

Eye Movements during Task Switching: Reflexive, Symbolic, and Affective Contributions to Response Selection

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Abstract

■ Active vision is a dynamic process involving the flexible coordination of different gaze strategies to achieve behavioral goals. Although many complex behaviors rely on an ability to efficiently switch between gaze-control strategies, few studies to date have examined mechanisms of task level oculomotor control in detail. Here, we report five experiments in which subjects alternated between conflicting stimulus–saccade mappings within a block of trials. The first experiment showed that there is no performance cost associated with switching between pro and anti saccades. However, follow-up experiments demonstrate that whenever subjects alternate between arbitrary stimulus–saccade mappings, latency costs are apparent on the first trial after a task change. More detailed analysis

of switch costs showed that latencies were particularly elevated for saccades directed toward the same location that had been the target for a saccade on the preceding trial. This saccade “inhibition of return” effect was most marked when unexpected error feedbacks cued task switches, suggesting that saccade selection processes are modulated by reward. We conclude that there are two systems for saccade control that differ in their characteristics following a task switch. The “reflexive” control system can be enabled/disabled in advance of saccade execution without incurring any performance cost. Switch costs are only observed when two or more arbitrary stimulus–saccade mappings have to be coordinated by a “symbolic” control system. ■

INTRODUCTION

Natural visual behavior requires an ability to flexibly switch between different gaze strategies while simultaneously monitoring their effectiveness in meeting task goals (Hodgson, Bajwa, Owen, & Kennard, 2000; Land, Mennie, & Rusted, 1999; Hayhoe, Bensinger, & Ballard, 1997; Yarbus, 1967; Buswell, 1935). Yet, despite this essential feature of active vision, few studies have directly examined this ability in detail.

Outside the field of oculomotor control there is an extensive literature on task switching (e.g., Monsell, 2003; Pashler, 2000; Rogers & Monsell, 1996; Allport, Styles, & Hsieh, 1994; Jersild, 1927). Typically, researchers have compared blocks of trials consisting of a single task, with blocks in which subjects have to alternate between tasks with conflicting stimulus–response mappings. On the first trial after a change in task, an increase in response times is observed. Even when long delays are added between trials, or task changes are made predictable, a robust “switch cost” is still found (e.g., Allport & Wylie, 2000; Meiran, 1996; Rogers & Monsell, 1996).

Several studies have demonstrated a counterintuitive asymmetry in switch costs when alternating between

tasks that vary in difficulty. Allport et al. (1994) used a Stroop task in which color names are presented to subjects printed in a conflicting colored ink (e.g., RED in green ink). Subjects are asked to alternate between reporting the printed word or the ink color. Response times are always shorter for word reading compared to ink color naming. Surprisingly, larger performance costs occur when switching from ink color naming to word reading. In other words, it is harder for subjects to switch from the difficult to the easy task.

Based on these findings, Allport et al. (1994) have proposed the concept of a task “set,” which specifies the behavioral schema, stimulus–response weightings, and attentional biases necessary for the performance of a particular task. In this framework, switch costs arise due to a passive process of interference from the previous task set. During performance of the nondominant Stroop task (ink color naming), it is assumed that the dominant task set (word reading) needs to be strongly inhibited. This inhibition persists following a task switch, explaining the asymmetry in switch costs.

Neuroimaging, neuropsychological, and neurophysiological studies have also begun to chart the organization of brain systems that mediate flexible control during a range of complex tasks and cognitive operations (e.g., Ruff, Woodward, Laurens, & Liddle, 2001; MacDonald,

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Cohen, Stenger, & Carter, 2000; Carter, Botvinick, & Cohen, 1999). It has been argued that research into oculomotor control may play an important role in this effort as the neural mechanisms and mathematical transformations subserving simple saccade tasks are already well charted (Husain, Parton, Hodgson, Mort, & Rees, 2003; Schall, Stuphorn, & Brown, 2002; Scudler, Kaneko, & Fuchs, 2002; Stuphorn, Taylor, & Schall, 2000). Perhaps, the closest oculomotor analogue of the verbal Stroop test is the anti saccade task. In this test, subjects have to execute a saccade away from the location of a salient stimulus onset and suppress the initiation of stimulus-driven eye movements. In one of their original articles on anti saccades, Hallett and Adams (1980) found that there was no difference in response latencies when pro and anti saccade trials were mixed within a block. They concluded that the “psychological details” under which eye movement tasks were run had little influence on movement latency. In contrast, Weber (1995) reported an increase in both latency and errors on the first trial following a switch between the two tasks.

An important difference between these two existing studies of pro/anti saccade switching is that the task was precued before the start of a trial in Hallett’s design, while in Weber’s study, the saccade target itself instructed either a pro or an anti saccade. Yet, the absence of a switch cost in Hallett’s original work is still puzzling in the light of the remarkable robustness of switch costs in the psychological literature (Pashler, 2000) and the assumed cognitive demands of the antisaccade task (Fischer & Weber, 1992; Fischer, Deubel, Wohlschlagel, & Schneider, 1999).

In Experiment 1 (Figure 1A), we present a replication of Hallett and Adams’ original finding that mixing pro and anti saccade tasks within a block of trials does not affect saccade latency.

