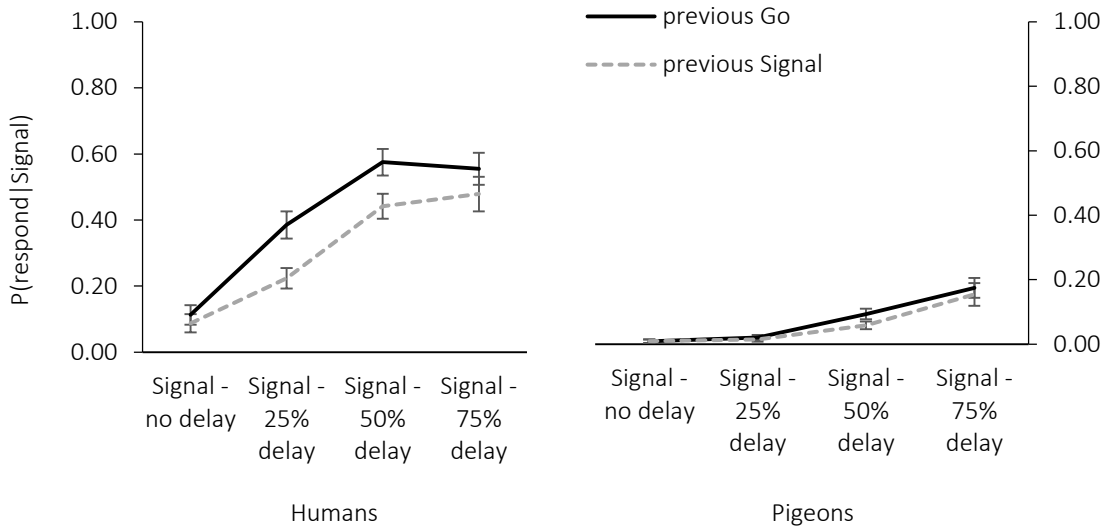

Figure 4.3.8. P(respond|Signal) in trials following a Go trial and trials following a Signal trial, depending on the current trial type (no-delay Signal, 25%-delayed Signal, 50%-delayed Signal or 75%-delayed Signal), for humans and pigeons.

Latency to respond

The latencies to click the stimulus (for the Change-Signal task, without having previously clicked the alternative key) are illustrated in Figure 4.3.9. Response latencies did not differ significantly between tasks, $F(1,25)=0.13$, $p=.72$, nor did the task that was performed influence the effect of Trial Type on response times, $F(4,100)=1.40$, $p=.26$. The factor Trial Type did affect latencies significantly, $F(4,100)=11.75$, $p<.001$, $\eta_p^2=.32$.

Bonferroni post-hoc comparisons showed that, for the Stop-Signal task, latencies of correct responses in Go trials were significantly longer than the latencies of incorrect responses to the Go stimulus in the three types of delayed Stop-Signal trials, all $p\leq.042$. Further, the latencies of 75%-delayed Stop-Signal trials were significantly longer than those in 50%-delayed Stop-Signal trials, $p=.011$, and in 25%-delayed Stop-Signal trials, $p=.006$. Latencies in no-delay Stop-Signal trials were marginally longer than those in 25%-delayed Stop-Signal trials, $p=.099$; all other comparisons between trials: $p\geq.15$.

For the Change-Signal task, latencies in Go trials were significantly longer than those of 50%-delayed and 75%-delayed Change-Signal trials, both $p\leq.001$. All other comparisons between trials were non-significant, all $p\geq.11$.

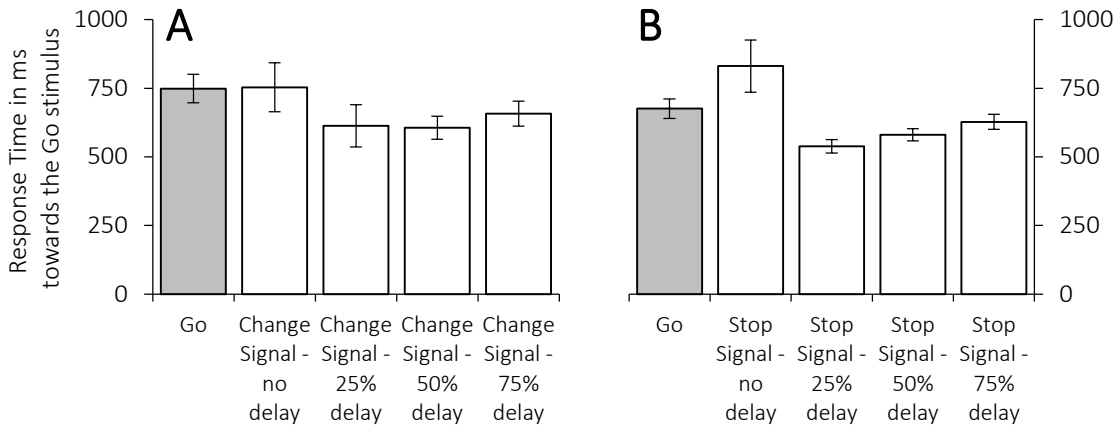

Figure 4.3.9. *Humans:* Latencies in ms to click the Go stimulus/signal, depending on Trial Type, in *A)* the Change-Signal task (given that there have not been any clicks at the alternative key) and *B)* the Stop-Signal task. Error bars represent standard errors.

When comparing latencies to respond to the stimulus in each Trial Type between tasks, latencies to correctly choose the stimulus in Go trials were not significantly different in the Change-Signal task and in the Stop-Signal task, all $p \geq .31$.

Eighteen humans produced sufficient data to analyse the effect of the previous trial type on response times towards the Go stimulus. For those participants, the previous trial (Go or Signal) did not significantly affect the latencies to respond to the Go stimulus, $F(1,16)=0.27$, $p=.61$; nor was there an interaction between the previous and the current trial type, $F(4,64)=1.10$, $p=.36$. The task that was performed did not affect these results, both $p \geq .28$. To compare performance to pigeons, the analysis of sequential effects was repeated including Go trials only. As shown in Figure 4.3.10, response times were significantly longer in Go trials following a Signal trial than in those following a Go trial (difference: 73ms, *SE*: 15ms), $F(1,29)=22.88$, $p<.001$, $\eta_p^2=.44$. This result was not affected by the task that was completed, $F(1,29)=1.42$, $p=.24$. Humans and pigeons differed significantly in the way the previous trial type affected response times on the current Go trial, interaction between previous trial type and species: $F(1,39)=12.75$, $p=.001$, $\eta_p^2=.25$ (see Figure 4.3.10).

Latency of correct responses in the Change-Signal task

As above for pigeons, I considered only those trials in which the first click was made at the correct key (Go stimulus on Go trials, alternative key on Change-Signal trials) and occurred after the onset of the Change signal, and subtracted the corresponding SSO of each type of Change-Signal trial from the response latency. The resulting latencies from signal onset are illustrated in Figure 4.3.11. Latencies did not differ significantly between the five Trial Types, $F(4,60)=1.97$, $p=.13$. There was no significant linear trend or non-linear trend in the data when considering all trials, $p>.071$, but the latency to make a correct response decreased linearly when considering only the four types of Change-Signal trials, $p=.029$.

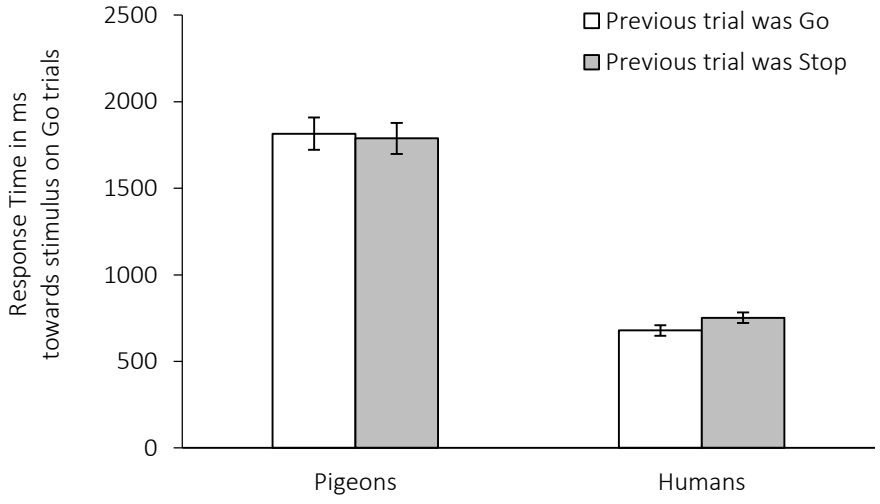

Figure 4.3.10. Response times towards the Go stimulus in Go trials, depending on whether the previous trial was a Go trial (white bars) or a Signal trial (grey bars), for pigeons and humans. Error bars represent standard errors.

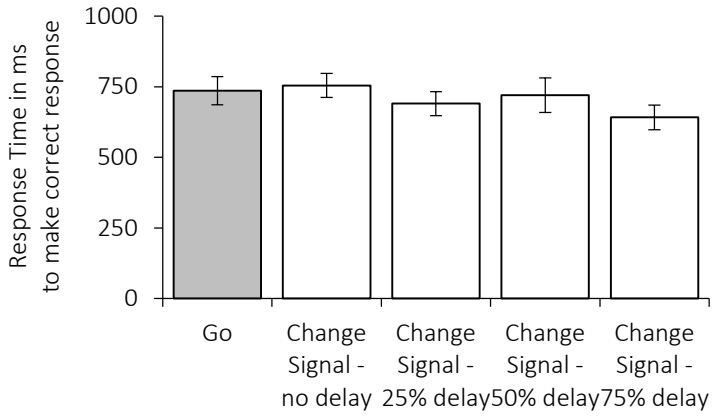

Figure 4.3.11. *Humans:* Latencies in ms to respond to the correct key after the signal had occurred in the Change-Signal task. *Note*: in no-delay Signal trials, the signal occurred immediately; in Go trials, no signal occurred, reported are the latencies to respond to the Go stimulus. Error bars represent standard errors.

The previous trial (Go or Signal) did not significantly affect the latencies to respond correctly, $F(1,15)=2.72$, $p=.12$, but there was a significant interaction between the previous trial type and the current trial type, $F(4,60)=2.65$, $p=.042$, $\eta_p^2=.15$. On Go trials, latencies to make the correct response were marginally longer following a Change-Signal trial than following a Go trial (difference: 55ms, *SE*: 25ms), but the difference was only significant when no corrections for multiple comparisons were applied to the post-hoc comparisons, $p=.048$ (Bonferroni-corrected: $p=.24$). In Change-Signal trials, response latencies were not significantly longer following a Change-Signal trial than following a Go trial, all $p\geq.070$. Humans and pigeons differed significantly in the way the previous trial type affected error rates on the subsequent trial, three-way interaction between previous trial type, current trial type and species: $F(4,80)=2.95$, $p=.037$, $\eta_p^2=.13$. However, Bonferroni post-hoc comparisons showed that humans only marginally showed a greater increase in response times following a Change-Signal trial than pigeons when the current trial was a Go trial, $p=.14$. Because none of the differences were significant in Bonferroni-corrected post-hoc comparisons, no separate figure of the results is provided.

Discussion

The performance of pigeons and humans in both the Stop-Signal and the Change-Signal task matched the predictions made by the independent horse-race model, which assumes that the process of initiating a response and the process of inhibiting a response are independent mechanisms, and behaviour is determined by the process that is completed first. Based on this assumption, one can expect to observe that performance should decrease with increasing signal onset.

This was the case for both pigeons and humans, who behaved remarkably similarly to each other: errors (that is, the probability of incorrectly performing the Go response in Signal trials) increased from trials without a delay in signal onset to trials in which the signal appeared after a delay of 25% of their mean response times to trials with a 50% delay to trials with a 75% delay. Similarly, the pigeons' likelihood to make a response at the signal increased with increasing signal onset, i.e., from trials in which the signal appeared immediately (in no-delay Signal trials) to trials with a 25% signal-onset delay to trials in which the signal appeared after a 50% delay and again after a 75% delay. Humans showed a trend in the same direction, in both the Stop-Signal and Change-Signal task.

More importantly, the independent horse-race model estimates that response latencies should be lower for Signal trials than for Go trials, which was the case for humans and pigeons in both tasks (albeit a bit more evident in the Stop-Signal task than in the Change-Signal task, and with the caveat that the few no-delay trials were anomalous in this respect). Both species also tended to show longer latencies to incorrectly make a response to the Go stimulus or the signal in Signal trials as the interval between the presentation of the Go stimulus (indicating the requirement to make a response) and the presentation of the signal (indicating to withhold that response) increased.

Taken together, the paradigm developed in Section 4.2 appears to elicit the commonly observed response-inhibition phenomena in both humans and pigeons. Additionally, the results provide quite good evidence that the independent horse-race model applies to associatively-mediated response inhibition as expressed by pigeons, both in the Stop-Signal and the Change-Signal task.

Another question addressed in this section was whether the Stop-Signal and Change-Signal tasks utilise the same inhibition mechanisms, or whether the mechanisms differ between tasks, either in the Change-Signal task requiring a more complex level of inhibitory control than the Stop-Signal task, or by it requiring less (or no) inhibitory control. There was no detectable difference in the pigeons' performance between the two tasks; their performance of response inhibition was no more or less successful in the Change-Signal task than it was in the Stop-Signal task, although the pigeons performing the Stop-Signal task did show a greater probability of responding after the signal appeared when the delay between the onset of the Go stimulus and the onset of the Stop signal was very long, see Figure 4.3.2. These results are broadly in accordance with Verbruggen and Logan's (2009b) claim that the two tasks employ similar response-inhibition mechanisms.

Nonetheless, as stated in the introduction to this chapter, adherence to the independent horse-race model does not imply a presence of inhibitory control, and the next question posed in this section was whether the process of executing the alternative response in the Change-Signal task is preceded by a process of inhibiting the initially indicated Go response at all. I assessed this issue by comparing the latencies to respond to the correct key in no-delay Change-Signal trials to those in delayed Change-Signal trials: if an additional process was required to stop the initially prepared response, the latency to execute the alternative response may be longer in delayed Signal trials than in no-delay Signal trials.

For both humans and pigeons, responding to the correct key took equally long in no-delay Change-Signal trials and Go trials. Although it has been found (Chikazoe et al., 2009) that response times can be longer when the response requirements are uncertain (as they would be in Go trials, as the presentation of the Go stimulus may or may not be followed by the Change signal) than when the requirements are certain (as they are in no-delay Change-Signal trials), equal response times in these two trial types are plausible. The subjects most likely only prepared and carried out one response option in both trial types (choosing the correct key), which required a fixed amount of time.

When subtracting the delay of the signal onset from the latencies of delayed Change-Signal trials, latencies to respond to the correct key were of comparable duration across all trials. This result is in accordance with the independent horse-race model: as it is assumed that the processes of initiating the Go response and initiating an alternative response run independently of each other (irrespective of whether the initiation of the alternative response is preceded by an inhibition of the prepared Go response or whether it immediately overrides the preparation of the Go response), the arrival of a Change signal would be expected to trigger the initiation of the alternative response immediately, so that the latency to make the alternative response in the Change-Signal task should be of equal length from the arrival of the signal.
Nonetheless, this outcome is quite interesting as it, on the one hand, confirms that the execution of the alternative response is triggered immediately upon signal onset and independently of the progress that initiates the Go response; on the other hand, it implies that there is no difference in latencies between trials in which only one response has to be prepared and executed (be it responding to the Go stimulus in Go trials, or choosing the alternative key in no-delay Change-Signal trials) and delayed Change-Signal trials in which, presumably, the initial Go response has to be inhibited and replaced by the alternative response. This phenomenon is not unknown in the human literature, where it has raised the question of whether a separate process of inhibiting the Go response is indeed needed before an alternative response can be initiated (cf. Boecker et al., 2013). Verbruggen et al. (2008b) explicitly addressed the issue of whether or not performance in Change-Signal tasks relies on response inhibition and concluded that, in accordance with the independent horse-race model, the inhibition process is indeed a necessary mechanism to stop the Go response on Signal trials. They reiterate that, because the inhibition process is performed independently of the process to initiate a response, both processes can occur in parallel, so that no additional time is needed to initiate the alternative response once the inhibition process is completed.

However, although the two mechanisms run independently of each other, Verbruggen et al. (2008b) noted that, at least when executive control is involved, the cognitive capacities required to perform them are most likely limited and shared by the two processes. Consequently, each process is

expected to take longer in the presence of the other process than when all capacities were allocated to a single process; that is, the process of executing the alternative response is assumed to take longer when the inhibition process is performed in parallel than when no inhibition is required. Consequently, reaction times might be equal in all trials in which the inhibition of the Go response is necessary (i.e., delayed Change-Signal trials), but in trials in which the response can be executed without the need to inhibit a previously prepared response (i.e., Go trials and no-delay Change-Signal trials), reaction times should be shorter than the reaction times in delayed trials. This was not the case for the pigeons or humans in this experiment; latencies were similar in length in all trial types regardless of whether and when a signal appeared, implying that the response latencies were determined by the duration of the response-initiation process and independent of the involvement of an inhibition mechanism. The logical consequences of this finding is that, for both pigeons and humans, the response-inhibition process did not reduce the capacities allocated to the process of response execution. This could be either because no inhibition process was involved in Change-Signal trials in this paradigm - perhaps instead, the initiation of the alternative response was sufficient to override the execution of the Go response, although Verbruggen et al. (2008b) ruled out the possibility that the execution of an alternative response can replace the execution of the Go response -, or because the parallel processes of inhibition and execution shared unlimited capacities. For executive-control processes, the general assumption is that capacities are limited, see Verbruggen et al. (2008b); but if associative processes governed behaviour, such constraints might not apply.