EXPERIMENT 1

Results

Saccade Latencies

A two-way ANOVA was carried out with block (uniform/switching) and task (pro/anti saccade) as factors. This revealed a significant difference in latencies between uniform and practice blocks. However, this difference was opposite to the predicted interference effect, with average anti saccade latency being faster in the switching blocks (means anti saccades, uniform: 272 ± 14 msec, switching: 230 ± 15 msec; pro saccade, uniform: 206 ± 11 msec, switching: 189 ± 14 msec).

The data from the switching blocks were further analyzed to see if there was a selective increase in response latencies on the first trial after the unexpected error that cued the task switch. A two-way repeated measures ANOVA with task (pro vs. anti saccades) and

trials after task switch (1–8) as factors revealed a significant effect of task on latencies (antisaccades longer than prosaccades), $F(1,11) = 30.19, p < .0001$, but no significant effect of trial, $F(7,70) = 1.48, p > .1$, or interaction between trial and task, $F(7,70) = 0.49$ (Figure 2).

Saccadic Accuracy and Errors

The spatial parameters of saccades in the task were also analyzed. Saccades were classified as errors if the initial saccade was directed toward the target location on antisaccade trials or toward the opposite location on prosaccade trials. Erroneous anti saccades on pro saccade trials were found to be very infrequent. For this reason, only errors in the anti saccade task were statistically analyzed. A one-way repeated measures ANOVA with trials after task change as the independent variable (1–8) revealed a significant effect of trial, $F(7,77) = 2.14, p < .05$. However, this effect did not take the form of the expected “switch cost.” A statistical contrast between the first trial after a rule change and the mean error rate on nonswitch trials (2–8 trials after rule change) revealed a significant reduction in pro saccade errors following the task switch, $F(1,11) = 11.34, p < .01$ (Figure 2).

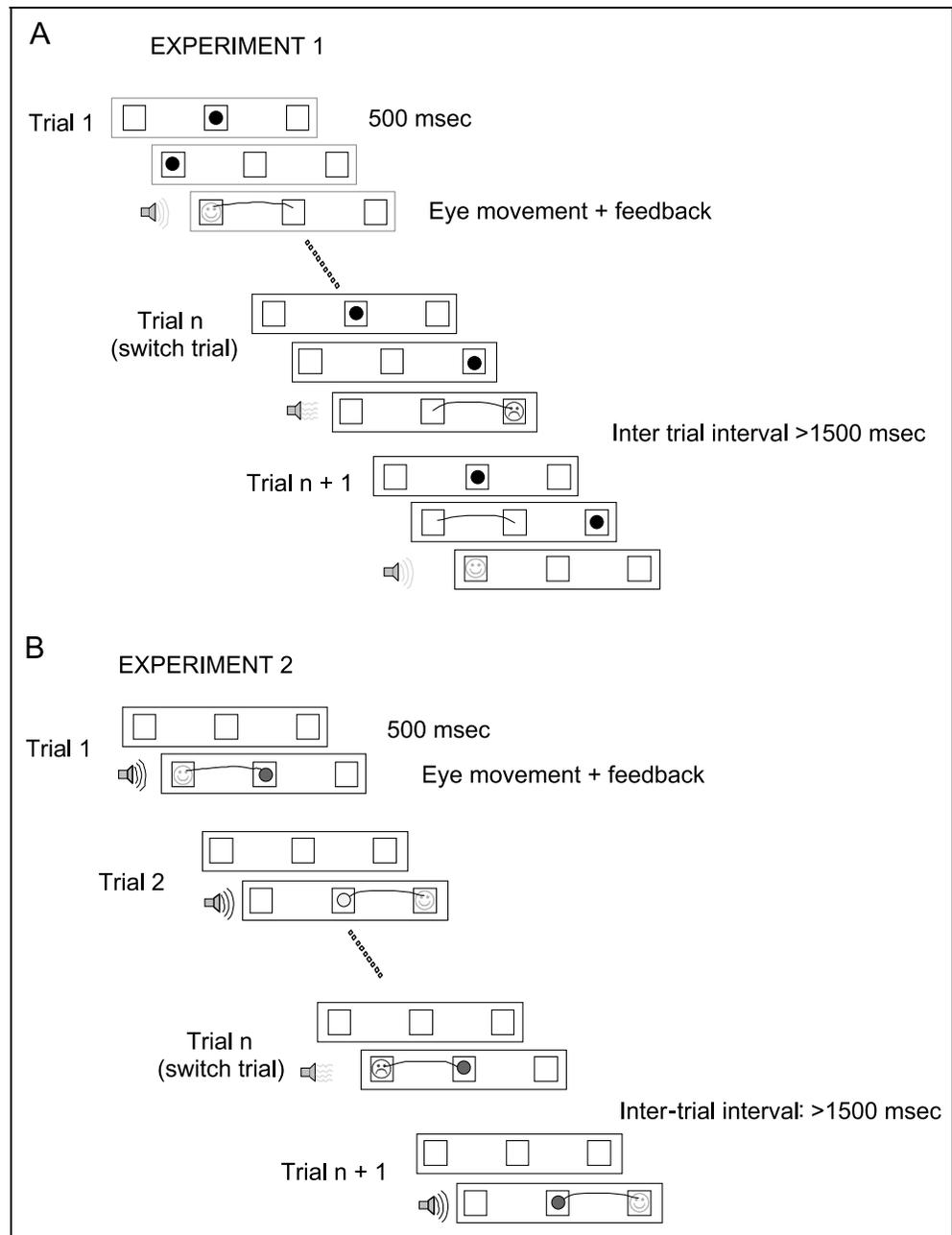
A similar analysis of primary saccade gain on correct response trials revealed no significant modulation in the amplitude of response gain dependent upon trials after task switch, $F(7,77) = 1.4$.

Discussion

Experiment 1 examined whether task switch costs occur when alternating between pro and anti saccades within a block of trials. The results showed that there is no increase in saccade latency on the first trial following a change in eye movement task compared to trials on which the task was the same as on the preceding trial. This was the case for both pro and anti saccade switches. In fact, a significant reduction in anti saccade errors was observed on trials immediately following a task switch.

We also found a significant reduction in the latency of saccades during switching blocks compared to the uniform practice blocks. Some caution should be attached to interpreting this aspect of the results. To ensure that subjects were well practiced on both tasks in isolation before attempting the switching blocks, all subjects completed the two uniform blocks first. As such, it is possible that the reduction in mean latency during switch blocks reflects a straightforward practice effect rather than enhanced performance as a consequence of the demand to switch. However, one recent functional imaging study reported more closely matched latencies and neural activation loci for pro and anti saccades when the two tasks are interleaved within an experimental block (Cornelissen et al., 2002). Another recent study compared pro/anti saccade switching in control subjects and schizophrenic patients (Barton et al., 2002). These authors also

Figure 1. (A) Pro/anti saccade switching task (Experiment 1) and (B) centrally cued task (Experiment 2). For the sake of clarity, the display contrast has been reversed in the figures.

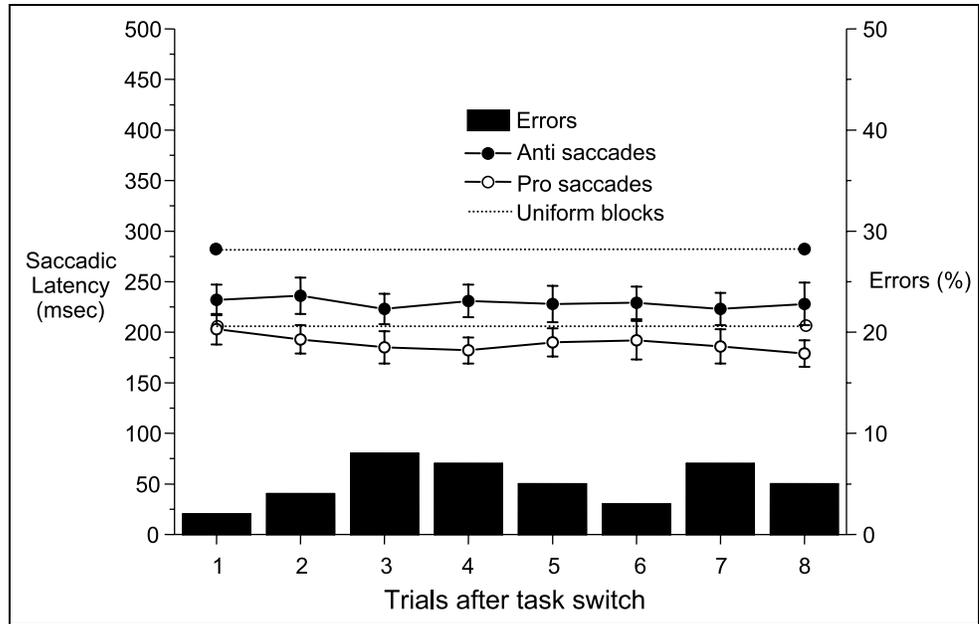


report a paradoxical reduction in anti saccade latency under task-switching conditions in both subject groups. Taken together with previous studies therefore, the present work suggests that there is a reliable improvement in anti saccade performance when pro and anti saccades are interleaved within a block. One explanation for this effect is that subjects allocate more attention to the task under switching conditions, leading to a benefit in performance of the anti saccade task.

The results of Experiment 1 also confirm that subjects can efficiently switch between pro and anti saccades without incurring any latency cost on switch trials (assuming that task changes are cued well in advance of the target onset) (Hunt & Klein, 2002; Weber, 1995; Hallet &

Adams, 1980). There are several explanations for the surprising absence of switch costs in pro/anti saccade switching. One possibility is that the oculomotor system is not susceptible to switch costs. The relatively close correspondence between sensory and motor reference frames in the eye movement system considerably reduces the complexity of the sensorimotor transformations required (Carpenter, 1988). But if simple eye movement tasks are immune to switch costs, then this should hold true regardless of the cue that is used to initiate saccades. As well as responding to peripheral onsets, humans and other primates can coordinate eye movements in response to cognitive or “symbolic” cues. In Experiment 2 (Figure 1B), subjects learned an arbitrary mapping

Figure 2. Means and standard errors of pro/anti saccade latencies and errors following a task switch (Experiment 1). The switch +1 trial is the first trial following the unexpected error that cues the change in task.



between a colored shape and an eye movement response to the left or right. As in Experiment 1, the mappings between stimulus and response then reversed at different points during the test. In all other respects, the instructions and procedure was identical to Experiment 1.