Evidence for an absence of inhibitory control might be taken from trial-sequence effects. In task-switching studies (cf. Chapter 3), the influence of executive control on behaviour is mostly observed in effects of trial sequence (i.e., switch costs) thought to reflect a mental reconfiguration of competing task sets. Similarly, the requirement to initiate or withhold a response on a given trial in Stop-Signal and Change-Signal tasks might elicit the activation of a mental goal to perform or inhibit that response, which might remain somewhat activated on trials that follow (similar to task-set inertia that can affect task-switching performance, cf. Monsell, 2003), leading to slowed responses and reduced

errors in subsequent trials. If this is the case, sequential trial effects might be visible in the data of human participants, who are assumed to construct mental task goals, but not in the data of pigeons, which are assumed not to do so. The comparison of performance in trials following a successful Go response and in trials following successful inhibition suggests that this might be the case: human participants slowed down in their response times in Go trials following response inhibition, and made fewer errors in Go trials (i.e., missing a response) following correct responding and fewer errors in Signal trials (i.e., responding to the stimulus) following successful response inhibition. Pigeons, however, did not alter their behaviour in such a way; although they showed an increased probability of incorrectly performing the Go response when the previous trial demanded that response, they showed no reliable difference in performance in trials affording the same response requirement (inhibiting or executing the Go response) as the previous trial compared to trials affording a different response requirement than the previous trial, which indicates that the pigeons did not perform any kind of mental goal adjustment. This result is further discussed in Chapter 5.

If performance in the Change-Signal task - at least for pigeons - was indeed not regulated by an inhibition process, it might be that subjects were able to respond correctly only if they had been prepared to perform either the Go or the alternative response from the start of a trial. Following Verbruggen et al. (2008b), such behaviour would lead to shorter reaction times with increasing signal-onset delay, that is, is would produce the pattern of performance depicted in Figures 4.3.4 and 4.3.11 (which only include correct trials). It would also imply that subjects either chose which response they were going to execute before the start of the trial, irrespective of the trial type (cf. Logan & Cowan, 1984), or had some notion of whether the trial was going to be a Go or a Change-Signal trial. The latter possibility is plausible in principle, since the likely type of the trial was indicated by the predictive cues; however, to foreshadow the analyses of the cue-dependent measures of performance in Section 4.4, these cues probably did not determine the behaviour of the pigeons and humans. Regarding the former possibility, Logan and Cowan (1984) noted that if responses were prepared ahead of the start of a trial (even if just for a proportion of trials), the probability of responding incorrectly in signal trials could

never be zero, regardless of how early the signal was presented. Instead, the probability would equal the proportion of trials on which subjects chose to respond to the Go stimulus regardless of the signal. For humans, this may have been the case; P(respond) for no-delay Change-Signal trials equals 0.13, indicating that the participants ignored the signal in 13% of trials. For pigeons, however, this number is very close to zero, which implies that pigeons did not select the response they were going to execute ahead of a trial.

One might assume a speed/accuracy trade-off: because in both Go trials and delayed Change-Signal trials, the Go stimulus was initially presented, the ambiguity about whether or not responding to the Go stimulus would be rewarded might have caused subjects to hesitate to make that response, so that the response latencies in all these trials were equally long. However, subjects would not be expected to hesitate before responding when the Change signal is presented, because the appearance of the signal unambiguously indicates that the alternative response has to be performed (cf. Chikazoe et al., 2009); thus, reaction times to perform the correct response in no-delay Change-Signal trials should be shorter than the reaction times in the other four types of trials. This was not the case in this experiment. Thus, the subjects either hesitated in every trial regardless of current response requirements, which, according to Aron (2011), requires executive control to enable the inhibition of any "spur of the moment" impulsive response, or they did not selectively adjust their behaviour. If the pigeons had learned to wait before making a response, the response times of the first peck in the Change-Signal test sessions that were analysed in this section, which included no-delay and delayed Change-Signal trials, should be longer than those in the previously administered Go/Change-training sessions (see Section 4.2), which included only no-delay Change-Signal trials. They were not; in fact, the latencies to respond to the Go stimulus in both Go trials and no-delay Change-Signal trials were significantly shorter in the pigeons' final ten Change-Signal test sessions (Go: 1154ms; no-delay Change-Signal: 1112ms) than in the final ten Go/Change training sessions (Go: 1227ms; no-delay Change-Signal: 1350ms), $F(1,5)=7.13$, $p=.044$, $\eta_p^2=.59$. The pigeons did not learn to hesitate before responding to increase accuracy.

The discussion of which cognitive processes likely determined the behaviour of pigeons and humans is continued in Section 4.5, following an analysis of the use of predictive cues in Section 4.4.

4.4 Does Signal-Specific Response Inhibition Transfer to Cues Predicting the Probability of the Signal?

Although the predictions of the independent horse-race model (Logan & Cowan, 1984; Verbruggen & Logan, 2009b) apply to the response-inhibition performance of pigeons and humans, reported in Section 4.3, this match alone does not allow any inferences about the involvement of executive control or associative processes in Stop-Signal and Change-Signal tasks, because the model makes no assumptions about the presence of specific cognitive abilities. Moreover, the results reported in Section 4.3 leave room to speculate about the involvement of inhibitory control in the Change-Signal task, as the observed performance might have been achieved without inhibiting a previously prepared response. Nonetheless, the fact that the performance of pigeons followed the model's predictions suggests that associative processes contribute to the pattern - or at least that the absence of executive control does not eradicate the pattern.

The influence of executive control on response inhibition may be observed in trial-to-trial effects reflecting mental goal activation that carries over between trials. In Section 4.3, I report that human participants showed both slower response times in Go trials if the trial was preceded by successful response inhibition than if the trial was preceded by correct response execution, and a decrease in error rates in trials that were of the same type (Go or Signal) as the previous trial; pigeons also showed a weak trend of improved accuracy in trials following trials of the same type, but did not alter the speed of responding in Go trials depending on the demands of the previous trial. However, given that, as stated in Section 1.3, the estimation of pigeons' response times can be unreliable with the apparatus available at the time of conducting this research, it is difficult to unambiguously attribute sequential trial effects to a mental goal adjustment elicited by executive-control processes. Associative processes might account for differences in performance that apparently occur at task level: considering specifically the paradigms used in this chapter, the two "tasks" of going and inhibiting (or changing) each afforded one specific response, allowing response-repetition effects (cf. Chapter 3) or priming effects to take effect. But there is also evidence that the influence of associative processes on inhibitory

control may more generally be observed at the level of task goals. For example, Bowditch et al. (2016) found that response-stopping can become associated with cues that predict the likelihood of a stop signal in the upcoming trial: seeing the cue might automatically initiate a stopping response even before any stop signal has appeared, which makes it plausible that even behaviour that seemingly involves proactive planning might be reduced to associative processes.

Consequently, in this section, I investigated whether presenting cues that were stochastically related to the events of the current trial (either performing the Go response, or stopping/changing the response) can come to deliver associatively-mediated inhibition. Specifically, I assessed whether a cue predicting either a Go trial or a Signal trial influenced the pigeons' or humans' response probabilities and response latencies towards the Go stimulus. If associative links are formed between the cues and the occurrence of a signal or, more directly, between the cues and the demand to withhold a Go response, then incorrect responses to the Go stimulus in Signal trials might be less likely, and correct responses in Go trials might occur more slowly in trials showing a cue that predicts a high probability of a signal occurring on that trial compared to trials in which the cue predicts a low probability that a signal might occur. Conversely, the likelihood of missing a response in Go trials should be lower for trials in which a cue indicating a low probability of a signal on that trial is presented compared to trials in which the cue indicates a high probability of the occurrence of a signal.

It has to be noted that, despite Bowditch et al.'s (2016) findings, it may be that, unlike signal-dependent response inhibition, cue-dependent inhibition relies on executive control; in this case, pigeons would not be expected to be able to adapt their behaviour depending on the nature of the cues that are presented. Instead, they might only express response inhibition in response to the Stop or Change signal.
If that was the case, it might further be that humans only show cue-dependent response inhibition if they are aware of the function of the cues and thus able to deliberately apply inhibitory control in response.

Results

Pigeons

I estimated changes in performance depending on the cues that were presented ahead of a trial by examining the probability of responding in Signal trials, both overall, P(respond), and after the signal occurred, P(respond|Signal), the probability of missing a response in Go trials, P(miss|Go), and the pigeons' latencies to respond to the Go stimulus in Go trials. P(respond) and P(miss|Go) correspond to the pigeons' error rates in Signal trials and Go trials, respectively. The data were analysed in four repeated-measures ANOVAs using Cue Type (Go cue, Neutral cue and Signal cue) and Session (blocked sessions 1-10, 11-20, 21-30, Probe Session 1 and Probe Session 2) as within-subjects factors and Task (Change-Signal or Stop-Signal task) as a between-subjects factor. Where applicable, the reported results were subject to Huynh-Feldt corrections. The results for all four dependent variables are shown in Figure 4.4.1; descriptive statistics are summarised in Table 4.4.1.

P(respond)

As shown in Figure 4.4.1 Panel A, the task that pigeons completed affected their likelihood of making a response in a Signal trial, $F(1,10)=7.20$, $p=.023$, $\eta_p^2=.42$, in that pigeons in the Stop-Signal task showed a greater probability of responding than those in the Change-Signal task. However, there was no significant difference in performance between the cue types that were presented, $F(2,20)=0.65$, $p=.54$, or between sessions, $F(4,40)=1.46$, $p=.24$. There were also no significant interactions between any factors, all $p \geq .16$.

Planned comparisons focussing on performance in the two probe sessions confirmed that P(respond) did not differ significantly between trials in which the Go cue was presented and trials in which the Signal cue was shown, either in the Stop-Signal task (Probe Session 1: uncorrected: $p=.097$, Bonferroni-corrected: $p=.29$; Probe Session 2: uncorrected: $p=.46$, Bonferroni-corrected: $p=1.0$) or in the Change-Signal task (Probe Session 1: uncorrected: $p=.11$, Bonferroni-corrected: $p=.73$; Probe Session 2: uncorrected: $p=.18$, Bonferroni-corrected: $p=.47$).

In light of the absence of statistically reliable cue effects on performance, the data were also examined using the Bayesian repeated-measures ANOVA

function in JASP (Love et al., 2015) including Cue Type as a within-subjects factor. For the Stop-Signal task, the estimated Bayes factor suggests that the data are 0.40:1 in favour of the null hypothesis; that is, the data are 2.5 times more likely to occur under a model assuming no effect of the three cues than under a model including Cue Type as a factor. When considering only the Go cue and Stop-Signal cue (and not including the neutral cue in the analysis), the estimated Bayes factor is 0.47:1 in favour of the null hypothesis; that is, the data are 2.11 times more likely to occur under a model assuming no effect than under a model assuming a difference between the Go and the Stop-Signal cue.

Table 4.4.1. *Pigeons:* Means [and standard errors] of P(respond) on Signal trials, P(respond|Signal) on Signal trials after the signal occurred, P(miss|Go) on Go trials, and latencies to respond to the Go stimulus, depending on Cue Type (Go, Neutral and Signal cue) and Test Sessions (three test blocks of ten sessions, in which the Go and Signal cues predicted the occurrence of a signal on the following trial to 75% accuracy, and two probe sessions, in which all cues predicted the occurrence of a signal on the following trial to 50% accuracy).

			Sessions				
		Cue	1-10	11-20	21-30	Probe 1	Probe 2
Stop Signal Task							
	P(respond)	Go Cue	0.08 [0.01]	0.10 [0.02]	0.08 [0.02]	0.07 [0.04]	0.11 [0.04]
		Neutral Cue	0.07 [0.01]	0.07 [0.01]	0.09 [0.01]	0.14 [0.03]	0.09 [0.03]
		Signal Cue	0.08 [0.01]	0.09 [0.02]	0.10 [0.07]	0.12 [0.03]	0.07 [0.04]
	P(respond|Signal)	Go Cue	0.05 [0.01]	0.08 [0.02]	0.05 [0.01]	0.02 [0.02]	0.06 [0.02]
		Neutral Cue	0.05 [0.01]	0.04 [0.01]	0.04 [0.01]	0.05 [0.02]	0.07 [0.02]
		Signal Cue	0.05 [0.01]	0.05 [0.01]	0.06 [0.01]	0.06 [0.02]	0.02 [0.02]
	P(miss|Go)	Go Cue	0.18 [0.05]	0.21 [0.08]	0.12 [0.04]	0.20 [0.09]	0.22 [0.13]
		Neutral Cue	0.16 [0.05]	0.21 [0.08]	0.12 [0.03]	0.19 [0.08]	0.15 [0.09]
		Signal Cue	0.18 [0.04]	0.19 [0.08]	0.09 [0.03]	0.18 [0.09]	0.08 [0.06]
	Latency to peck the Go stimulus in Go trials	Go Cue	1561 [124]	1661 [147]	1562 [142]	1662 [169]	1486 [175]
		Neutral Cue	1616 [139]	1741 [163]	1537 [122]	1425 [179]	1620 [346]
		Signal Cue	1591 [135]	1670 [171]	1598 [162]	1707 [180]	1599 [263]

Table 4.4.1 continued.

Change-Signal Task							
	P(respond)	Go Cue	0.04 [0.01]	0.05 [0.01]	0.03 [0.02]	0.08 [0.03]	0.06 [0.03]
		Neutral Cue	0.05 [0.02]	0.04 [0.01]	0.03 [0.01]	0.07 [0.03]	0.06 [0.03]
		Signal Cue	0.04 [0.01]	0.05 [0.02]	0.03 [0.01]	0.03 [0.02]	0.03 [0.03]
	P(respond|Signal)	Go Cue	0.02 [0.01]	0.01 [0.02]	0.01 [0.01]	0.02 [0.02]	0.02 [0.02]
		Neutral Cue	0.03 [0.01]	0.01 [0.01]	0.01 [0.01]	0.05 [0.03]	0.02 [0.02]
		Signal Cue	0.02 [0.01]	0.02 [0.02]	0.02 [0.01]	0.00 [0.01]	0.00 [0.01]
	P(miss|Go)	Go Cue	0.27 [0.06]	0.31 [0.06]	0.31 [0.09]	0.39 [0.08]	0.38 [0.08]
		Neutral Cue	0.29 [0.05]	0.29 [0.07]	0.31 [0.09]	0.38 [0.11]	0.39 [0.11]
		Signal Cue	0.33 [0.05]	0.35 [0.05]	0.34 [0.08]	0.40 [0.08]	0.38 [0.08]
	Latency to peck the Go stimulus in Go trials	Go Cue	1924 [124]	1979 [147]	2112 [142]	2020 [169]	2166 [175]
		Neutral Cue	1941 [139]	1972 [163]	2114 [119]	1886 [233]	2415 [471]
		Signal Cue	2076 [141]	2036 [154]	2130 [157]	2166 [115]	2052 [293]

For the Change-Signal task, the estimated Bayes factor implies that the data are 1.67 times more likely to occur under a model assuming no effect than a model assuming an effect of all three cues (0.6:1 in favour of the null hypothesis) and equally likely to occur under a model assuming no effect as under a model assuming a difference between the Go and the Change-Signal cue (0.99:1 in favour of the null hypothesis).

P(respond|Signal)

As shown in Figure 4.4.1 Panel B, the task that pigeons completed affected their likelihood of making a response in a Signal trial, $F(1,10)=6.77$, $p=.026$, $\eta_p^2=.40$, in that pigeons in the Stop-Signal task showed a greater probability of responding than those in the Change-Signal task. However, the cue type that was presented did not influence performance, $F(2,20)=0.53$, $p=.60$, nor did the session, $F(4,40)=0.45$, $p=.78$. There were no significant interactions between any factors, all $p \geq .08$.

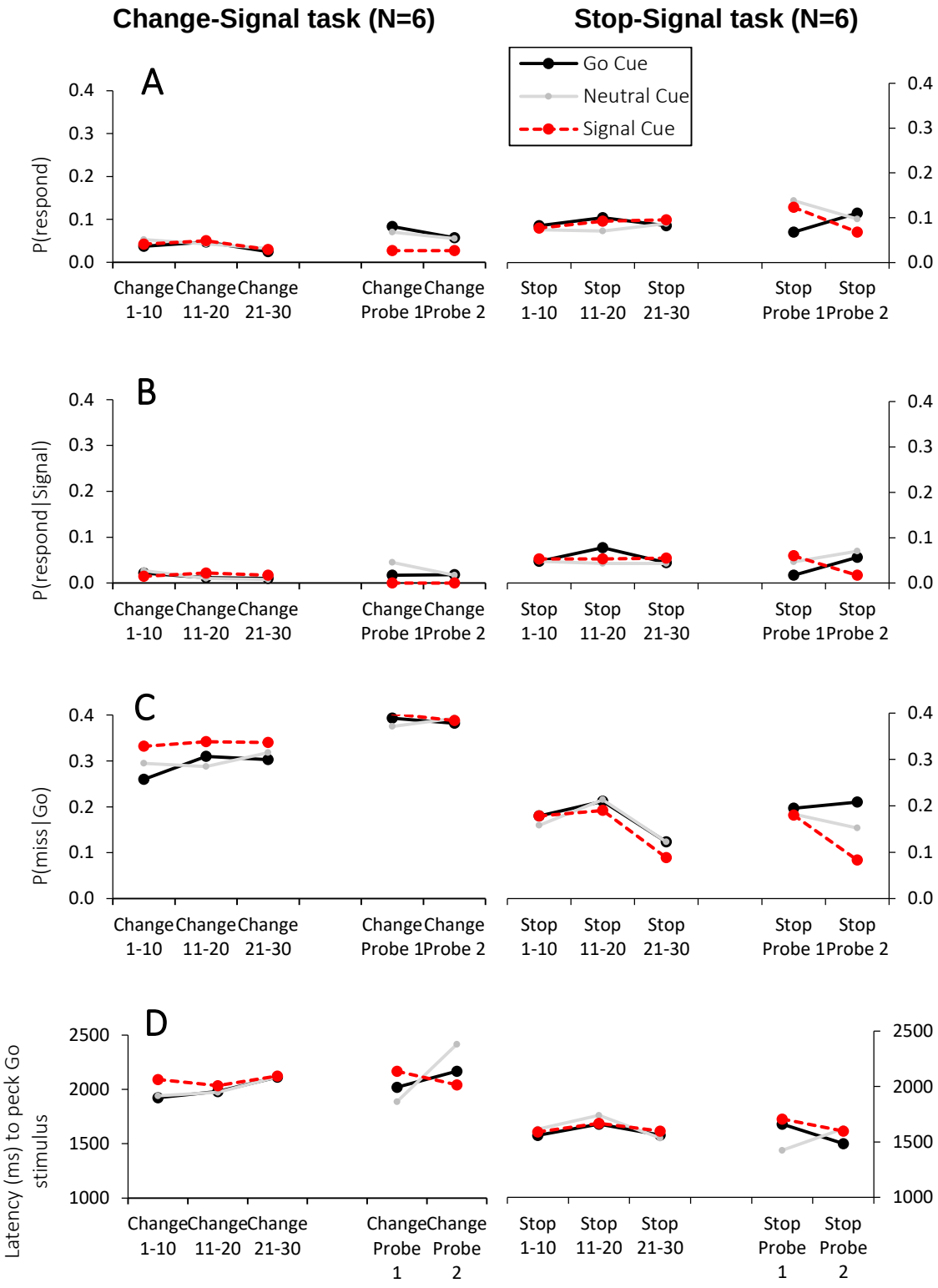

Figure 4.4.1. *Pigeons: A)* The overall probability of responding on Signal trials, P(respond), *B)* the probability of responding on Signal trials after the signal had occurred, P(respond|Signal), *C)* the probability of missing a response to the Go stimulus on Go trials, P(miss|Go), and *D)* the mean latency to respond to the stimulus on Go trials, depending on the cue that was shown in a trial (Go, Neutral, or Signal cue), across 30 cued sessions and 2 probe sessions (the cued sessions are blocked for easier visualisation).

Planned comparisons focussing on performance in the two probe sessions confirmed that P(respond|Signal) did not differ significantly between trials in which the Go cue was presented from trials in which the Signal cue was shown, neither in the Stop-Signal task (Probe Session 1: uncorrected: p=.076, Bonferroni-corrected: p=.23; Probe Session 2: uncorrected: p=.12, Bonferroni-corrected: p=.36) nor in the Change-Signal task (Probe Session 1: uncorrected: p=.36, Bonferroni-corrected: p=1.0; Probe Session 2: uncorrected: p=.36, Bonferroni-corrected: p=.1.0).

As above, the absence of any cue effects were further examined by performing a Bayesian repeated-measures ANOVA in JASP (Love et al., 2015) including Cue Type as a within-subjects factor. For the Stop-Signal task, the estimated Bayes factor suggests that the data are 0.43:1 in favour of the null hypothesis; that is, the data are 2.33 times more likely to occur under a model assuming no effect of the three cues than under a model including Cue Type as a factor. When considering only the Go cue and Stop-Signal cue (and not including the neutral cue in the analysis), the estimated Bayes factor is 0.51:1 in favour of the null hypothesis; that is, the data are 1.96 times more likely to occur under a model assuming no effect than under a model assuming a difference between the Go and the Stop-Signal cue.

For the Change-Signal task, the estimated Bayes factors estimates that the data are 2.63 times more likely to occur under a model assuming no effect than a model assuming an effect of all three cues (0.38:1 in favour of the null hypothesis) and 1.18 times more likely to occur under a model assuming no effect than a model assuming a difference between the Go and the Change-Signal cue (0.85:1 in favour of the null hypothesis).

P(miss|Go)

As shown in Figure 4.4.1 Panel C, the probability of missing a response on Go trials was marginally influenced by the task that pigeons completed, F(1,10)=4.35, p=.064, but not by the presented cue type, F(2,20)=0.12, p=.87, nor by the session, F(4,40)=1.23, p=.31. There were no significant interactions between any of the three factors, all p≥.15.

Planned comparisons focussing on performance in the two probe sessions confirmed that P(miss|Go) did not differ significantly between trials in which the Go cue was presented from trials in which the Signal cue was shown, neither in

the Stop-Signal task (Probe Session 1: uncorrected: p=.47, Bonferroni-corrected: p=1.0; Probe Session 2: uncorrected: p=.13, Bonferroni-corrected: p=.38) nor in the Change-Signal task (Probe Session 1: uncorrected: p=.79, Bonferroni-corrected: p=1.0; Probe Session 2: uncorrected: p=.91, Bonferroni-corrected: p=1.0).

As above, the absence of any cue effects were further examined by performing a Bayesian repeated-measures ANOVA in JASP (Love et al., 2015) including Cue Type as a within-subjects factor. For the Stop-Signal task, the estimated Bayes factor suggests that the data are 0.39:1 in favour of the alternative hypothesis; that is, the data are 2.56 times more likely to occur under a model including Cue Type as a factor than under a model assuming no effect of the three cues. When considering only the Go cue and Stop-Signal cue (excluding the neutral cue), the estimated Bayes factor is 0.38:1 in favour of the alternative hypothesis; that is, the data are 2.66 times more likely to occur under a model assuming a difference between the Go and the Stop-Signal cue than under a model assuming no effect.

For the Change-Signal task, the estimated Bayes factors estimates that the data are 1.07 times more likely to occur under a model assuming an effect of all three cues than a model assuming no effect (0.93:1 in favour of the alternative hypothesis) and 1.61 times more likely to occur under a model assuming a difference between the Go and the Change-Signal cue than a model assuming no effect (0.62:1 in favour of the alternative hypothesis).

Reaction times towards the Go stimulus in Go trials

As shown in Figure 4.4.1 Panel D, the pigeons' latencies to respond to the Go stimulus were not affected by the cue type presented, F(2,20)=0.58, p=.55, or by the session, F(4,40)=0.41, p=.71, nor was there a significant interaction between the two factors, F(8,80)=1.49, p=.23. Pigeons doing the Change-Signal task were slower to respond to the Go stimulus than pigeons in the Stop-Signal task, F(1,10)=5.20, p=.046, η_p^2=.34; however, this factor did not interact with any other factor, all interactions p≥.31.

Planned comparisons focussing on performance in the two probe sessions confirmed that response times towards the Go stimulus did not differ significantly between trials in which the Go cue was presented from trials in which the Signal cue was shown, neither in the Stop-Signal task (Probe Session

1: uncorrected: p=.80, Bonferroni-corrected: p=1.0; Probe Session 2: uncorrected: p=.25, Bonferroni-corrected: p=.76) nor in the Change-Signal task (Probe Session 1: uncorrected: p=.26, Bonferroni-corrected: p=.77; Probe Session 2: uncorrected: p=.61, Bonferroni-corrected: p=1.0).

As above, the absence of any cue effects were examined by performing a Bayesian repeated-measures ANOVA in JASP (Love et al., 2015) including Cue Type as a within-subjects factor. For the Stop-Signal task, the estimated Bayes factor suggests that the data are 0.39:1 in favour of the null hypothesis; that is, the data are 2.56 times more likely to occur under a model assuming no effect of the three cues than under a model including Cue Type as a factor. When considering only the Go cue and Stop-Signal cue (excluding the neutral cue), the estimated Bayes factor is 0.63:1 in favour of the null hypothesis; that is, the data are 1.59 times more likely to occur under a model assuming no effect than under a model assuming a difference between the Go and the Stop-Signal cue.

For the Change-Signal task, the estimated Bayes factors estimates that the data are 1.27 times more likely to occur under a model assuming an effect of all three cues than a model assuming no effect (0.78:1 in favour of the alternative hypothesis) and 1.19 times more likely to occur under a model assuming an effect than a model assuming no difference between the Go and the Change-Signal cue (0.84:1 in favour of the alternative hypothesis).

Humans

As was done for the pigeons above, the human data were analysed in four repeated-measures ANOVAs using Cue Type (Go cue, Neutral cue and Signal cue) and Block (Test Blocks 1-4, 5-9, 10-14, and Cue-Probe Session) as within-subjects factors and Task (Change-Signal or Stop-Signal task) as a between-subjects factor. Where applicable, the reported results were subject to Huynh-Feldt corrections. The results for all four dependent variables are shown in Figure 4.4.2; descriptive statistics are summarised in Table 4.4.2.

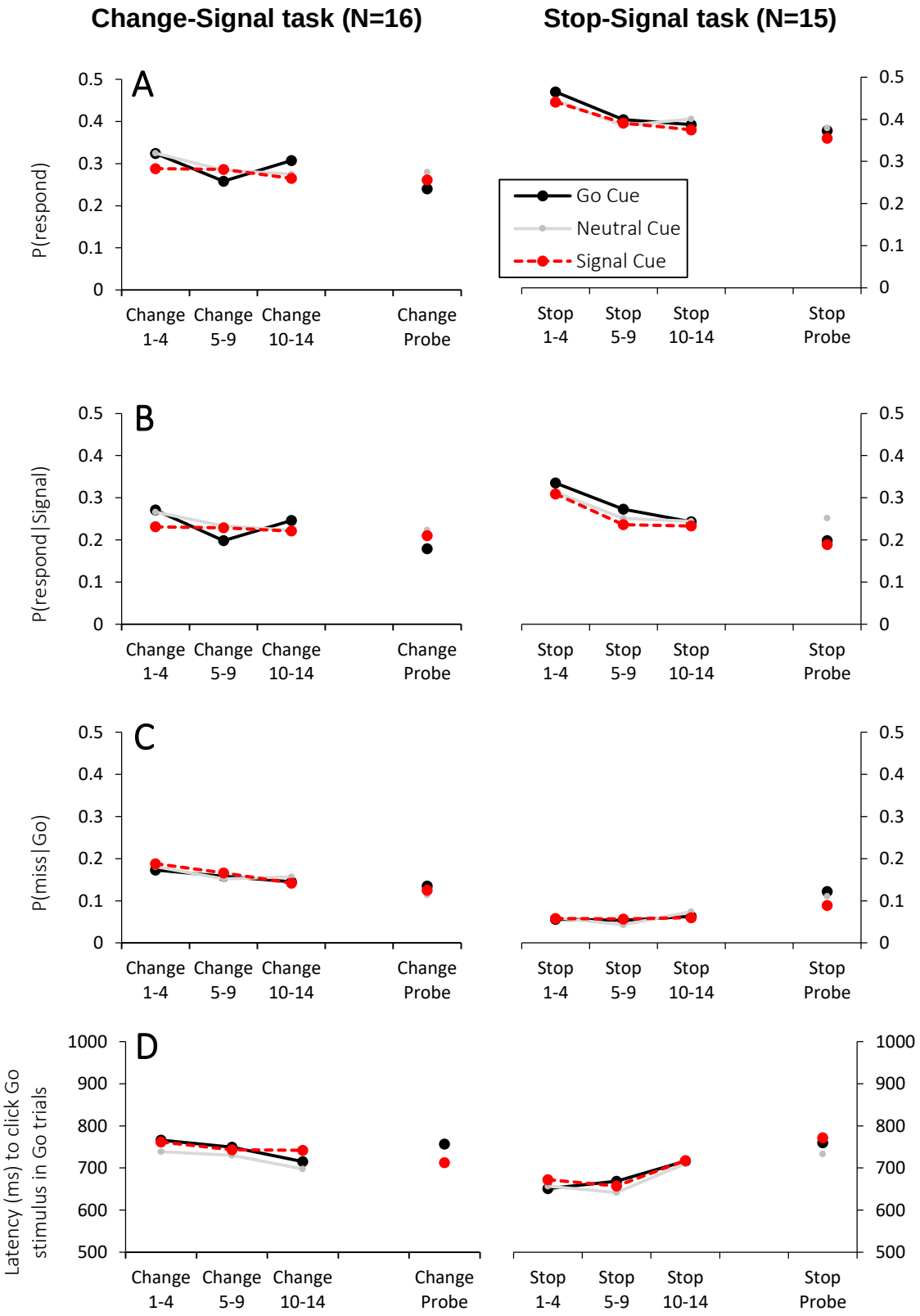

Figure 4.4.2. *Humans: A)* The overall probability of responding on Signal trials, P(respond), *B)* the probability of responding on Signal trials after the signal had occurred, P(respond|Signal), *C)* the probability of missing a response to the Go stimulus on Go trials, P(miss|Go), and *D)* the mean latency to respond to the stimulus on Go trials, depending on the cue that was shown in a trial (Go, Neutral, or Signal cue), across 14 cued blocks and a cue-probe block (the cued blocks are blocked for easier visualisation).

P(respond)

As shown in Figure 4.4.2 Panel A, the task that participants completed affected their likelihood of making a response in a Signal trial, $F(1,29)=12.31$, $p=.001$, $\eta_p^2=.30$; the probabilities also decreased significantly across successive blocks, $F(3,87)=5.90$, $p=.003$, $\eta_p^2=.17$. However, the cue type that was presented did not affect the probability of making a false response in Signal trials, $F(2,58)=1.46$, $p=.24$. There were no significant interactions between any factors, all $p \geq .42$.

Table 4.4.2. *Humans:* Means [and standard errors] of P(respond) on Signal trials, P(respond|Signal) on Signal trials after the signal occurred, P(miss|Go) on Go trials, and latencies to respond to the Go stimulus, depending on Cue Type (Go, Neutral or Signal cue) and Test Blocks (three blocks in which the Go and Signal cues predicted the occurrence of a signal on the following trial to 75% accuracy, and a cue-probe block, in which all cues predicted the occurrence of a signal on the following trial to 50% accuracy).

		Blocks			
		1-4	5-9	10-14	Probe
Stop-Signal Task					
P(respond)	Go Cue	0.47 [0.04]	0.40 [0.02]	0.39 [0.02]	0.37 [0.03]
	Neutral Cue	0.45 [0.03]	0.39 [0.03]	0.40 [0.03]	0.38 [0.03]
	Signal Cue	0.44 [0.03]	0.39 [0.02]	0.38 [0.03]	0.36 [0.05]
P(respond|Signal)	Go Cue	0.34 [0.06]	0.27 [0.03]	0.24 [0.04]	0.20 [0.04]
	Neutral Cue	0.31 [0.04]	0.25 [0.04]	0.24 [0.04]	0.25 [0.04]
	Signal Cue	0.31 [0.05]	0.24 [0.04]	0.23 [0.04]	0.19 [0.06]
P(miss|Go)	Go Cue	0.06 [0.03]	0.05 [0.04]	0.06 [0.03]	0.12 [0.07]
	Neutral Cue	0.06 [0.02]	0.04 [0.02]	0.07 [0.04]	0.11 [0.06]
	Signal Cue	0.06 [0.02]	0.06 [0.04]	0.06 [0.03]	0.09 [0.06]
Latency to click the Go stimulus in Go trials	Go Cue	651 [23]	669 [25]	717 [41]	760 [69]
	Neutral Cue	657 [31]	642 [21]	710 [45]	733 [49]
	Signal Cue	673 [30]	657 [40]	718 [47]	772 [66]

Table 4.4.2 continued.

Change-Signal Task					
P(respond)	Go Cue	0.32 [0.03]	0.26 [0.03]	0.31 [0.03]	0.24 [0.03]
	Neutral Cue	0.33 [0.03]	0.28 [0.03]	0.28 [0.03]	0.28 [0.04]
	Signal Cue	0.29 [0.03]	0.29 [0.03]	0.27 [0.03]	0.26 [0.03]
P(respond|Signal)	Go Cue	0.27 [0.04]	0.20 [0.03]	0.25 [0.03]	0.18 [0.03]
	Neutral Cue	0.27 [0.03]	0.23 [0.04]	0.22 [0.03]	0.22 [0.04]
	Signal Cue	0.23 [0.03]	0.23 [0.04]	0.22 [0.03]	0.21 [0.03]
P(miss|Go)	Go Cue	0.17 [0.05]	0.16 [0.05]	0.15 [0.05]	0.14 [0.05]
	Neutral Cue	0.18 [0.05]	0.15 [0.06]	0.16 [0.06]	0.11 [0.05]
	Signal Cue	0.19 [0.06]	0.17 [0.05]	0.14 [0.05]	0.13 [0.06]
Latency to click the Go stimulus in Go trials	Go Cue	766 [65]	749 [59]	715 [43]	757 [72]
	Neutral Cue	739 [56]	730 [55]	698 [46]	713 [60]
	Signal Cue	762 [61]	743 [51]	742 [53]	713 [64]

Planned comparisons focussing on performance in the probe block confirmed that P(respond) did not differ significantly between trials in which the Go Cue was presented from trials in which the Signal Cue was shown, neither in the Stop-Signal task, p=.65, nor in the Change-Signal task, p=.18.

As for pigeons, the absence of any cue effects were further examined by performing a Bayesian repeated-measures ANOVA. For the Stop-Signal task, the estimated Bayes factor suggests that the data are 0.19:1 in favour of the null hypothesis; that is, the data are 5.25 times more likely to occur under a model assuming no effect of the three cues than under a model including Cue Type as a factor. When considering only the Go and Stop-Signal cues (excluding the neutral cue), the estimated Bayes factor is 0.38:1 in favour of the null hypothesis; that is, the data are 2.61 times more likely to occur under a

model assuming no effect than under a model assuming a difference between the Go and the Stop-Signal cue.

For the Change-Signal task, the Bayes factors estimates that the data are 4.15 times more likely to occur under a model assuming no effect than a model assuming an effect of all three cues (0.24:1 in favour of the null hypothesis) and 1.19 times more likely to occur under a model assuming no effect than a model assuming a difference between the Go and the Change-Signal cue (0.84:1 in favour of the null hypothesis).

P(respond|Signal)

As shown in Figure 4.4.2 Panel B, the task that was completed did not affect the likelihood of responding in the presence of the signal, $F(1,29)=0.42$, $p=.53$; nor did the cue type that was presented, $F(2,58)=0.58$, $p=.56$. However, the probability of responding differed between blocks, $F(3,87)=7.31$, $p=.001$, $\eta_p^2=.20$, in that it decreased as the experiment progressed. There were no significant interactions between any of the three factors, all $p \geq .28$.

Planned comparisons focussing on performance in the probe block confirmed that P(respond|Signal) did not differ significantly between trials in which the Go Cue was presented from trials in which the Signal Cue was shown, neither in the Stop-Signal task, $p=.81$, nor in the Change-Signal task, $p=.25$.

For the Stop-Signal task, the estimated Bayes factor suggests that the data are 0.45:1 in favour of the null hypothesis; that is, the data are 2.24 times more likely to occur under a model assuming no effect of the three cues than under a model including Cue Type as a factor. When considering only the Go and Stop-Signal cues (excluding the neutral cue), the estimated Bayes factor is 0.41:1 in favour of the null hypothesis; that is, the data are 2.46 times more likely to occur under a model assuming no effect than under a model assuming a difference between the Go and the Stop-Signal cue.

For the Change-Signal task, the estimated Bayes factors estimates that the data are 3.75 times more likely to occur under a model assuming no effect than a model assuming an effect of all three cues (0.27:1 in favour of the null hypothesis) and 1.81 times more likely to occur under a model assuming no effect than a model assuming a difference between the Go and the Change-Signal cue (0.55:1 in favour of the null hypothesis).

P(miss|Go)

As shown in Figure 4.4.2 Panel C, the probability of missing a response on Go trials was not significantly influenced by the task that was completed, $F(1,29)=2.09$, $p=.16$, nor by the presented cue type, $F(2,58)=0.13$, $p=.86$, nor by the block of trials, $F(3,87)=0.15$, $p=.78$. There were no significant interactions between any of the three factors, all $p \geq .21$.