EXPERIMENT 2

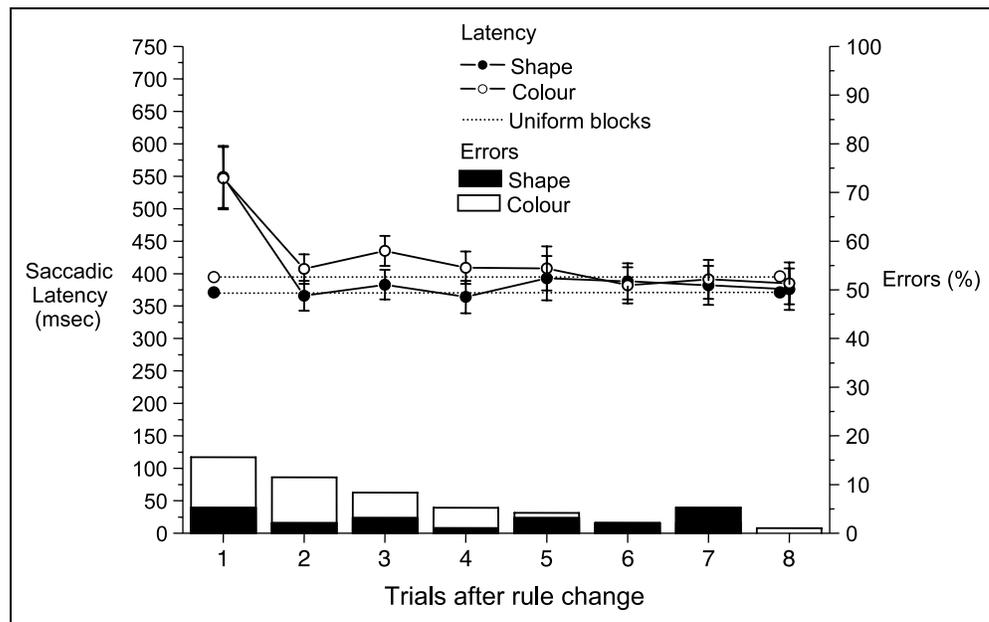
Results

Latencies

Mean latency of saccades did not differ significantly between the practice block and the switching blocks. The data from the switch blocks were then analyzed on a

trial by trial basis relative to the first trial after the unexpected error that cued the task change. A two-way one-within, one-between factor ANOVA with cue (shape vs. color) and trials after task change (1–8) as factors revealed a significant effect of trial after switch, $F(7,77) = 18.07, p < .001$. A statistical contrast between the first trial after the switch and the mean response latency on Trials 2–8 following the rule change confirmed that the increase in latency was exclusive to the first trial after the unexpected error that indicated the task change, $F(1,11) = 39.04, p < .001$ (Figure 3). The magnitude of this switch cost did not differ significantly between shape and color cueing methods.

Figure 3. Latencies and errors for centrally cued saccades following a task switch (Experiment 2).



All of our subjects were unpracticed in the switching task. To determine if the size of switch costs varied with practice, we performed another two-way ANOVA with block number (first or second) and trial (one to three) as factors. This showed that there was no significant difference in latency between the two blocks, $F(1,11) = 1.19$, neither was there an interaction between block and trial after task change, $F(2,22) = 2.01$, $p > .1$, indicating that the magnitude of the switch cost did not vary from the first to the second block.

Saccade Accuracy and Errors

A switch cost was also apparent in the rate at which subjects executed erroneous saccades after a task change. These errors occurred on a total of 6% of trials. However, the vast majority of these errors were corrected for, such that subjects redirected their gaze to fixate the correct response box and received a correct feedback (Figure 4). Perseverative response errors, in which subjects selected the wrong location with a fixation of criterion duration (800+ msec) were very rare (<1% of trials).

A two-way ANOVA, with trials after task change (1–8) and cue (shape vs. color) indicated that saccade direction errors were significantly increased on the first trial after a task change, $F(7,70) = 3.07$, $p < .01$. Although color cues appeared to induce more saccade errors than shape cues, this trend did not reach significance (Figure 3). Finally no significant modulation in saccadic gain was observed on

correct response trials dependent upon trials after task change, $F(7,77) = 0.91$.

Saccade Inhibition of Return

During the course of the experiment and subsequent analyses, it became apparent that the switch cost observed after a task change was location specific. Eye movement latencies were particularly slow when the cue instructed a saccade back to the location at which the unexpected error signal had been presented on the preceding trial. This observation was confirmed using a post hoc two-way analysis of variance with trial type (switch or no switch) and response (same or opposite direction as preceding trial) as factors. This analysis revealed a significant two-way interaction effect between trial type and response, $F(1,11) = 7.96$, $p < .025$. Saccadic latencies were increased when subjects had to respond with a saccade back to the location at which the error feedback had been presented on the preceding trial (Figure 5). This is similar to the saccadic inhibition of return effect previously reported for return saccades to a previously attended location (Trappenberg, Dorris, Munoz, & Klein, 2001; Ro, Pratt, & Rafal, 2000; Posner, Rafal, Choate, & Vaughan, 1985). However, in this case the effect appears to be dependent on the occurrence of a task switch or a negative feedback.