Planned comparisons focussing on performance in the probe block confirmed that P(miss|Go) did not differ significantly between trials in which the Go cue was presented from trials in which the Signal cue was shown, neither in the Stop-Signal task, $p=.36$, nor in the Change-Signal task, $p=.68$.

For the Stop-Signal task, the estimated Bayes factor suggests that the data are 0.28:1 in favour of the null hypothesis; that is, the data are 3.53 times more likely to occur under a model assuming no effect of the three cues than under a model including Cue Type as a factor. When considering only the Go and Stop-Signal cues (excluding the neutral cue), the estimated Bayes factor is 0.47:1 in favour of the null hypothesis; that is, the data are 2.14 times more likely to occur under a model assuming no effect than under a model assuming a difference between the Go and the Stop-Signal cue.

For the Change-Signal task, the estimated Bayes factors estimates that the data are 5.20 times more likely to occur under a model assuming no effect than a model assuming an effect of all three cues (0.19:1 in favour of the null hypothesis) and 2.73 times more likely to occur under a model assuming no effect than a model assuming a difference between the Go and the Change-Signal cue (0.37:1 in favour of the null hypothesis).

Reaction times towards the Go stimulus in Go trials

As shown in Figure 4.4.2 Panel D, latencies to respond to the Go stimulus were not affected by the task that was completed, $F(1,29)=0.43$, $p=.52$, or by the block, $F(3,87)=0.88$, $p=.40$ (although participants in the Stop-Signal task became increasingly slower as the experiment went on, $p=.018$). The presented cue type marginally affected latencies towards the Go stimulus, $F(2,58)=2.63$, $p=.081$. There was no significant interaction between the three factors, all $p \geq .11$.

Planned comparisons focussing on performance in the probe block confirmed that response times towards the Go stimulus did not differ significantly between

trials in which the Go cue was presented from trials in which the Signal cue was shown, either in the Stop-Signal task, p=.72, or in the Change-Signal task, p=.47.

For the Stop-Signal task, the estimated Bayes factor suggests that the data are 0.22:1 in favour of the null hypothesis; that is, the data are 4.53 times more likely to occur under a model assuming no effect of the three cues than under a model including Cue Type as a factor. When considering only the Go and Stop-Signal cues (excluding the neutral cue), the estimated Bayes factor is 0.37:1 in favour of the null hypothesis; that is, the data are 2.71 times more likely to occur under a model assuming no effect than under a model assuming a difference between the Go and the Stop-Signal cue.

For the Change-Signal task, the estimated Bayes factors estimates that the data are 4.63 times more likely to occur under a model assuming no effect than a model assuming an effect of all three cues (0.22:1 in favour of the null hypothesis) and 2.46 times more likely to occur under a model assuming no effect than a model assuming a difference between the Go and the Change-Signal cue (0.41:1 in favour of the null hypothesis).

Discussion

Neither pigeons nor humans showed any indication of altering their behaviour when provided with information about the likely nature of an upcoming trial. That is, performance was similar regardless of whether the cue predicted a high or a low likelihood of the appearance of a signal in the upcoming trial. Bayesian analyses of the influence of the cues on performance remained inconclusive, as there was no strong support for either the null hypothesis that the cues did not affect performance, or the hypothesis that the cues altered behaviour. Although the graphs in Figure 4.4.1 might suggest that the presentation of a predictive cue influenced the pigeons' ability to inhibit an unwanted response, the data were too variable to carry any statistical meaning. For example, the apparent differences in the probability of responding in Signal trials in probe session 1 of the Change-Signal task (Figure 4.4.1 Panel A) were caused by the behaviour of a single pigeon that responded to every trial that was accompanied by a Go cue, whereas the other five pigeons completing this task had a much lower probability of doing so (in fact, four of them never responded after the Change

signal had appeared in the probe sessions). Nonetheless, the procedure of averaging the performance of those six pigeons led to the apparent decrease in performance for trials showing a Go cue.

Had the pigeons or humans differentiated between the cues, one would expect both their response times towards the Go stimulus and the probability of missing a response in Go trials to increase in the presence of the Signal cue (compared to presenting the Go cue) and the probability of responding to the signal to increase in the presence of the Go cue (compared to presenting the Signal cue). This pattern should have been especially apparent in the probe sessions, in which the cues did not reliably predict the nature of the upcoming trial any more. But, statistically speaking, performance in the cued blocks was similar to that in the probe blocks, in which the cues were uninformative.

Consequently, there is no discernible evidence that pigeons differentiated between the cues that predicted with varying probabilities whether the next trial would be a Signal trial. However, since humans also gave no such indication, one can only speculate about what this finding implies about the cognitive requirements for exerting cue-based response inhibition. There is so far no concrete evidence that pigeons are unable to utilise the cues; it may be that they simply did not do so in the current paradigm, or with the amount of training they received. Assuming that pigeons were unable to use the information of the cues consequently means that the same would have to be assumed for humans, who are certainly able to use predictive cues, as they have done so in Bowditch et al. (2015). Further, although pigeons do not always attend to information that would reduce the ambiguity of a problem (e.g., Roberts, Feeney, McMillan et al., 2009; Smith, 2009), they are able to do so under the right circumstances (e.g., Dinsmoor, Sears, & Dout, 1976; Silberberg, & Fantino, 2010; Zentall & Stagner, 2012). Thus, it cannot be concluded that a mere failure to come under the control of predictive cues indicates that cued inhibitory control requires higher cognitive abilities than the associative processes that pigeons are restricted to.

Only two human participants (one in each task) reported that they had become aware of the predictive function of the cues. In an attempt to gain more insight into the cognitive processes that elicit cue use, their performance was considered separately. Although both participants appeared to demonstrate

some sensitivity to the identity of the cues, mainly in the later blocks of the experiment and the probe block, the data from a single person per task did not carry the statistical power to make a definite statement, and Bayesian analyses of the effects remained inconclusive about the influence of the cues. Thus, it may simply be the case that the paradigm used in this chapter cannot adequately capture cueing effects. The question of whether or not cue awareness is necessary to utilise the cues, or whether behaviour might come under the control of automatic associations of the cue with the occurrence of a signal (or direct associations with the action of withholding a response), cannot be answered with the data that was generated with this paradigm.

What the results of this section do indicate, however, is that cue-dependent response inhibition, although potentially mediated by associative learning as previous research suggests, is not acquired as easily or quickly associatively as the response inhibition following an explicit signal that is reported in Section 4.3. This is not too surprising given that a peck or click at the stimuli had immediate consequences (either a reward or timeout), whereas a peck or click at the cues did not. Awareness of the predictive function of the cues may enhance their influence on inhibitory control, but it is currently not certain whether such awareness is needed to enable an individual to perform cue-dependent response inhibition.

4.5 Discussion - Associative Processes in a Response-Inhibition Paradigm

The experiments in Chapter 4 were conducted to estimate the influence of executive control and associative processes on response inhibition in both a Stop-Signal and a Change-Signal task. The results of Section 4.3 brought up a few interesting possibilities in this regard: first, executive control might not be needed to perform accurately in these tasks, as pigeons succeeded and showed similar patterns of behaviour in both tasks as humans did, and these patterns matched the predictions about performance made by the currently most prominent model of response inhibition, the independent horse-race model (Logan & Cowan, 1984). Secondly, although it is generally assumed that both tasks engage similar response-inhibition mechanisms (Verbruggen et al., 2008b), the pattern of responding in the Change-Signal task exhibited by both pigeons and humans, in combination with the observed absence of trial-sequence effects in pigeons, may suggest that no response-inhibition mechanism has in fact been employed in this task - and the many similarities between the two tasks speak towards the possibility that performance in the Stop-Signal task might equally be accomplished without the involvement of inhibitory-control processes.

Regarding the first of the above possibilities, although there are a great number of similarities in the performance of humans and pigeons, one will need to consider the differences in the performance between the two species to make a definite statement about the cognitive capacities involved in response inhibition. The most prevalent performance difference was found in the way humans and pigeons used the information of one trial to prepare for response execution or inhibition in the next trial, described in Section 4.3. The human participants persistently slowed down in their response latencies in Go trials after a Signal trial relative to Go trials following a Go trial, and greatly reduced the probability of wrongly responding to the Go stimulus in Signal trials following a Signal trial. Pigeons did not reliably do so. The human participants expressed in the post-experiment questionnaire that they had been aware of the function of the green and red stimuli (as a signal to Go or Stop/Change), and this awareness of the different response demands might have enabled them to mentally adjust the balance between focussing on performing the Go response and diverting

attention away from this action to detect the potential occurrence of a signal (Verbruggen & McLaren, in preparation).

Furthermore, executive control processes might contribute to different degrees towards reactive response inhibition in response to a signal and towards proactive inhibition by which subjects prepare for the possibility of having to inhibit a response. As reported in Section 4.4, neither pigeons nor humans reliably altered their behaviour based on information provided by cues predicting the likelihood that the Go response had to be withheld in a given trial. However, the mere lack of cue utilisation cannot be interpreted as an inability to respond to the predictive cues if performance is governed by associative processes, especially since previous research does suggest otherwise (Bowditch et al., 2015). Although it may be argued that an awareness of the function of the cues facilitated the appropriate adjustment of behaviour - two participants detected the contingencies between cues and the occurrence of a signal, and those two showed a pattern of behaviour that could be interpreted in favour of cue sensibility -, the data gained from the experiment in this thesis were insufficient to allow for a definite statement in this regard.
Bowditch et al. (2015) argued that inhibition both in response to a signal and in response to a cue may be reactive, that is, neither require a proactive preparation to inhibit one's response. This may well be the case; it may be that the subjects in the experiment reported in this chapter simply did not receive enough exposure to each of the cues to form a stable association with a cue and either the occurrence of a signal or, more directly, the goal to withhold a response, whereas the experienced number of Signal trials was sufficient to promote awareness of the contingencies of the stimulus and signal, and the associated demand to execute or withhold the Go response. Alternatively, it may be that cue-dependent response inhibition, like the trial-dependent adjustment of mental action goals discussed above, relies on the subjects' ability to utilise the information provided by the cues, and that subjects can only reliably adjust their behaviour in preparation for a potential need to inhibit a response if they possess executive control. Unfortunately, the results in this chapter provide no conclusive evidence in regard to this assumption, so that no definite statement can be made at the moment in regard to the cognitive requirements that allow proactive response inhibition.

In summary, the results reported in this section provide a first insight into different patterns of performance as a result of different cognitive mechanisms. In the beginning of this chapter, it was speculated that the influence of executive control might be visible in behavioural adjustments that are a consequence either of the inhibition requirements of the previous trial, or of available information about the likelihood that a signal will occur in a trial. The latter could not reliably be detected in either pigeons or humans with the current paradigms, and there may be a multitude of reasons for this failure to detect cue effects, which made it, at least for the moment, impractical to pursue the investigation of cue effects on pigeons' response-inhibition performance in any further experiments. However, the former is worth examining in more detail, since the results of this chapter potentially provide some support for the assumption that executive control manifests itself in trial-to-trial adjustments, which was exhibited by humans, but not by pigeons. As stated previously in Section 2.3, it is possible that the assessment of the pigeons' response times was unreliable and would not adequately capture any effects that might have been observable in the pigeons' performance with more accurate ways of measurement. Even though the pigeon's response times did reflect the predictions of the independent horse-race model, the possibility exists, especially if it can be assumed that trial-to-trial effects might be small.

In Chapter 5, I report an additional experiment I conducted to investigate whether pigeons may be able to adjust their behaviour from one trial to the next under different circumstances than the computerised tests that were used in the experiments reported in this chapter. This additional experiment was not reliant on a timed pecking response and, in addition, its design necessitated that a response was initiated before the appearance of the signal, in an attempt to ensure that inhibition had to be applied to correct that response. Because of these two advantages over the paradigms reported in this chapter, the experiment reported in Chapter 5 might provide further insights to the questions as to whether pigeons can perform post-signal adjustments to their behaviour, and whether the associatively-mediated withholding of a response requires inhibition.

CHAPTER 5: CAN PIGEONS INHIBIT A RESPONSE IN A CONTINUOUS RESPONSE-INHIBITION PARADIGM?

In Chapter 4, I established that pigeons and humans show similar patterns of performance in a Stop-Signal and Change-Signal task. However, although it is generally assumed that in humans both tasks require a mechanism of response inhibition (Verbruggen et al., 2008b) and performance in both is regarded as a measure of executive control, there is evidence that the response-inhibition mechanism governing Stop-Signal and Change-Signal performance has an associative component (Verbruggen & Logan, 2008a, 2009a; Verbruggen et al., 2014; Best et al., 2016). The pigeons' success in both tasks in Chapter 4 suggest that performance can be mediated entirely by associative processes and without the involvement of controlled inhibition.

The possibility that the paradigms in Chapter 4 had been solved without the executive process of inhibitory control poses a potential threat to their validity in attributing behaviours to certain cognitive mechanisms, i.e., in attributing the ability to inhibit an initiated response to executive control. In order to test this assumption, it has to be assured that the pigeons indeed initiate a Go response, necessitating an act of response inhibition when its execution becomes inappropriate. A suitable paradigm has to be designed in such a way as to force the subjects to initiate a response before the command to withhold it arrives.

The tasks used in Chapter 4 required subjects to perform a discrete action towards the Go stimulus (in Change-Signal task, this was also the case for the alternative key). Further, once a response location was chosen in the Change-Signal task, the act of inhibiting a response to that location might have been difficult for pigeons, because the alternative response location was - to the pigeon - spatially separated, and required a head or full-body movement of the pigeon to be brought into sight. In combination, the paradigm might have been unsuitable to elicit inhibitory control for pigeons, even if they might have been able to exert it under different circumstances.

A more promising approach might be the use of a paradigm that allows continuous response adjustment. For example, Verbruggen and McLaren (in

preparation) established a continuous Change-Signal paradigm to assess inhibitory control in children and adolescents of different ages. Unlike conventional paradigms, their task did not require a discrete action towards the Go stimulus and a separate action following the appearance of the Change signal, but instead participants were allowed to adjust their behaviour in one continuous motion. In their computer-based paradigm, participants had to quickly move the mouse cursor towards a target presented in one corner of the computer screen; sometimes, that target started moving towards the opposite screen corner after the children started dragging the mouse cursor towards it, forcing them to change the trajectory of the cursor to reach the target.

Verbruggen and McLaren's (in preparation) paradigm has been adapted for the use with pheasants (Madden, personal communication), by tracking their movement towards a target within a confined space. The pheasants entered a small arena at one end and crossed it to reach one of two food wells presented in the two corners at the other end of the arena. The right-hand food well was visibly baited, whilst the left-hand one was covered. In two of the six repeat trials of this experiment, as the birds crossed the arena, the right-hand food well was covered and the food in the left-hand well became accessible, so that the pheasants had to change their path to approach the usually unavailable left-hand food well to retrieve the food reward. As expected, the pheasants showed increased response times to reach the target location in these circumstances, and showed a distinct bias to approach the initially presented well for a short while after the accessible food well changed.

Verbruggen and McLaren (in preparation) claimed that the trajectories of the subjects' movement in space allow inferences about the mechanisms of response inhibition. They argued that the inhibitory control afforded in one trial can influence performance on the following trial if subjects perform mental goal adjustments between two trials. Such adjustments might induce similar effects on performance as the mental task-set reconfigurations that contribute to switch costs in task-switching paradigms: whilst focussing on the previous task set might allow subjects to perform that task more quickly on repeat trials, it decreases the ability to quickly and flexibly change to the other task set on switch trials (cf. Monsell, 2003). The same is thought to apply to response

inhibition (Verbruggen et al., 2008a; Bissett & Logan, 2011, 2012): humans might continuously calibrate the balance between focussing on completing the Go task on one side and, on the other side, diverting attention from the Go task to detect potential signals that that response has to be inhibited (cf. Elchlepp et al., 2016). Adjustments in favour of the goal to perform a response might not only increase the readiness to perform the required response on Go trials but also on Signal trials, whilst adjustments towards the mental goal to withhold a response might facilitate inhibition in Signal trials but lead to slower response execution when the Go response is required in Go trials. Such adjustments did appear to underlie the response patterns of the older children in Verbruggen and McLaren's (in preparation) study; the turning points in Change trials, at which the trajectories of the mouse cursor started moving towards the changed target location, were biased towards the Go location more if the previous trial had been a Go trial than if the previous trial had been a Change trial.

Conversely, if subjects possess poor executive control (for example, if the subjects are very young children), performance might be influenced less by trial-to-trial adjustments of abstract task goals but more by a residual activation of the motor system (cf. Awh, Belopolsky, & Theeuwes, 2012; Verbruggen, McAndrew, Weidemann, Stevens, & McLaren, 2016), in that there might be a bias to execute the exact motor response that was performed in the previous trial (including, on Signal trials, any initial movement towards the Go target). Such an influence can be assumed to be quite strong if the Go and the changed response targets always afford the same motor response (if, for example, the Go response is always a movement to the right, and the changed response is always a movement to the left). This was the case in the study of Verbruggen and McLaren (in preparation), and indeed, if the trial before a Change trial had also been a Change trial, their youngest participants moved the mouse cursor in a more curved line - with the turning point being closer to the initially indicated target location - than if the preceding trial had been a Go trial. This might indicate that the demand of the previous trial to perform a curved motion (from the start position in the direction of the initial location and then to the changed location) influenced that movement in the next trial.

It has to be noted that a potential inertia of motor responses can behaviourally be differentiated from a tendency to repeat a previously rewarded response, for example, in the specific case of Verbruggen and McLaren's and Madden's paradigms, returning to the most recently rewarded target location (cf. response-repetition effect, Chapter 3). In the latter case, the previously rewarded target location might be approached directly; it would be expected that the trajectories in Go trials following Go have a more direct path to the Go location than the trajectories in Go trials following a Change, and consequently the turning points in Go trials following Go would be expected to occur earlier in a trial than the turning points in Go trials following a Change.
For clarity, the patterns of performance that are expected to occur given each of the above three potential behavioural strategies is illustrated in Figure 5.1. In addition to mental goal adjustments, residual motor activation and a bias to approach the previously rewarded location, a non-directional approach is included as a fourth potential factor; it is discussed later on.

Executive-control processes can reduce the effects of any of the mentioned causes. To disentangle the potential causes of any bias towards a target location as a consequence of the previous trial, it is thus once again helpful to examine the pattern that emerges when behaviour is not guided by executive control. The pheasants in Madden's (personal communication) study completed one trial per day, which prevented the analysis of any trial-to-trial goal adjustments; therefore, I assessed the performance of pigeons in this task. As pigeons are not assumed to be able to formulate the kind of mental goal sets that may underlie human behaviour, any difference in their trajectories towards a goal location in Go and Change trials should be a consequence either of residual motor activation of the response that was executed in the previous trial, or of a bias to move towards the most recently rewarded target location. Any such effects should be evident in the comparison of Go trials that were preceded by another Go trial with Go trials that were preceded by a Change trial (Verbruggen et al., 2008a; Bissett & Logan, 2011, 2012).

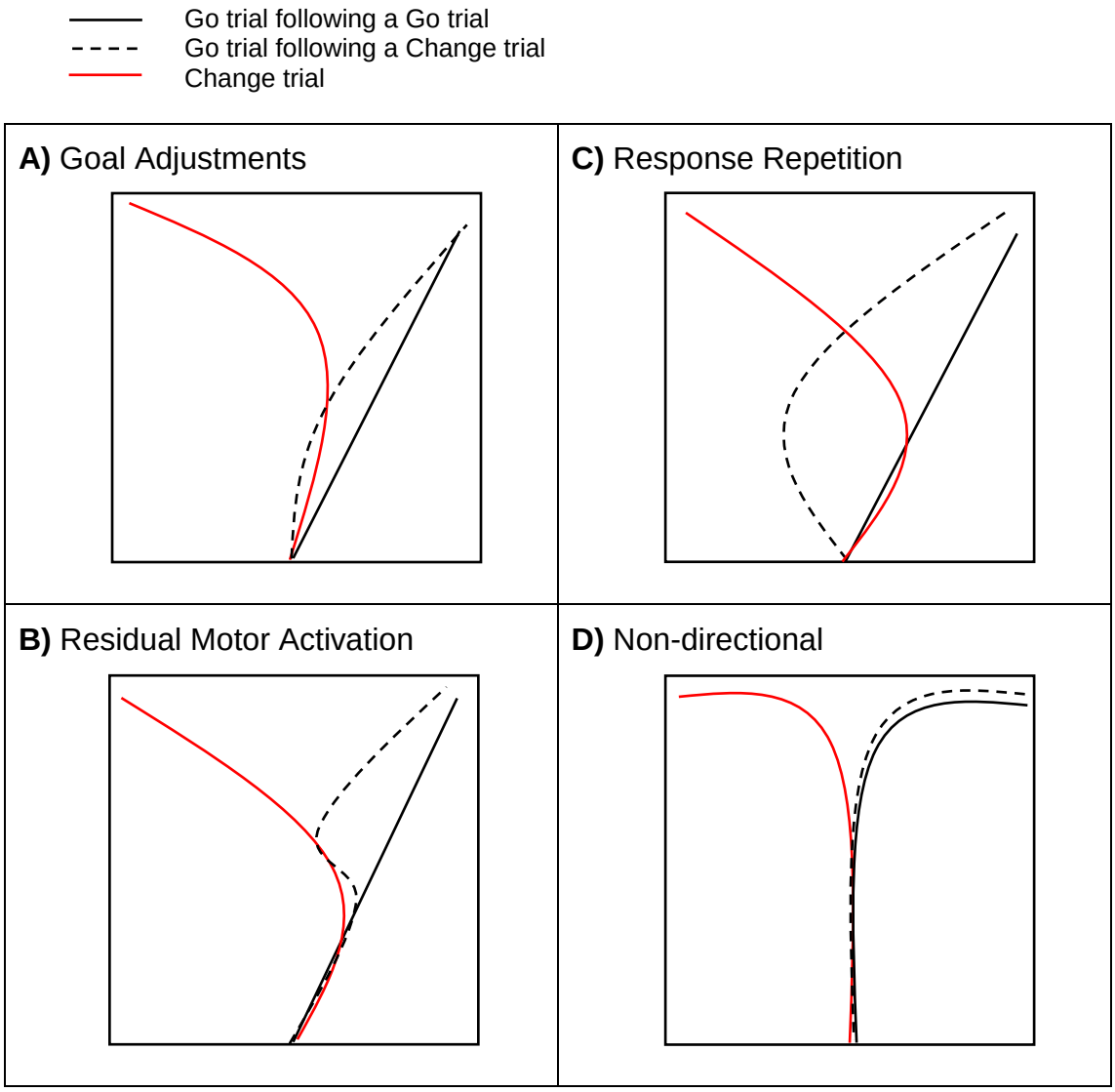

Figure 5.1. Expected trajectories in Go trials (following a Go or following a Change trial) and Change trials when behaviour is governed by *A)* inter-trial goal adjustments, *B)* residual activation of motor programs, or *C)* a tendency to approach the previously baited food well, or *D)* when the arena is entered without direction. *Note*: the target location was on the right in Go trials and on the left in Change trials.

Following Madden's procedures, I built an arena (described below) containing two food locations. In two thirds of trials - the Go trials -, the right-hand-side location (the Go location) was baited and a pigeon was rewarded for approaching it. In the remaining third of trials, after the pigeon started its approach, the initially available Go location was covered and the left-hand-side food location became available. In these trials, in order to gain a reward, the pigeon had to stop any movement towards the right location and instead approach the newly exposed location. The necessary continuous response adjustment in this setup has one obvious benefit over the response

requirements of the paradigm developed in Chapter 4: because the task requires movement in space, the pigeons were forced to initiate a response towards a goal (a food location) on every trial. This made it possible to assess the pigeons' ability (both in terms of success and speed) to correct their behaviour after initialising a response. Another advantage of the paradigm used in this chapter over the one used in Chapter 4 is that no extended training period was required to establish associations between arbitrary colours and symbols and the command to inhibit a response. The paradigm used in this chapter utilised the pigeons' natural behaviour of approaching a food source; no further reward or punishment was required to elicit a response towards the target. As a result, a substantially larger sample of subjects could be tested.

Methods

Subjects

Forty-nine pigeons entered this experiment (including all the pigeons that took part in the experiments reported in Chapters 2, 3 and 4); 38 completed the entire procedure. Housing conditions were the same as described in Chapter 2. Each pigeon was tested in isolation. Inside the testing arena, the pigeons had no access to water or grit, but they received water and grit *ad libitum* in the aviaries and holding areas.

Apparatus

Figure 5.2 Panel A is a scale plan of the experimental apparatus; for a 3D-sketch, see Figure 5.2 Panel D. The arena was mounted onto a sheet of 135x100cm melamine-covered chipboard (Contiboard®) with six pillars of planed soft wood, each 10x10x45cm in size. The outer walls of the arena were made of 6mm plywood of 30cm in height; the long walls were 124cm long, the short walls were 80cm long. Because the poles were taller than the walls, a curtain made of blue cloth was drawn between the poles along the long walls (seen in Figure 5.2 Panel B) to restrict the pigeons' vision to the inside of the arena. The arena that was accessible to the pigeons measured 82x76cm. The pigeons entered the arena from one of the short walls via a 40cm long and 26cm wide runway corridor (seen in Figure 5.2 Panel C). The corridor and the interior walls adjacent to it were made of 6mm plywood and plastic-covered

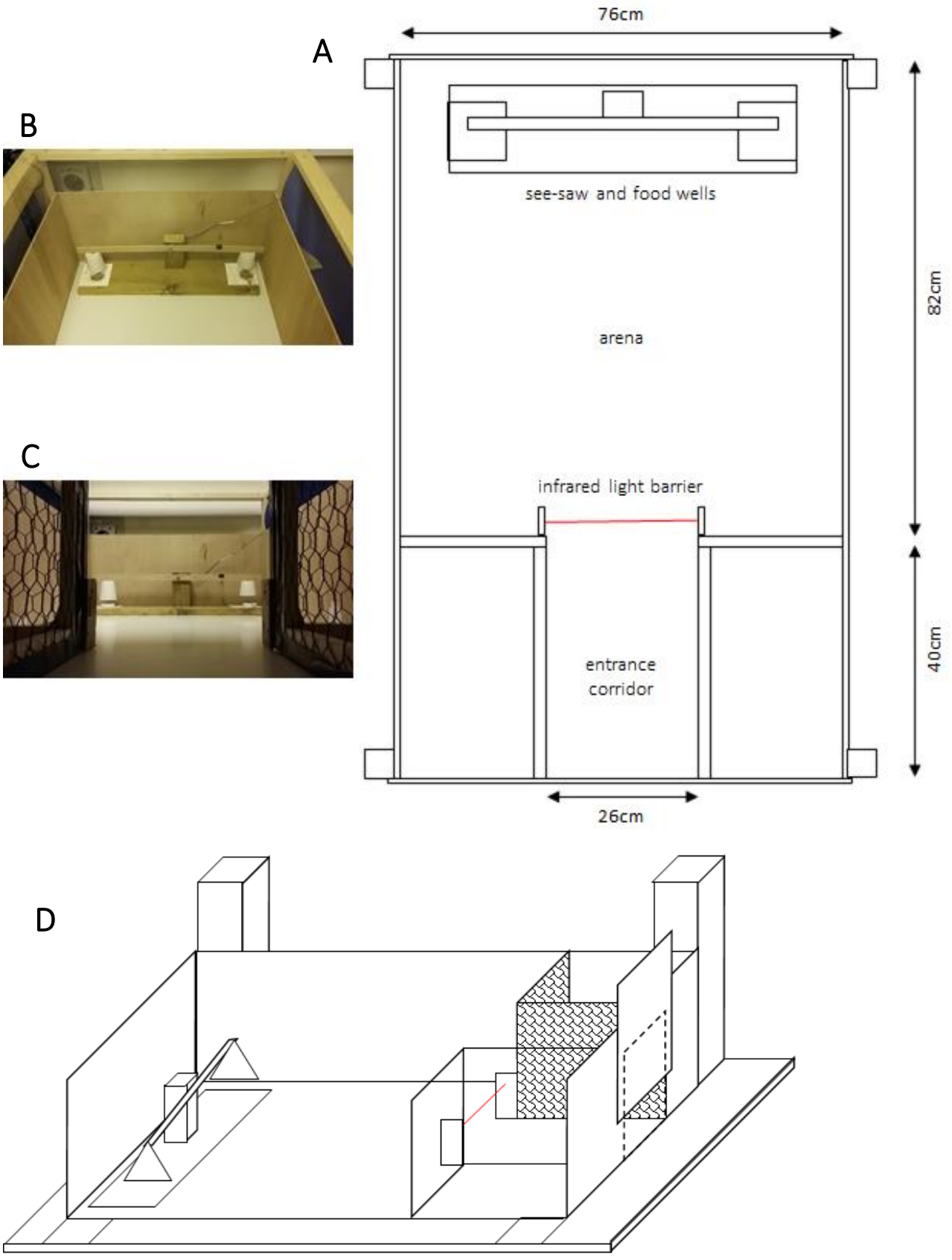

Figure 5.2. *A*) Scale plan (1:10) of the testing arena. *B*) View from above at the see-saw. Both wells are uncovered in this picture. *C*) The pigeon's view from the inside of the entrance corridor into the arena. Both wells are uncovered in this picture. *D*) Design of the testing arena shown from the side (not to scale, for exact proportions see Panel A). See text for details.

25mm chicken wire, enabling the pigeons to view the arena from inside the corridor. A see-saw device was mounted along the opposite short wall of the arena. The see-saw consisted of a plywood beam
of 50cm length that was fixed onto a block of wood by a bolt. A small plastic cup was attached to each end of this axis, cut to size to cover another plastic lid glued in place underneath that served as a food well. The two wells were approximately 35cm apart from each other in the corners of the arena. The see-saw could be operated to cover one of the two food wells. In its default position, the see-saw covered the left (as seen from the corridor entrance) food well, exposing the right well. Its axis rested on the armature of a solenoid integrated into the see-saw hinge, which retracted when the solenoid was activated, allowing the see-saw to tip over to cover the right food well and expose the left well. Directly adjacent to the right side of the corridor exit on the inside of the testing area, an LED diode was mounted 7cm from the ground and continuously generated an infrared light beam. The beam was detected by a lux meter mounted at the same height on the left side of the corridor exit. The lux meter recorded any changes in the incoming infrared beam and submitted this information to an Arduino® One microchip board; if the there was an interruption in the light beam, the Arduino One board operated the solenoid attached to the see-saw. The arena was covered by a Plexiglas® roof hinging onto one of the long walls. It opened to the top to allow the experimenter to manually remove the pigeon from the arena. The runway corridor was covered by a scrap-board roof. A video camera was mounted onto this roof to overlook the testing arena.

Procedure

Before testing, all pigeons received a 15-minute habituation session in which the see-saw was fixed in place to expose both food wells, which were both baited. One pigeon at a time was placed into the entrance corridor of the arena and was allowed to freely explore the testing arena and feed from the two food wells. A pigeon received up to three habituation sessions until it fed from both food wells in the same session. If a pigeon had not visited both wells by the third session, it was excluded from any further test sessions.

Following a successful visit to both food wells within 15 minutes, the pigeon received a 5-minute session in which, again, both food wells were accessible and baited. If the pigeon visited both wells within the 5-minute interval, it was

moved on to the test sessions. This 5-minute feeding session was also repeated up to three times, until the pigeon had fed from both wells in the same session. As above, if a pigeon failed to do so within three sessions, it was excluded from any further test sessions. 38 of the 49 pigeons successfully completed the habituation sessions; the remaining 11 pigeons did not explore the arena.

Test trials were administered in two sessions, each session consisting of 4 blocks of 3 trials, totalling 24 trials per pigeon. The first two trials in each block were 'Go' trials: the see-saw was fixed to expose the right food well (covering the left well) and a pigeon was allowed to feed freely from that well after approaching it. The third trial in the sequence was a 'Change' trial: at the start of this trial, the see-saw was in the same position as in Go trials but rested loosely on the solenoid armature, and it was allowed to flip to the other side when the pigeon crossed the infrared light beam at the arena entrance and so operated the solenoid. In these trials, the pigeon was allowed to feed from the newly exposed left food well; the right well was covered after the see-saw had tipped over.

A trial ended either once the pigeon had consumed all the food from the available food well or, if the pigeon failed to approach a well, after a maximum of three minutes. In the latter case, the trial was repeated up to two more times until the pigeon approached the exposed food well; if it had not done so by the third trial repetition, the session was aborted. If this was the case, the pigeon repeated the entire block of three trials in its next session.

All trials were recorded using the video camera.

Data Collection

To estimate the pigeons' ability to correct their behaviour after initiating movement towards a food location, I recorded the latency from releasing a pigeon into the entrance corridor until it fed from the exposed food well. Furthermore, using the video recordings of each trial, I recorded the position of a pigeon's beak and its trajectory as it moved within the arena and mapped its path to the food well using the Open Source Physics Tracker© video tracking software (Brown, 2009). From these data, I extracted the latency to reach the accessible food well from the point of being released into the entrance corridor; I also extracted the coordinates of the turning point at which a pigeon's

trajectory was distinctly directed towards the accessible food well, defined as the final local minimum (in Go trials) or maximum (in Change trials) of the x-coordinate of the pigeon's beak before the value of this coordinate continuously increased or decreased respectively until the correct food well was reached. I also recorded the time to reach that turning point since entering the arena and crossing the infrared light beam. The axes of coordinates were standardised so that the entrance point from the corridor into the arena was marked by the coordinates (0,0); the available food well in Go trials was located at (1,1) and the available food well in Change trials was located at (-1,1).

As the trials were administered in two sessions of 12 trials, the first trial and the thirteenth trial were not preceded by either another Go or a Change trial, so they were excluded from analyses. Thus, there were 8 Go trials preceded by Go, 6 Go trials preceded by Change and 8 Change trials that went into analyses.

Where applicable, the reported results of the statistical analyses were subject to Huynh-Feldt corrections.

Results

Figure 5.3 shows the average trajectory path that a pigeon's beak took from the entrance of the arena to the accessible food well for each trial. To account for individual differences in the latencies to reach the correct food well, the trajectories of each trial were standardised by Vincentisation (Vincent, 1912; Ratcliff, 1979; Genest, 1992); the graphs depict the twenty 0.05-quantile points of the latency to reach the available food well. These were averaged across the eight (or six) trials of each trial type for each pigeon (shown as grey lines in Figure 5.3), and then again averaged to calculate the group mean trajectories. The coordinates of every pigeon's average turning points (the moment of starting to approach the available food well) in each trial type are illustrated in Figure 5.4.