Discussion

A very large switch cost was observed on eye movement latencies following the reversal in mappings between a symbolic cue and an eye movement response that lasted for one trial after a task change. Subjects also made an increased number of saccades in the wrong direction on switch trials, although most of these errors were quickly corrected for, such that the eyes landed on the correct location and subjects received a correct feedback. The presence of switch costs in this experiment demonstrates that the absence of switch costs in Experiment 1 reflects a specific characteristic of the pro/anti saccade switching task and is not a feature of all simple eye movement tasks.

Experiment 2 also found a novel effect not reported in previous studies of task switching. Latencies were found to be particularly elevated when the first cue after a task change instructed a saccade in the same direction as on the preceding trial. This saccade inhibition of return effect (Trappenberg et al., 2001; Ro et al., 2000; Posner et al., 1985) was not present on nonswitch trials. However, because we used unexpected errors to cue task changes, it is possible that the effect might be either switch or error modulated. To investigate this hypothesis, we conducted a third experiment using different cues to instruct the task change.

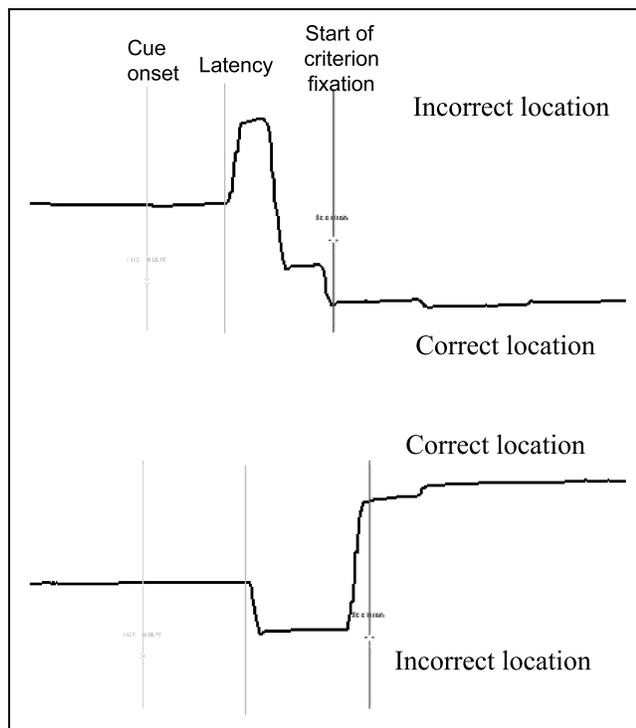
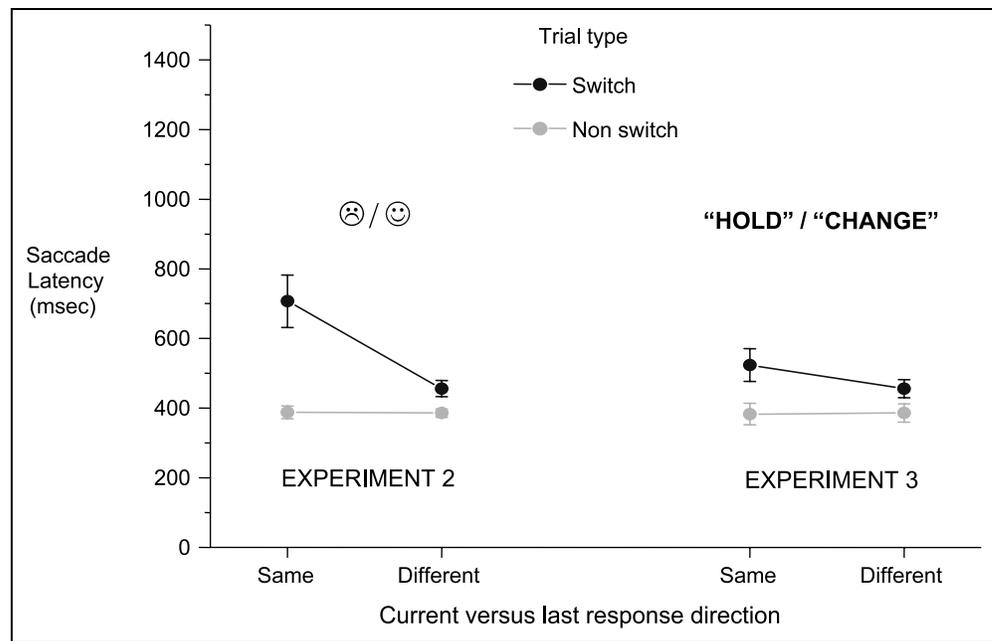


Figure 4. Corrective saccadic eye movements (Experiment 2).

Figure 5. Switch/reward-modulated inhibition of return when rule changes were cued by either an unexpected error (Experiment 2) or a direct instruction (Experiment 3).



EXPERIMENT 3

Results

Latencies and Errors

As in Experiment 2, saccadic latencies were increased on the first trial after a task change, $F(7,49) = 3.94$, $p < .005$. Saccade errors were also found to be significantly increased on the first trial after the task change, $F(7,42) = 6.70$, $p < .001$. As in Experiment 2, the vast majority of these errors were corrected for such that decision errors were very rare.