The x-coordinate of the pigeons' average turning points in Change trials (M=0.14, SD=0.22, Figure 5.4 Panel C) was significantly greater than zero, $t(37)$=3.80, adjusted p=.003, η_p^2=.28, indicating that pigeons were closer to the Go food well than to the changed food well when their trajectory irreversibly

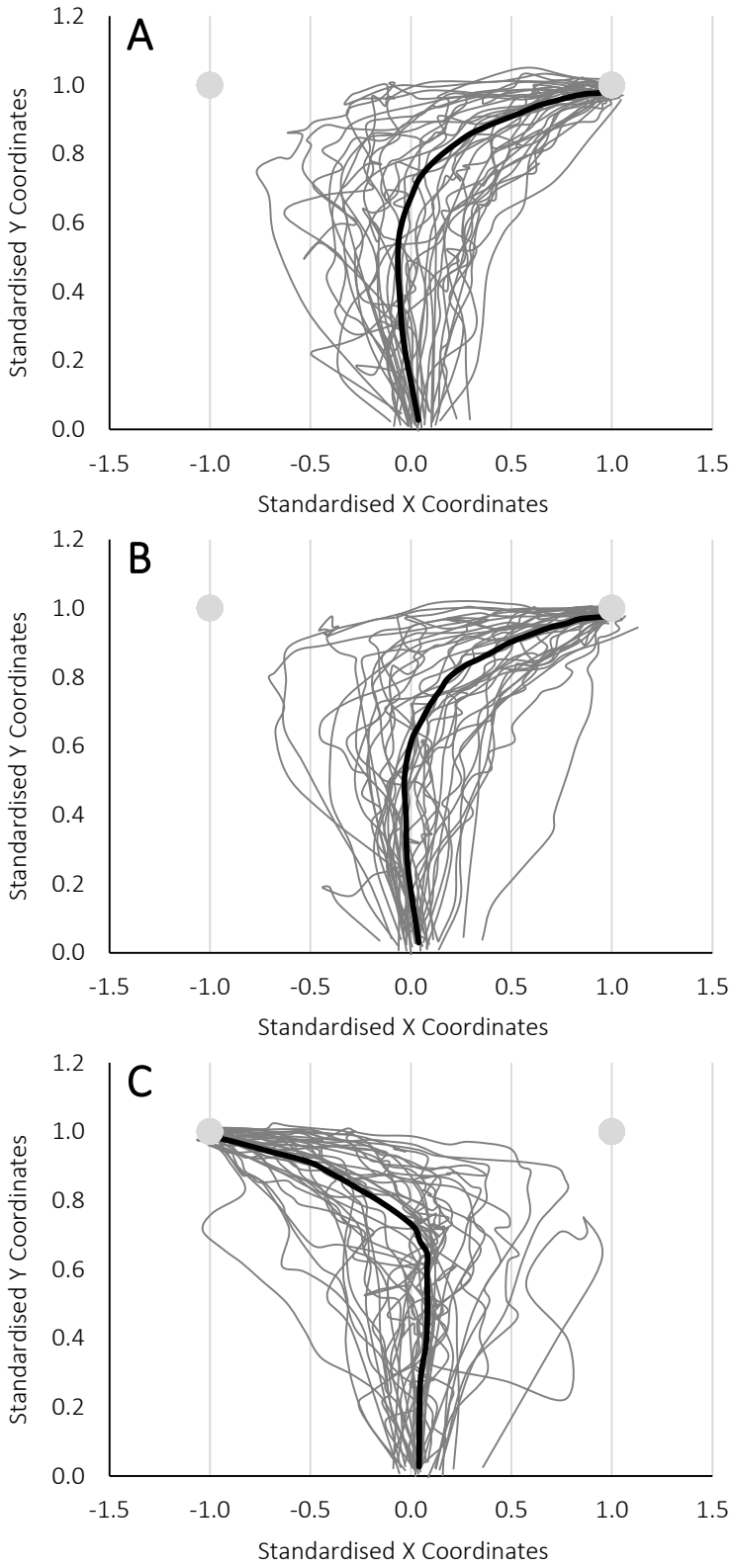

Figure 5.3. Average trajectories towards the baited food well in *A)* Go trials following another Go trial, *B)* Go trials following a Change trial and *C)* Change trials. Grey lines: mean trajectories of individual pigeons, black lines: overall mean trajectory. *Note:* the grey circles depict the locations of the two food wells; in Go trials the accessible well was at (1,1), the location of the accessible well in Change trials was at (-1,1).

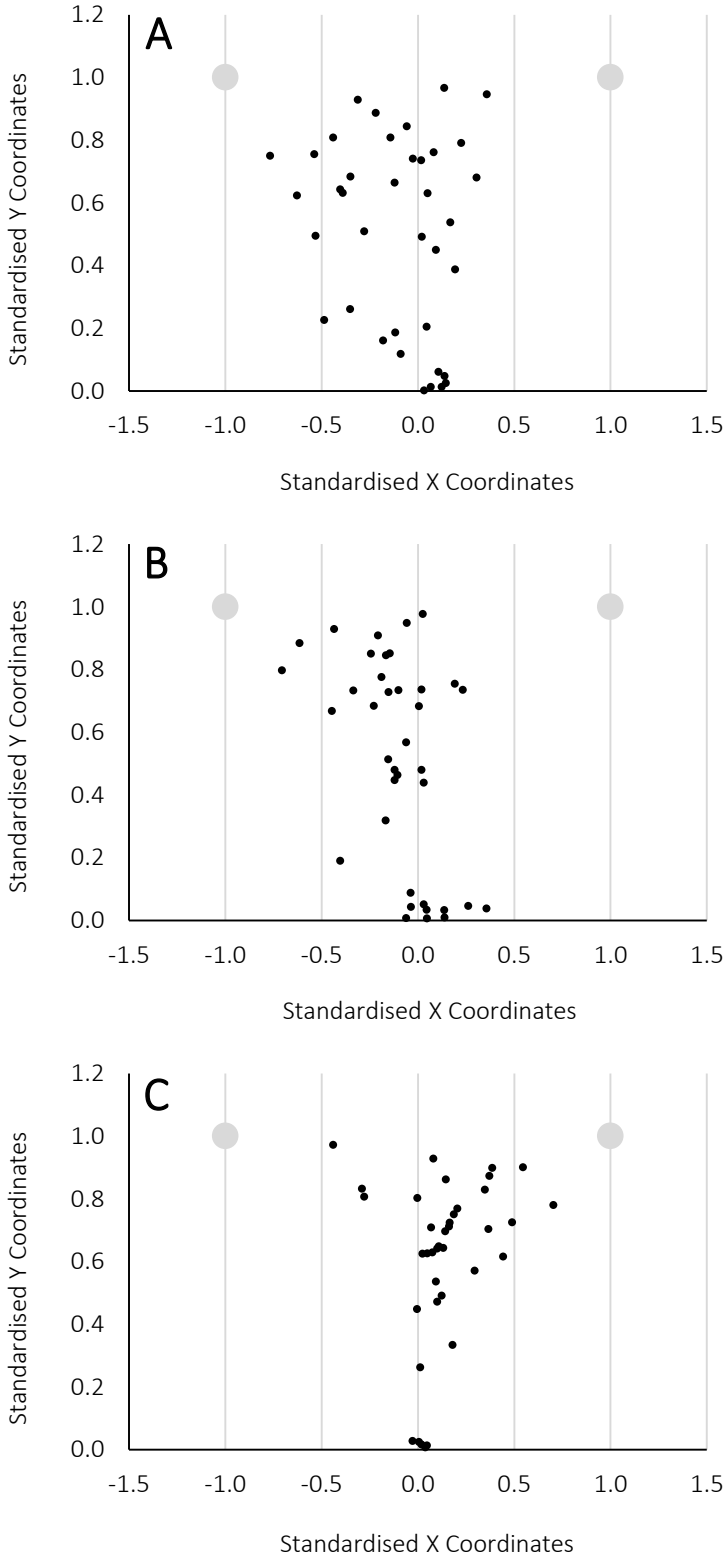

Figure 5.4. The individual pigeons' average turning point (coordinates of the first location at which the distance to the available food well decreased and did no further increase subsequently) in *A)* Go trials following another Go trial, *B)* Go trials following a Change trial and *C)* Change trials. *Note:* the grey circles depict the locations of the two food wells; in Go trials the accessible well was at (1,1), the location of the accessible well in Change trials was at (-1,1).

started approaching the changed well. For Go trials, the average turning point (as the x-coordinate at which a subject started decreasing the distance to the Go well without any further increase in distance) was marginally lower than zero for Go trials following a Go trial (M=-0.10, SD=0.23, Figure 5.4 Panel A; $t(37)$=2.41, adjusted p=.063, η_p^2=.14), and significantly lower than zero for Go trials following a Change trial (M=-0.11, SD=0.28, Figure 5.4 Panel B; $t(37)$=-2.71, adjusted p=.030, η_p^2=.17), indicating that the pigeons were somewhat closer to the inaccessible food well than to the Go food well when starting to approach the Go well.

To assess whether there were any differences in the trajectories in Go-following-Change and Change-following-Go trials, the x-coordinates of the pigeons' trajectories on Change trials were mirrored along the y-axis, so that the location of the correct food well had the coordinates of (1,1), like the correct well in Go trial types. The x-coordinates of the pigeons' mirrored turning points in Change trials did not differ significantly from the x-coordinate of their turning points in Go trials, $F(2,74)$=0.24, p=.72; Bonferroni post-hoc comparisons to Go trials: both p=1.0. The turning points in the two types of Go trials did not differ depending on whether that trial was preceded by a Go trial or a Change trial, p=1.0. Likewise, there was no difference between the two types of Go trials and the Change trials in the (mirrored) x-coordinates at the point of entering the arena and in the subsequent twenty 0.05-quantile points of the pigeons' mean trajectories, interaction between trial type and trajectory of x-coordinates: $F(40,1480)$=1.46, p=.23.

The y-coordinate of the average turning points for all three trial types also differed significantly from zero (which represents the entrance point into the arena); Go trials following a Go trial: M=0.51, SD=0.31, Figure 5.4 Panel A; $t(37)$=10.21, adjusted p<.001, η_p^2=.74; Go trials following a Change trial: M=0.51, SD=0.34, Figure 5.4 Panel B; $t(37)$=9.40, adjusted p<.001, η_p^2=.71; Change trials: M=0.60, SD=0.28, Figure 5.4 Panel C; $t(37)$=13.36, adjusted p<.001, η_p^2=.83. These coordinates did not differ significantly between trial types, $F(2,74)$=1.25, p=.28.

Figure 5.5 shows the latencies from being released into the entrance corridor to reaching the accessible food well. Additionally, the average time to reach the turning point, that is, the time from entering the arena and crossing the light beam to distinctly moving towards the newly available food well, is shown as grey bars.

The turning-point latencies were analysed in a repeated-measures ANOVA using Trial Type (Go trial following another Go trial, Go trial following a Change trial, Change trial) as a within-subjects factor. They differed significantly between Go and Change trials, $F(2,74)=6.70$, $p=.004$, $\eta_p^2=.15$. Bonferroni post-hoc comparisons confirmed that the pigeons started approaching the correct food well equally fast in both types of Go trials regardless of whether the previous trial had been a Go (M=6.2sec, SD=1.2) or a Change trial (M=6.5sec, SD=1.2), p=1.0; that is, there was no effect of the response requirements in the previous trial on reaching the turning point in Go trial. However, the pigeons took longer to start approaching the correct food well in Change trials (M=11.4sec, SD=2.2), comparisons to Go trials: both $p \leq .023$.

The time from the turning point to reaching the correct food location (shown as white bars in Figure 5.5) did not differ significantly between trials, $F(2,74)=1.68$, $p=.20$. Once the pigeons were on a distinct path towards the correct food well, they reached it in roughly the same time in all trials.

To assess whether the difference in the latencies to reach the turning point might be due to being more familiar with approaching the Go location, the analysis was repeated including only the data from the last block of trials, at which point the pigeons had experienced seven Change trials. The time to reach the turning point in the last block did not differ significantly between trial types, $F(2,74)=1.91$, $p=.17$; the pigeons turned towards the correct food location not significantly different in Go trials following a Go (M=3.7sec, SD=0.9), Go trials following a Change (M=4.2sec, SD=1.1), and Change trials (M=8.5sec, SD=3.2).

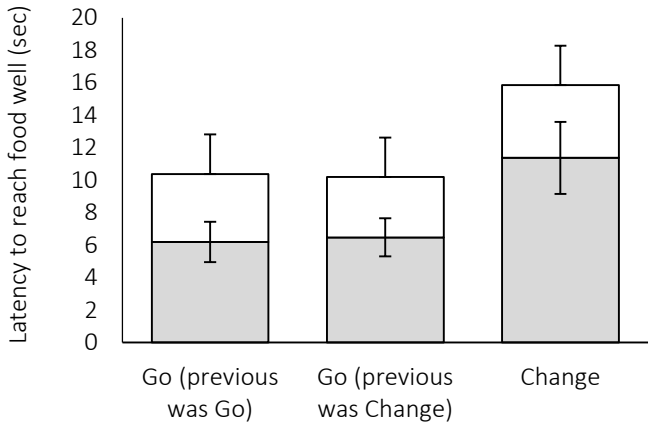

Figure 5.5. Latencies in seconds to reach the correct food well in Go trials (following another Go trial or following a Change trial) and Change trials. The grey areas denote the average time to reach the turning point at which a pigeon started approaching the available food well. Error bars represent standard errors. *Note:* Change trials were always followed a Go trial.

Discussion

The paradigm used in Chapter 4 could have been completed without the involvement of a response-inhibition mechanisms. Therefore, in an effort to necessitate the inhibition of a prepared response, the design of the experiment in this chapter forced pigeons to initiate a Go response before the signal to alter that response was given. The paradigm required pigeons to approach a baited food well, a behaviour that is, presumably, highly prevalent in the pigeons' natural behavioural repertoire and executed quickly, and might thus require a considerable amount of inhibitory control to be overcome.

The pigeons took significantly longer to start approaching the correct food location in Change trials, and their trajectories suggest that they were inclined to initially approach the (incorrect) Go location in those trials before adjusting their movement towards the changed location. I return to the response times later; but first, I focus on the trajectory data.

Verbruggen and McLaren (in preparation) claimed that the influence of inhibitory control, at least in their subjects, would be visible in a clear movement towards the Go location followed by a sharp curve towards the changed location. As can

be seen in Figure 5.3 Panel C, some pigeons do seem to change direction abruptly, but the group as a whole showed no trajectory of abruptly changing directions from moving towards the Go target to the changed target; neither did they show a tendency to approach the Go well in a straight line in Go trials. Instead, judging by the overall trajectory curves in Figure 5.3, it appears that the general trend was to move towards the centre of the arena in all trials, and then to approach the accessible food well from there.

To determine the cognitive mechanism that determined the pigeons' behaviour, I evaluated the effect of the previous trial on movement trajectories. Similar to the post-signal effects on response latencies and P(respond) discussed in Sections 1.2 and 4.3, the influence of the response requirement of the previous trial on performance in the current trial can have several possible causes. For example, differences in trajectories depending on the previous trial type can be due to mental goal adjustments (Elchlepp et al., 2016), residual motor activation (Verbruggen & McLaren, in preparation), or a bias to repeat the previous response (cf. Chapter 3). Each potential cause should have a different effect on the expressed trajectories, as illustrated in Figure 5.1.

The pigeons' average turning points at which the distance to the correct food well only decreased, indicating that the pigeons approached the appropriate well, was indeed biased towards the previously rewarded food location, both in Change trials and in Go trials following a Change trials, which would support the response-repetition account. For Go trials following a Go trial, however, this account (as well as the other two potential mechanisms described above) predicts a direct path towards the Go location from the moment of entering the arena - but for the pigeons, the average turning point for Go trials following another Go trial were not closer to the Go location than the turning points in Go trials following a Change trial (indicated by similar values of the x-coordinates); they were also not closer to the entrance of the arena (and thus earlier in a trial) for Go trials following Go than for Go trials following Change (indicated by similar values of the y-coordinate). In fact, the pigeons crossed the arena about half-way (see Figure 5.3 Panel A) before turning towards the Go well. As mentioned above, this pattern suggests that, instead of employing any of the strategies proposed above which would induce a bias towards the Go location, the pigeons tended to move towards the centre of the arena in all trials, and

then approached the accessible food well from there. Accordingly, Figure 5.1 Panel D presents the pattern of behaviour that would be expected if there was no bias towards either target location, and subjects instead proceeded without a goal direction into the arena. As is evident when comparing the mean trajectories in Figure 5.3 with those predicted in Figure 5.1, the pigeons likely pursued this approach. It also explains the observation that the turning points in each trial were biased towards the incorrect food location: if a pigeon entered the arena not in a straight line but towards the side of the correct location, it would be able to reach the correct food well with minimal adjustments to its path - and the recorded turning point for these occasions would be close to the arena entrance and close to zero. If the pigeon, upon entering the arena, proceeded in the direction of the incorrect well, it would have to change its trajectory, at the latest point when reaching the wrong corner of the arena - the turning point for these trials would all be on the opposite side to the correct food well. Averaging the turning points across trials would thus produce coordinates that are skewed towards the opposite side of the correct food location.

The apparent lack of direction in the pigeons' trajectories can possibly be explained by their comparatively long response latencies to reach a correct food well. As shown in Figure 5.5, the pigeons took ten to fifteen seconds to complete a trial, whereas the pheasants in Madden's experiment took around five to ten seconds (Madden, personal communication). Whilst it is possible that this difference between species is due to a somewhat larger arena for the pigeons (the distance from the entrance to the other side of the arena was 124cm for the pigeons and 75cm for the pheasants), long latencies make it difficult to assess whether the pigeons engaged a mechanism of response inhibition to adjust their responses when necessary. The paradigm in this chapter did not impose any negative consequences for approaching the incorrect food well or for responding slowly, so that there was no pressing need to quickly readjust any incorrect behaviour.

It could have been the case that the pigeons generally completed the movement towards the Go location until they reached it and only approached the other food well after discovering that the Go well was inaccessible. Some pigeons did seem to do so in all eight Change trials, but there is no overall pattern across all subjects that would indicate that the pigeons generally approached the Go well first (and failed to employ inhibitory control) and then

corrected their behaviour. Instead, the non-directional trend in their overall trajectories suggests that, as in the experiment in Chapter 4, the pigeons did not inhibit a prepared response in order to be able to perform the correct response.

Despite this apparent overall trend, it is not the case that experience had no effect on behaviour - as mentioned above, the pigeons took considerably longer to reach the turning point in the Change trials than in the Go trials. In all trials, the distance from the entrance to the two food wells was equal; thus, if there had been no bias in approaching either well, those latencies should have been equal in Go and Change trials. The fact that this was not the case shows that the pigeons more readily approached the Go well than they approached the Change well.

Because Change trials occurred less frequently than Go trials, the required response in Change trials (i.e., approaching the left food well) might not have been as well practised as the Go response, making pigeons slower. Thus, the slower response latencies, and the pigeons' initial tendency to move towards the Go location could be seen as a matter of familiarity with the response requirements, rather than as evidence for the inhibition of an incorrect response. Indeed, in the last block of trials, the pigeons' latencies to reach the turning point in each trial type did not differ significantly between trial types; that is, after having had experienced seven Change trials previously, the pigeons approached the changed food location as quickly as the Go location, although the greater variability in the Change latencies suggests that the pigeons might still had a tendency to approach the Go well, which had been baited twice as often.

Separately, familiarity with the Go response might be the key to the question as to why the pigeons did not show the same strong tendency to approach the Go location as the pheasants in Madden's (personal communication) experiment, which performed the same task under very similar conditions. In contrast to the 24 trials that were given to the pigeons, the pheasants only completed six trials, each administered on a different day. Only two of those trials were Change trials, one of which was the very last trial; that is, when entering their first Change trial, the pheasants had experienced only two Go trials, and at the start

of their second Change trial, the pheasants had previously experienced four Go trials and one Change trial.

Some specifics about the design of the arena might have further contributed to differences in strategies between pheasants and pigeons. It might be that the pigeons were unable to determine which one of the two wells was open and contained food when they entered the arena, so that a strategy of entering the arena in a straight line and thus minimising the distance to each well was the most efficient way of resolving uncertainty. Another likely possibility is that the pigeons, although able to view both food wells from within the entrance corridor, did not start to move towards one food location until they had entered the arena, which was the same moment that the light beam initiating a change was crossed. A possible improvement of the design in this regard would be to change the point at which the light beam is crossed. In Verbruggen and McLaren (in preparation) study, the children had started a distinct movement towards the Go target before the change was induced; perhaps installing the light beam at a position closer to the Go location - for example, at the coordinates of (0.25,0.25) - would initiate a comparable goal-directed movement for the pigeons. Increasing the ratio of Go trials to Change trials might additionally promote more direct trajectories towards the Go location.

All in all, although it was initially thought that this paradigm might provide a more direct way of assessing response inhibition in pigeons than the paradigm used in Chapter 4, it appears that it had problems if its own. Nonetheless, if the procedure used in the present chapter are refined, it can have merits; for example, it allows a quick assessment of a large sample size without the need for extensive training in an operant chamber. The computer-based approach reported in Chapter 4, which allows relatively close mirroring of the procedures used with adult humans, might be better suited to measure inhibitory processes if it can be implemented practically, as it can with pigeons.

CHAPTER 6: GENERAL DISCUSSION

Executive control provides humans (and perhaps other capable animals) with the outstanding cognitive ability to plan their actions and flexibly adjust these plans to current intrinsic and extrinsic demands. This ability has been studied extensively, with two of the most widely used paradigms being the task-switching (Monsell, 2003) and the Stop-Signal paradigm (Logan & Cowan, 1984).

In task-switching paradigms, it is assumed that the influence of executive control is evident in task-switch costs, and that humans perform a mental task-set reconfiguration (Monsell, 2003; Monsell & Mizon, 2006), by which the specific stimulus-response rules of the current task are retrieved into working memory, and the rules of the previous task are deleted. It has been proposed that this process of replacing one set of rules with a different set of rules, despite its cost to performance, shields an individual's attention against external distraction (Dreisbach & Haider, 2008, 2009; Dreisbach & Wenke, 2011) and thus limits the execution of incorrect responses.
Indeed, in the experiments reported in this thesis (and in line with the literature on task-switching performance in humans, cf. Monsell, 2003; Kiesel et al., 2010; Vandierendonck et al., 2010), the participants who based their behaviour on the task rules that defined the paradigm showed substantial switch costs. In further evidence for the shielding function of switch costs (Dreisbach, 2012), these costs were mainly observed in responses towards response-incongruent stimuli, to which the correct response varied between tasks, and occurred irrespective of whether or not a stimulus or a response was repeated from one trial to the next. This result suggests that the behaviour of those participants was indeed sensitive only to the abstract task structure of the paradigm, and any interference from potentially conflicting stimulus-response contingencies was minimised by executive-control operations.

Similarly, Stop-Signal paradigms are thought to depend on executive control, enabling an individual to inhibit the execution of a response after it has been prepared; Change-Signal paradigms additionally demand the preparation and execution of an alternate response. Although there is now considerable doubt

that the proposed "horse-race" between the process that governs response execution and the process that governs response inhibition relies on executive control (cf. van Gaal et al., 2009; Verbruggen & Logan, 2008a, 2009a), other phenomena might reflect the influence of executive control, such as the observation that response latencies increase in trials following successful inhibition (Rieger & Gauggel, 1999; Bissett & Logan, 2011, 2012; Elchlepp et al., 2016) and accuracy increases in trials that demand the same process (either response execution or inhibition) as the previous trial (Verbruggen & McLaren, in preparation). The human participants in the experiments reported in this thesis showed these effects.

However, as pointed out in Chapter 1 and subsequent chapters, the behavioural effects that are captured with task-switching and Stop-Signal paradigms might not necessarily reflect executive-control processes, but could emerge when behaviour is guided by associative processes.

For example, it could be expected that, without executive control, subjects would not perform any of the mental inter-trial adjustments that presumably enable successful task switching. Specifically, associative learning could guide acquisition without a mental representation of competing sets of task rules (and consequently without requiring task-set reconfiguration; Dreisbach, 2006, 2007; Forrest, 2012; Forrest et al., 2014) - behaviour would be based on the experience with specific stimuli and their associated responses. Similarly, in Stop-Signal tasks, subjects relying on associative processes should not be able to perform any adjustments of their mental inhibition threshold (Bissett & Logan, 2011; Stuphorn & Emeric, 2012; Verbruggen & McLaren, in preparation) in anticipation of having to inhibit a response. In fact, any potential trial-to-trial effects in either paradigm should be limited to specific aspects of the presented stimuli or the performed response, but should not be visible at the level of an abstract task structure (cf. Chapters 3 and 4).

6.1 How Do Executive Control and Associative Processes Affect Performance?

The main focus of this thesis was to examine whether the above predictions could be confirmed by studying the performance of pigeons. One important assumption of this approach was that the behaviour of pigeons is guided purely by associative processes. It is widely assumed, on the basis of substantial evidence, that this is the case (Mackintosh, 1988), and the cognitive capacities of pigeons and their evident limitations relative to human performance are well documented (e.g., Lea & Wills, 2008; Lea et al., 2009, Wills et al., 2009; Smith et al., 2011; Smith et al., 2012; Maes et al., 2015). The studies reported in this thesis provide further evidence that the pigeons indeed relied exclusively on associative processes to acquire and perform accurately in a given task: in Section 2.2, I show that a small change in the way forced-choice response options were displayed determined success or failure to learn a discrimination task. Additionally, in Section 4.1, I report the observation that the specific method of reinforcement greatly influenced whether pigeons acquired a behavioural response. As discussed in the relevant sections, these observations support the contention that the behaviour of the pigeons primarily relied on Pavlovian processes.

In the assessments of task-switching effects reported in Chapter 3, pigeons demonstrated a marked absence of task-switch costs. A series of further experiments confirmed these findings; due to the similarity in the results, these experiments were not reported in greater detail in this thesis, but their results are summarised in Appendix A5. In one experiment, each task was indicated by a single cue (so that every cue switch signalled a task switch, which can contribute largely to task-switch costs in humans; Monsell & Mizon, 2006; Vandierendonck et al., 2010), to assess whether the number of cue-task mappings would affect the emergence of switch costs in the performance of pigeons. In another experiment, the task-switching paradigm included only response-incongruent stimuli, to which humans show increased switch costs (Kiesel et al., 2010; Forrest, 2012). In a final experiment, the inter-trial interval was reduced from 15 to 30 seconds to one to two seconds, and the presentation of a start key was omitted, to assess whether a shorter latency

between trials and before the arrival of the stimulus would increase switch costs - in humans, shorter intervals reduce the time to prepare a task switch, which leads to a decrease in performance in task-switch trials (Logan, 2003; Monsell, 2003; Altmann, 2004). None of these variations produced detectable switch costs in pigeons.

Despite the consistent lack of task-switch costs, the pigeons' performance in the task-switching paradigm was greatly affected by the response-congruency of the stimuli and by response-repetition effects, which both occur independently of any task demands and are best explained in terms of associative processes (cf. Chapter 3). That is, the congruency effect reflects interference from conflicting stimulus-response mappings; the response-repetition effect seems to relate mainly to the appetitive value of a recently reinforced stimulus location.

The results of the experiments with pigeons are quite intriguing on their own - but in order to be able to make a more comparative assessment, I examined whether humans could come under the control of the same associative processes.

Previous studies in humans have tried to determine the influence of associative processes on performance by limiting the extent to which participants could engage executive control. For example, information about the task structure of the task-switching paradigm was withheld (e.g., Dreisbach, 2006; 2007; Forrest, 2012; Forrest et al., 2014), and participants were only provided with stimulus-response contingencies or had to learn the specific contingencies via trial and error.

I took a similar approach in this thesis: in an attempt to limit the extent to which humans employed executive control to complete the paradigms but instead engaged associative learning, all participants were encouraged to learn the correct responses to each stimulus as they performed the tasks.

The underlying assumption of this procedure (and of key studies in this area, e.g., Dreisbach, 2006; 2007; Forrest, 2012; Forrest et al., 2014) was that participants who report that their responses had not been guided by any abstract rules had relied on associative processes to perform accurately. But is there any evidence in the experiments reported in this thesis that this was indeed the case?

In the task-switching experiments reported in this thesis, the performance of most Rules-Ignorant participants could be attributed to a rule-based strategy of some sort, although the rules that had been generated deviated (sometimes greatly) from the objective task rules. One may be cautious about how much the rules that the participants reported indeed governed their behaviour as they performed the experiment. It is not uncommon that specific rules are simply offered as a post-hoc explanation of how responses could be generated but had not in fact been applied by the participant. It is impossible to find out if this might have been the case; nonetheless, all of the participants who reported a rule-based strategy expressed similar sequential trial effects, including reliable task-switch costs. In addition to the strategic (yet Rules-Ignorant) task-switchers, some participants reported that they had tried to memorise the stimulus-response contingencies, and others reportedly found no pattern that would link a specific stimulus to a response - those two groups of participants were of the greatest interest from a comparative point of view, as they probably were the groups that relied most on associative learning.

Unlike pigeons, (but like the participants in Forrest's, 2012, studies), those participants who memorised the contingencies expressed switch costs in their performance. Their performance also differed from that of the pigeons in that response-repetition effects greatly affected performance in task-repeat trials but were absent in task-switch trials. This result, as explained in detail in Section 3.4, might show the differential effects of Pavlovian and instrumental processes: the pigeons were more sensitive to the appetitive value of a cue-stimulus-location compound, preferring to approach response locations that were recently paired with reward, whereas humans acquired the cue-stimulus-response contingencies in a way that incorporated the closer associative relation between those cues that indicated the same task and consequently facilitated performance in trials repeating equivalent cues. Importantly, this finding shows that task-switch costs can occur in human performance even when their responses were not based on task rules but on stimulus-response contingencies.

In fact, only those participants who had assumed that responses were randomly marked correct were entirely unaffected by a change in tasks. Although in some

regards the pattern of their performance showed similarity to that of the pigeons' performance, these humans performed at chance level overall, which speaks against the possibility that they had come under the control of the same cognitive processes as the highly accurately performing pigeons. These participants also showed an absence of any congruency effect, and varied greatly in their general response patterns. It can be assumed that they did not learn anything about the effective stimulus-response contingencies or the underlying tasks, neither guided by rules nor by associative processes - which seemed to be the only way to eradicate switch costs in human performance. These participants most likely responded randomly, with a strong tendency to repeat the response that was indicated as correct in the previous trial (cf. Section 3.4).

In the Stop-Signal and Change-Signal paradigms, despite having to learn the function of specific stimuli via trial and error, all human participants were able to report the contingencies between the Go stimulus and the demand to execute the Go response, and between the Stop/Change signal and the demand to withhold the Go response. The participants in these two tasks also showed reliable inter-trial adjustments that reflected an abstract representation of the goals to execute or inhibit a response, namely increased response latencies in trials following successful inhibition and increased accuracy in trials that demand a repetition of the same process (either response execution or inhibition). The pigeons showed no such trial-to-trial effects, either in the computerised task reported in Chapter 4, or in the physical task reported in Chapter 5. Although the pigeons showed an increased probability of wrongly executing a response when the execution of that response had been rewarded in the previous trial, this behaviour does not necessarily imply an adjustment of the subjects' inhibition threshold - it merely reflects a greater readiness to perform a recently reinforced response, regardless of current trial demands (similar to the response-repetition effect on the pigeons' task-switching performance, cf. Section 3.3). Any adjustments in inhibitory control would be expected to primarily facilitate the ability to detect the signal and inhibit an inappropriate response, and not to lead to a more rigid (and error-prone) execution of the Go response.

In summary, although the pigeons showed some sequential trial-to-trial effects, both in the task-switching and in the response-inhibition paradigms, these effects were due only to the repetition of specific stimulus features or responses, but did not extend to repetitions at the level of abstract tasks, i.e., performing the same discrimination task during task switching or executing the same goal-oriented response (response inhibition or execution) in the Stop-Signal and Change-Signal task.

For humans, the majority of participants generated and followed abstract rules. Nonetheless, a small group of participants in the task-switching experiments tried to learn the contingencies, and had no awareness of the task rules that were in place. The performance of this group differed noticeably from that of the participants who had followed rules: like pigeons, they were greatly affected by stimulus- and response-specific attributes. However, unlike for pigeons, the processes that mediated learning in these humans led to a performance benefit in task-repeat trials compared to task-switch trials (cf. Section 3.4). Taken together, humans were apparently able to acquire part of the task-switching paradigm associatively, in an instrumental fashion that is sensitive to the presented stimulus-response contingencies and the associative equivalence of task cues; however, a strategy of continued hypothesis-testing might nonetheless have influenced the effect of associative processes on the performance of those humans. The pigeons on the other hand were able to acquire the paradigm via Pavlovian processes, on the basis of the affective value of the presented combination of cue, stimulus and response location.

6.2 Do Executive-Control Paradigms Measure Executive Control?

Before addressing the question stated in the heading of this section, it has to be reiterated that conventional task-switching studies examine response times, whereas I primarily considered error rates. However, task-switching effects reliably occur in both measures of performance (Monsell, 2003; Forrest, 2012), and it was shown in Section 3.1 that this was also the case in the experiments carried out for this thesis. Similarly, Castro and Wasserman (2015) reported an absence of switch costs not only for errors but also for the response times of pigeons. In the Stop-Signal and Change-Signal studies reported in this thesis, both response times and the probability of responding were relevant, and, as reported in Chapter 4, I was able to capture at least some response-inhibition effects in both these measures in pigeons and humans.

In task-switching paradigms, regardless of whether performance is assessed via response times or error rates, executive-control processes are thought to result in task-switch costs, as a reflection of mental task-set reconfiguration. However, since it has been shown that switch costs can also occur in humans who did not use task rules (cf. Chapter 3; Forrest, 2012; Forrest et al., 2014), assessing switch costs in isolation may not be a suitable indicator of an individual's level of executive control. Systematic errors in task-switch trials might be the result of an insufficient application of the relevant task rules; furthermore, large response-repetition effects (especially in the absence of response-repetition costs in task-switch trials) in addition to switch costs might point towards the influence of associative processes on performance (cf. Sections 3.3 and 3.4).

Executive control during task switching might be most evident in effects that occur exclusively at the task level, which would result from the preparation of a particular task-set of stimulus-response contingencies ahead of a trial. In addition, it can be expected that executive control of behaviour will reduce the influence of specific stimulus-response contingencies, so that task effects (e.g., switch costs) will affect behaviour in a magnitude comparable to (if not exceeding) the influence of stimulus congruency or response repetitions.

For Stop-Signal and Change-Signal tasks, performance in line with the independent horse-race model is not a good indicator of the executive-control processes that might be involved in achieving response inhibition (Verbruggen & Logan, 2008b, 2009b; Verbruggen et al., 2014; Best et al., 2016; Bowditch et al., 2016). More informative might be inter-trial effects on performance (cf. Chapters 4 and 5), which would give insight into whether a subject performs any trial-to-trial adjustments of a mental inhibition threshold to optimise the trade-off between accurately performing the Go response and diverting attention from this task to detect the sudden appearance of a stop signal (Rieger & Gauggel, 1999; Chikazoe et al., 2009; Aron, 2011; Bissett & Logan, 2011, 2012; Elchlepp et al., 2016; Verbruggen & McLaren, in preparation). Such adjustments should be observable at the task-goal level (i.e., the goals to execute or inhibit a response) and less so at the level of specific stimuli or responses (i.e., repeating the same response).

6.3 Limitations and Further Research

It was of course almost inevitable that, due to their comparative nature, the paradigms that were developed for the experiments reported in this thesis are subject to some caveats. For example, as pointed out in the previous section, the task-switching experiments mainly focussed on the analysis of error rates instead of the more conventional measure of response times.
In this section, I summarise a few further limitations, and their potential solutions, which unfortunately could not be implemented within the constraints of this thesis. In addition, I propose additional experiments that might contribute to our knowledge in this research area.

Task Switching

One common issue with comparative studies is that the animals often undergo extensive training periods before completing the task of interest, which was also the case in the experiments conducted for this thesis. It might be argued that overtraining led to the absence of effects that might otherwise have been observable. While this is possible, it is unlikely that overtraining was the cause of the lack of task-switch costs: not only has previous research (Stoet & Snyder, 2008) shown that extended training could not eradicate switch costs, at least for humans, but also, in the experiments reported in Sections 2.2 and 3.3, those (Rules-Ignorant) participants who had received training showed numerically greater switch costs than those who had not. It could be the case that this observation is limited to humans, in such a way that training would facilitate the development of a certain level of task awareness in humans (cf. Section 3.4) but does not apply to subjects that learn associatively. Although there is no previous research on this subject, it seems counterintuitive to argue that experiencing the stimulus-response contingencies of each task in isolation would diminish any switch costs that had potentially been present if the contingencies of both tasks had been acquired at the same time. Furthermore, it is difficult to explain how a too extensive training period might erase effects that are presumed to rely on executive control, but not the effects that are thought to relate to associative processes, such as response-congruency effects or response-repetition benefits; the extended experience with the stimulus-

response contingencies during training would be expected to primarily affect the magnitude of the latter effects.

There is a further caveat about the methodology of the paradigm, which might have prevented the emergence of switch costs in the performance of pigeons: after correctly responding to a trial, the pigeons had to move away from the display to obtain a reward, which might have disrupted any effects of task repetitions and switches. A possible way around this problem might be the administration of rows of trials without continuous reward, or (as was done in regards to the issue of potential overtraining) to test humans under similar disruptive conditions when receiving feedback for their response and examine the effects of such a procedure on their performance.

Quite an obvious limitation on the human side of the task-switching experiments was the inevitable fact that there was no way of controlling the size of the groups of Rules-Aware and Rules-Ignorant participants, since group membership could only be determined at the end of the experiment. The resulting large variation in group sizes and the consistently low number of Rules-Ignorant participants could potentially have affected the power and informative value of any findings. There may be several possible ways of influencing the proportion of participants who did and did not infer the task rules, for example by introducing a second task and thus increasing the cognitive load of participants as they perform the task-switching task, by employing incidental-learning paradigms in which participants are deceived about the real purpose of the experiment and about which behaviour is really of interest, or by, similar to an information-integration approach, defining the discrimination categories in a way that cannot easily be verbalised. Neuropsychological methods such as transcranial magnetic stimulation (TMS) might be a further possibility.