Saccade Inhibition of Return

Saccade inhibition of return was examined using a two-way ANOVA with trial type (switch or hold) and response (same or opposite direction as preceding trial) as factors. In contrast to Experiment 2, there was no significant interaction between trial type and response in Experiment 3, $F(1,7) = 2.49$, $p > .1$. Although the mean values showed a tendency toward a switch-modulated inhibition of return effect on latencies, this was not consistent across subjects and was greatly reduced in magnitude relative to Experiment 2 (Figure 5).

Discussion

Replacing positive and negative feedbacks with explicit cues to hold or change tasks was found to reduce the magnitude of the saccadic inhibition of return effect reported in Experiment 2. We conclude from this that inhibition of return can be modulated by reward/affective feedbacks.

Neurophysiological studies, mainly in macaque monkey, have also shown that reward feedbacks exerts a

strong influence on saccadic eye movement programming (Glimcher, 2002; Kobayashi, Lauwereyns, Sakagami, & Hikosaka, 2002; Leon & Shadlen, 1999; Platt & Glimcher, 1999). Further research into the interaction between neural reward and response selection systems is likely to be critical in understanding how the brain implements autonomous decision making and behavioral control (Glimcher, 2002; Montague & Berns, 2002). However, the role of reward processing has been largely overlooked in human behavioral research into attention and motor control. What is apparent from the existing literature is that inhibition of return is an amodal phenomenon operating within different sensory (Spence, Lloyd, McGlone, Nicholls, & Driver, 2000) and motor domains (Briand, Larrison, & Sereno, 2000). It is perhaps not surprising therefore that the effect can also be modulated by affective factors. Other research into human decision making has emphasized the importance of emotional or affective cues in selecting between competing responses (Bechara, Damasio, Tranel, & Damasio, 1997; Damasio, 1996) and similar mechanisms may apply during selection of eye movements.

Although reward-dependent inhibition of return was reduced in magnitude in the present experiment, a small trend toward the effect was observed with explicit instructional cues. One possibility is that the auditory feedback tone accompanying the instruction to change rule had negative affective associations for some subjects. It is also conceivable that any unpredicted or surprising event might elicit an affective/arousal response to some degree. This is consistent with the idea that emotional systems act as an “interrupt” mechanism, initiating re-evaluative cognitive processes when outcome predictions are breached (Mandler, 1980).

Another interesting question for future research is whether face feedback stimuli are particularly likely to illicit an affective response. Accumulating evidence suggests that there are brain systems dedicated to processing emotional information in faces (e.g., O’Doherty et al., 2003; Haxby, Hoffman, & Gobbini, 2000). Also consistent with this possibility, a recent patient study using the current task indicates that damage to one of these face sensitive regions (orbitofrontal cortex), abolishes reward dependent inhibition of return (Hodgson et al., 2002).

Despite a reduction in the magnitude of saccadic inhibition of return, a large cost was nevertheless observed on the first trial after a task change in Experiment 3. But the reason why switch costs were absent in Experiment 1 remains puzzling. One possibility is that reflexive saccades are so automatic that they are never associated with switch costs. Experiment 4 was designed to test this hypothesis by replacing reflexive saccades with a novel eye movement task. In this new task, a target movement to the left instructed subjects to execute an eye movement toward a location directly

above fixation (Figure 6). When the target stepped right, subjects have to make a saccade downwards. If the null results of Experiment 1 were due to the use of reflexive prosaccades as the secondary task, then switch costs should be observed when antisaccades are alternated with this novel vertical saccade task.

EXPERIMENT 4

Results

Latencies

Anti saccade latencies were significantly shorter than vertical saccade latencies in the task-switching blocks, $F(1,7) = 9.47, p < .05$. Trial by trial analysis revealed a significant increase in latencies on the first trial following a task change [main effect of trial after task switch, $F(7,49) = 4.59, p < .001$]. As in Experiment 2 this effect was confined to the first trial after the rule change [means comparison for Trial 1 relative to Trials 2–8, $F(1,7) = 10.36, p < .02$]. Further, there was a significant

Figure 6. Vertical saccade task (Experiment 4).