As mentioned in the previous section, focussing purely on task-switch costs in cued task-switching experiments might not be a valid indication of the executive processes behind a subject's task-set-shifting ability. Cued task-switching paradigms, such as the one used in this thesis, might reduce the amount of control that is usually employed to fixate on one task set and suppress a competing task set (cf. Dreisbach, 2012), because a task switch is possible on

every trial; participants need to be able to release the suppression of one task set (and apply inhibition to the irrelevant task set) rapidly. Thus, the rigid application of a certain task set might be prevented when the applicability of this task becomes less predictable (see also the variable adjustment of response-inhibition thresholds; cf. Elchlepp et al., 2016; Verbruggen & McLaren, in preparation).

One way to increase the amount of control of interference in the application of particular task sets would be to introduce invalid cues into the cued task-switching procedure. If participants prepare on every trial for the possibility to have to change the task, they might delay the configuration of a task set until the arrival of the task cue. Then, introducing an unexpected mismatch in the task that was indicated by the cue and the task that will actually have to be performed on the stimulus (indicated, for example, by pairing the stimulus with a different cue) might induce additional performance costs.

Humans who base their responses on task rules often show inverted switch costs when a cue is suddenly invalidated (Hübner, Kluwe, Luna-Rodriguez, & Peters, 2004; Wendt, Luna-Rodriguez, Reisenauer, Jacobsen, & Dreisbach, 2012): they show impaired performance on unexpected task-repeat trials compared to unexpected task-switch trials. This finding is regarded as an indication that on unexpected repeat trials the task set of the previous trial has been inhibited in preparation for the presumed task switch, and the subsequent requirement to overcome this inhibition when the task suddenly repeats is more cognitively demanding than initialising such inhibition on unexpected switch trials. Given the results reported in this thesis, it is unlikely that pigeons (or more interestingly, humans acquiring the task associatively) would prepare a response at task level and consequently suffer such performance costs; they would probably only initiate a response once the cue-stimulus compound is presented.

Another way to obtain a more rigorous control over behaviour, and enhance the inhibition of unwanted task sets to restrict interference, might be to use a voluntary task-switching paradigm. In such paradigms, participants are able to choose the task they want to perform. This procedure often eliminates exogenous influences on task-switch costs, because task switches are prepared well in advance and can thus be performed with little cost to performance; any residual cost is thought to reflect true executive-control

processes (Vandierendonck et al., 2010). Furthermore, if voluntary task-switching paradigms induce stricter control operations, an unexpected demand to change one's chosen task, and the necessary task-set reconfiguration required to do so, might induce large performance costs (cf. Weaver, Foxe, Shpaner, & Wylie, 2014).

One commonly observed consequence of the stricter control of behaviour by task rules in voluntary task-switching is that participants tend to perform more task-repeat trials than task-switch trials, even when instructed to perform each task equally as often (Arrington & Logan, 2004; Vandamme, Szmalec, Liefooghe, & Vandierendonck, 2010). This could be seen as evidence that the perceived stimulus-response contingencies are hierarchically organised into mental task sets. For pigeons, this does not seem to be the case: in unpublished pilot work by Brooks (personal communication), pigeons showed no preference to attend to an array of stimuli affording one discrimination task before moving on to an array of stimuli belonging to a different discrimination task.

Response Inhibition

In regards to the Stop-Signal and Change-Signal paradigms reported in Chapter 4, it is worth investigating further why neither pigeons nor humans reliably adjusted their behaviour in response to cues that predicted how likely a signal would be to appear in the current trial, which would have been expected at least of the human participants, regardless of whether their performance had been based on executive control or governed by associative processes (cf. Bowditch et al., 2016). This observation might be a product of weaknesses of the paradigm; therefore, it would be helpful to conduct a systematic investigation of whether cue effects can occur at all using the paradigms described in Section 4.2. For example, it could be assumed that an awareness of the function of the cues would elicit cue effects in humans; if participants who are explicitly instructed about the cues utilised them, this result would give room for further speculations about the absence of cue effects in the subjects included in the experiment reported in Chapter 4.

However, the main caveat concerning the response-inhibition paradigms used in this thesis is that it might not be certain whether the pigeons had indeed prepared the Go response at the time that the signal to withhold it arrived; if they had not, an inhibition of its execution would not have been necessary.
A potential way to avoid this issue and elicit a greater likelihood that a Go response is indeed prepared may be to demand a series of responses, any one of which might potentially have to be withheld. In doing so, the aversiveness of pre-emptively performing a response should be reduced for any one response, and responses would be expected to be initiated less hesitantly. An experiment of this kind, combining the benefits of testing pigeons in an operant chamber (as for the experiments in Chapter 4) with the requirement to perform the first response before a Stop signal is shown (as in Chapter 5) is being carried out at the University of Exeter at the moment, and first results confirm the findings presented in Chapter 4.

As it stands, the results presented in this thesis strongly question whether response inhibition based on external signals does in fact require executive control. Nonetheless, more and more animal studies are being conducted with the purpose of assessing inhibitory, or impulse, control in a variety of species (e.g., MacLean, Hare, Nunn et al., 2014). To limit the extent of studies declaring executive-control abilities in animals, a recent proposal (Beran, 2015) has pointed out the importance of discriminating between passive response inhibition, which may not require any advanced cognitive abilities, and active inhibitory control, which depends on an individual's ability to restrict its behaviour intentionally based on intrinsic motivational factors. Response inhibition primarily relates to the suppression of a particular response in reaction to external demands and is assessed in go/no-go, Stop-Signal, A-not-B or detour tasks (Beran, 2015). Inhibitory control on the other hand requires an active choice to withhold a certain behaviour despite having the option to execute it. It can be assessed in tasks that present a choice between several response options, such as delayed-gratification tasks - although there may be some restriction in the behaviours a subject can carry out at any point in time, for example when subjects choose the option to wait a short or a long time (e.g., Fortes, Vasconcelos, & Machado, 2015) without any opportunity to change their choice after the initial decision; this behaviour would be more accurately defined

as an intended restriction rather than impulse control when being faced with an attractive distractor. True inhibitory control might be evident in the way by which subjects withstand the impulse to pursue a constantly present, highly desirable distractor (Beran, 2015).

6.4 Conclusions

In a series of experiments, I have shown that pigeons could acquire adaptive behaviour in executive-control paradigms and hence that associative-learning processes are sufficient to account for such behaviour. However, some task-specific effects that are normally seen in humans and can be attributed to executive-control processes were absent, or greatly reduced, in pigeons. Those effects either reflect the mental operations that are performed to ensure that a specific set of stimulus-response-contingencies is applied and any contingencies belonging to a different set are suppressed, or reflect mental preparations for the possibility that the requirement to execute a certain response suddenly changes. In particular, in Chapter 3, it is shown that the benefits of repeatedly applying the same set of stimulus-response contingencies also extend to instrumental learning, if the equivalence of cues indicating the same set of contingencies is recognised. However, without such cue equivalence, and when Pavlovian processes dominate learning, performance comes without such benefits (or, in reverse, without the costs of switching from one set to another). Furthermore, as shown in Chapters 4 and 5, the behavioural effects of preparing for an unpredicted change in response requirements appear to be absent if behaviour is based purely on associative processes.

Conversely, associatively mediated performance was largely influenced by the stimulus-response contingencies that were effective in each paradigm. Repeating the same response in consecutive trials facilitated the performance of pigeons and associatively learning human participants in the task-switching paradigm, and performing a particular Go response increased the pigeons' likelihood of executing that response in the following trial in Stop-Signal and Change-Signal paradigms.

In summary, the implications of the experiments reported here is that the influence of executive-control processes in task-switching paradigms or in Stop-Signal and Change-Signal tasks is primarily reflected in effects at the level of abstract task requirements and not at the level of stimulus or

response attributes, and should therefore be assessed in preparatory behavioural adjustments that occur before the arrival of any stimulus.

APPENDICES

Appendix A1. Participant questionnaire used in the experiment reported in Section 3.1. All answers were given verbally and noted down by the experimenter.

1. What do you think this experiment was testing?
2. Did you notice anything unusual or experience any problems with the programme during the experiment?
3. Did you lose concentration for any significant amount of time at any point during the experiment (i.e., for more than a few seconds)?
4. Can you describe the stimuli you saw during the experiment?
5. How were you remembering how to respond to each stimulus, e.g., did you use any strategies when you were doing the experiment? If so, what were they?
6. Do you think there was any relationship between any of the stimuli and the correct responses? (Can the participant name either of the rules for classification?)
7. Do you think there was a relationship between the initial coloured circle and the stimulus that followed?
8. Did you use the initial coloured circle to prepare for the stimulus that followed?
9. Do you have any other comments about this experiment?

Appendix A2. Participant questionnaire used in the experiment reported in Section 3.2. The questions were presented on screen at the end of the experiment and required either a Yes/No answer, which was given by clicking the respective button on screen, or a typed response.

This is the end of the experiment. Please answer the following short questions about the task. Press the space bar to continue.

1. The stimuli you saw consisted of different elements. For example, each stimulus showed one of four colours - red, green, yellow and blue. Did you pay attention to the colour when you made a response? *(Yes/No)*
    1.1. *(optional, presented if a participant answered "yes" to question 1)* Did you need to know the colour to be able to choose the correct response? *(Yes/No)*
2. The stimuli either showed a horizontal or a vertical pattern of lines. Did you pay attention to the orientation of the lines when you made a response? *(Yes/No)*
    2.1. *(optional, presented if a participant answered "yes" to question 2)* Did you need to know the orientation to be able to choose the correct response? *(Yes/No)*
3. The stimuli either showed a pattern of thick lines or thin lines. Did you pay attention to the thickness of the lines when you made a response? *(Yes/No)*
    3.1. *(optional, presented if a participant answered "yes" to question 3)* Did you need to know the thickness to be able to choose the correct response? *(Yes/No)*
4. *(optional, presented if a participant answered one of the questions 1, 2 and 3 with "yes" and the other two with "no")*
    4.1. *(presented if a participant answered "yes" to question 1.1)* You said that you needed to know the colour to be able to choose the correct response. Please explain in which way this information helped you make a response. Please type in your response giving as much detail as possible and then press ENTER to submit your answer. *(open field)*

4.2. *(presented if a participant answered "yes" to question 2.1)*

You said that you needed to know the orientation to be able to choose the correct response. Please explain in which way this information helped you make a response. Please type in your response giving as much detail as possible and then press ENTER to submit your answer. *(open field)*

4.3. *(presented if a participant answered "yes" to question 3.1)*

You said that you needed to know the thickness to be able to choose the correct response. Please explain in which way this information helped you make a response. Please type in your response giving as much detail as possible and then press ENTER to submit your answer. *(open field)*

5. *(optional, presented if a participant answered at least two of the questions 1, 2 and 3 with "yes")*

   You said that you needed to know several elements of the stimulus to be able to choose the correct response. Please explain in which way knowing each of these stimulus elements helped you make a response. Please type in your response giving as much detail as possible and then press ENTER to submit your answer. *(open field)*

6. *(optional, presented if a participant answered all of the questions 1, 2 and 3 with "no")*

   Did you have a certain strategy to help you choose a response? Please explain how you picked the correct response. Please type in your response giving as much detail as possible and then press ENTER to submit your answer. *(open field)*

Thank you very much! Please fetch the experimenter.

Appendix A3. Participant questionnaire used in the experiment reported in Section 3.3. The questions were presented on screen at the end of the experiment and required either a Yes/No answer, which was given by clicking the respective button on screen, or a typed response.

This is the end of the experiment. Please answer the following short questions about the task. Press the space bar to continue.

1. If the next participant of this study asked you what he or she should do to get as many trials correct as possible, what would you tell him or her? Please type in your response giving as much detail as possible and then press ENTER to submit your answer. *(open field)*
2. The stimuli you saw consisted of different elements. For example, each stimulus showed one of four colours - red, green, yellow and blue. Did you need to know the colour to be able to choose the correct response? *(Yes/No)*
3. The stimuli either showed a horizontal or a vertical pattern of lines. Did you need to know the orientation to be able to choose the correct response? *(Yes/No)*
4. The stimuli either showed a pattern of thick lines or thin lines. Did you need to know the thickness to be able to choose the correct response? *(Yes/No)*
5. Was it necessary to remember the correct response to the stimulus that appeared in the trial just before to know how to respond? For example, if the current and the previous image looked the same, did you repeat the response you had just given before? Or, if the image looked different from the previous one, did you choose the opposite response to before? *(Yes/No)*
    5.1. *(optional, presented if a participant answered "yes" to question 5)* Please explain in which way knowing the response to the stimulus in the previous trial helped you make a response. Please type in your response giving as much detail as possible and then press ENTER to submit your answer. *(open field)*

Thank you very much! Please fetch the experimenter.

Note: after the participant completed this questionnaire, the experimenter presented a screenshot of a trial showing an incongruent stimulus superimposed on a cue for task A (horizontal, high-spatial-frequency stimulus on a red cue). The participant was informed about the correct response to this stimulus (e.g., left; the response contingencies were counterbalanced across participants). Then the experimenter showed a screenshot of the next trial, containing the other incongruent trial on a cue for task B (vertical, low-spatial-frequency stimulus on a blue clue). The participant was asked to name the correct response on this trial, and to explain why this response was chosen.

Appendix A4. Participant questionnaire used in the experiment reported in Section 4.3. The questions were presented on screen at the end of the experiment and required either a Yes/No answer, which was given by clicking the respective button on screen, or a typed response.

This is the end of the experiment. Please answer the following short questions about the task. Press the space bar to continue.

1. One of the circles on the side was a dim colour, the circle on the other side was brightly coloured. Sometimes, the bright circle changed its colour. Did this colour change affect you in the way you made a response? *(Yes/No)*
    1.1. *(optional, presented if a participant answered "yes" to question 1)* Please explain how this colour change might have influenced you when making a response. Please type in your answer giving as much detail as possible. *(open field)*
2. There was always a grey circle in the middle, sometimes with vertical or horizontal stripes. Did this grey circle affect you in the way you made a response? *(Yes/No)*
    2.1. *(optional, presented if a participant answered "yes" to question 2)* Please explain how the circle in the middle might have helped you make a correct response. Please type in your answer giving as much detail as possible. *(open field)*
3. If the next participant of this study asked you what he or she should do to get as many trials correct as possible, what would you tell him or her? Please type in your answer giving as much detail as possible. *(open field)*

Thank you very much! Please fetch the experimenter.

Appendix A5. Results of further studies on the effects of various manipulations on pigeon task-switching effects. *A*) Only one instead of two cues per task were presented ("One Cue"); *B*) the inter-trial interval was decreased from 15-30 seconds to 1-2 seconds ("Short ITI"); *C*) only incongruent trials were presented ("Simple").

A) One Cue

The purpose of this experiment was to assess whether switch costs emerge in the performance of pigeons when each task was indicated by a single cue; in humans, a great proportion of switch costs can be attributed to a switch of the task cue (Monsell, 2003; Forrest, 2012).

Methods and Results

Fourteen pigeons participated in this experiment. Eight pigeons had previously completed the experiment reported in Section 3.1; six naïve pigeons were trained on the two individual tasks in the same way as described in Section 2.3. They experienced all four task cues during training but, during task-switching test trials, only one cue per task was presented.

The experiment consisted of 20 sessions of 73 trials each, designed in the same way as described in Section 3.1, with the difference that each of the two tasks was indicated by only one cue rather than two cues each. Four different cue-task combinations were possible: 1) Task A - Blue, Task B - Red; 2) Task A - Blue, Task B - Green; 3) Task A - Yellow, Task B - Red; 4) Task A - Yellow, Task B - Green. These were counterbalanced across individuals.

Table A5.1 shows the results of a repeated-measures ANOVA on error rates, using Session (1 to 20), Trial Type (Cue/Task Repeat or Task Switch) and Stimulus Congruency (Congruent or Incongruent) as within-subject factors. To assess whether performance of the naïve pigeons was comparable to the experienced birds, a between-subject factor accounting for the two groups of pigeons was included in the ANOVA.

	Pigeons (n=14)			
	F	df	p	η_p^2
Experience	0.45	1,12	.52	.04
Session	1.36	19,228	.17	.10
Trial Type	0.59	1,12	.46	.05
Congruency	26.43	1,12	**<.001**	.69
Trial Type * Congruency	0.15	1,12	.70	.01

Table A5.1. ANOVA results of study One Cue.

B) Short ITI

This experiment was carried out to assess whether a very short inter-trial interval (ITI) would lead to the occurrence of switch costs in pigeons. Stoet and Snyder (2003a, 2003b, 2008) reported the emergence of significant switch costs in macaques when the ITI was reduced from 345ms to 170ms.

Methods and Results

After completing the experiment reported in Section 3.1 and the One Cue experiment mentioned above in this appendix, the fourteen pigeons entered this experiment. It consisted of 10 sessions of 145 trials, of which roughly one third were switch trials. The Inter-trial interval was reduced from between 15 to 30 seconds to one to two seconds. The cue-stimulus compound was presented immediately after a peck at the observation key, that is, the cue was not shown on its own first as it had been done in the previous experiments.

Table A5.3 shows the results of a repeated-measures ANOVA on error rates, using Session (1 to 10), Trial Type (Task Repeat or Task Switch) and Stimulus Congruency (Congruent or Incongruent) as within-subject factors.

	Pigeons (n=14)			
	F	df	p	η_p^2
Session	2.52	9,117	**.026**	.16
Trial Type	1.26	1,13	.28	.09
Congruency	32.30	1,13	**<.001**	.71
Trial Type * Congruency	1.63	1,13	.22	.11

Table A5.3. ANOVA results of study Short ITI.

C) Simple

The purpose of this experiment was to assess whether switch costs emerge in the performance of pigeons when the correct response to each stimulus depended on the current task; in humans, switch costs mainly emerge in response to such response-incongruent stimuli (Monsell, 2003; Forrest, 2012).

Methods and Results

After completing the experiment reported in Section 3.1 and the two experiments mentioned above in this appendix, the fourteen pigeons entered this experiment. It consisted of 10 sessions of 73 trials each, designed in the same way as described in Section 3.1, with the difference that only incongruent stimuli were presented.

Table A5.2 shows the results of a repeated-measures ANOVA on error rates, using Session (1 to 10) and Trial Type (Task Repeat or Task Switch) as within-subject factors.

	Pigeons (n=14)			
	F	df	p	η_p^2
Session	0.27	9,117	.98	.02
Trial Type	0.19	1,13	.67	.01

Table A5.2. ANOVA results of study Simple.

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