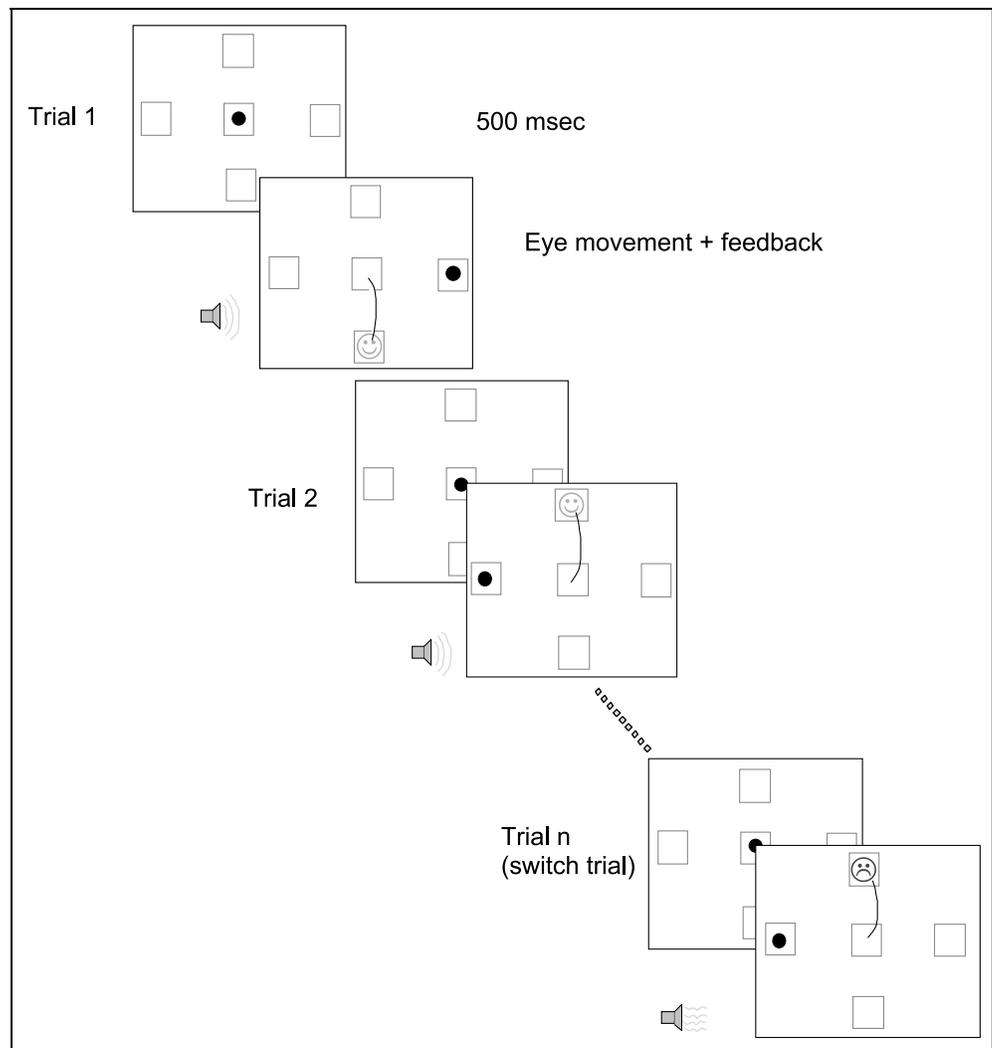
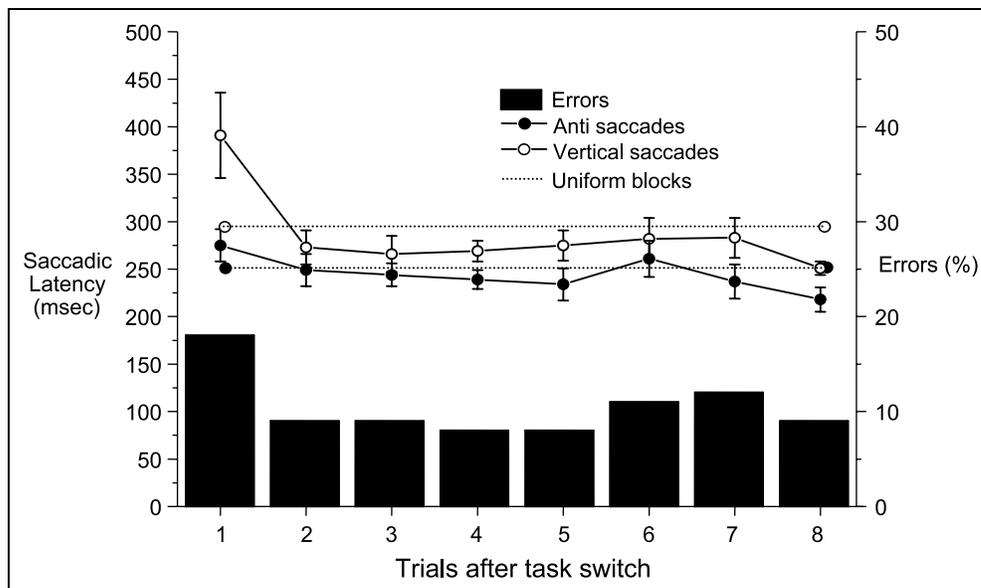


Figure 7. Saccade latencies and errors following a task switch (Experiment 4).



interaction between task (anti saccades \times vertical saccades) and trial after task change, with a much larger effect following switches from the anti saccade task to the vertical saccade task, $F(7,49) = 2.48, p < .05$ (Figure 7).

Saccadic Accuracy and Corrective Eye Movements

Erroneous saccadic eye movements, either to the target or an incorrect response location occurred on 10% of trials. Eighty-nine percent of these errors were prosaccade errors on vertical saccade trials. However, analysis revealed no significant difference in saccade error rates dependent upon trials after switch or between the uniform and switching blocks (Figure 7).

Discussion

Experiment 4 showed that when antisaccades are alternated with a conflicting arbitrary stimulus–saccade coupling, significant switch costs occur. Interestingly, this cost was much larger in Experiment 4 when switching away from anti saccades to the vertical saccade task. Anti saccade latencies were also significantly shorter than vertical saccades during the mixed task blocks, suggesting that anti saccades were the dominant of the two tasks. Previous studies of task switching using the ink/word naming Stroop task had reported the reverse asymmetry in switch costs between dominant and non-dominant tasks. The results reported here indicate that this asymmetry may not hold true across different response domains and modalities. Switch costs can be smaller when switching from the more demanding to the easier of two tasks.

The results of this experiment are also consistent with the idea that reflexive eye movements may be so automatic and hardwired that they are not associated with

task switch costs (Hunt & Klein, 2002). An alternative explanation is that there is always an increase in the latency on the first trial in a new run of vertical eye movements regardless of the nature of the intervening horizontal saccade task. To test this, we repeated Experiment 4 using reflexive pro saccades as the alternate task.

EXPERIMENT 5

Results

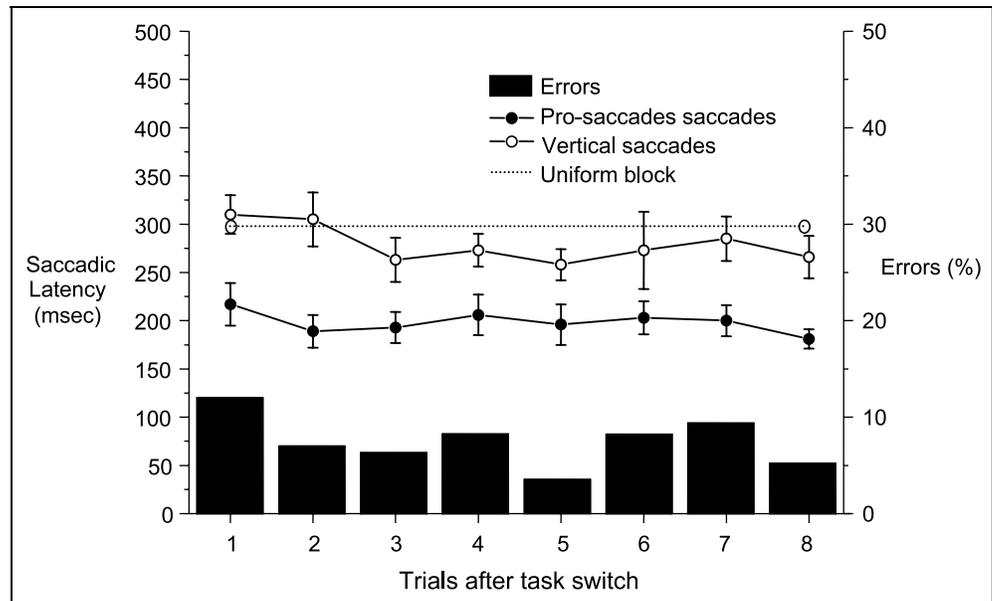
The latencies of pro saccades were significantly shorter than vertical saccades, $F(1,7) = 27.03, p < .001$. However, there was no significant effect of trials after task switch on response latency in either task, $F(7,49) = 1.45, p > .1$. There was also no interaction effect between trial and task, $F(7,49) = 0.72$. As with Experiment 4, the majority of saccade errors (90%) comprised pro saccade errors on vertical saccade trials. Neither saccade errors nor any other dependent variable showed any significant variation dependent upon trials after a task change (Figure 8).

Discussion

In contrast to Experiment 4, no switch costs were found in Experiment 5 when switching between reflexive saccades and a secondary task involving an arbitrary mapping between a peripheral onset and a vertical saccade. The significant switch costs reported in Experiment 4 cannot be attributed to alternating between horizontal and vertical saccades per se. It is the nature of the horizontal saccade task that is critical in predicting whether switch costs are observed on a new run of vertical saccades.

We propose in the light of these experiments that whenever two arbitrary stimulus–saccade mappings have

Figure 8. Saccade latencies and errors following a task switch (Experiment 5).



to be alternated between trials, significant switch costs will be found. However, as long as sufficient time is allotted in between responses, tasks involving a constant arbitrary mapping can be alternated with reflexive responding without incurring a latency cost. In short, subjects are able to hold a single arbitrary mapping “on-line” while enabling or disabling reflexive responding.

One question that these experiments do not address is whether with enough practice subjects can turn an arbitrary stimulus–response mapping into a reflexive one. One way to test this possibility would be to use stimuli that already have a well-established meaning (e.g., arrows) and use extended practice periods prior to presentation of switching tasks involving single or dual novel associations.

GENERAL DISCUSSION

Our results are consistent with the existence of two systems for saccade control that differ in their characteristics following a task switch. The first is “reflexive” and can be enabled or disabled in advance of a new run of trials. The second might best be termed “symbolic” and permits entirely arbitrary mappings between the environment and behavior. When a single arbitrary mapping has to be held on-line while switching to and from reflexive responding, no increase in latency is measurable when switching between tasks (Experiments 1 and 5). However, whenever two conflicting arbitrary mappings have to be coordinated, a switch cost is seen lasting one stimulus–response linkage (Experiments 2–4).

An open question concerning task switch costs is whether they are due to the additional time required to implement top-down control over new stimulus–response mappings or whether they reflect the presence of passive interference from the preceding task set

(Monsell, 2003). To address this question, we have recently tested an additional four subjects on Experiment 2 using an increased intertrial interval after a task change (4 sec compared to 1.5 sec). Despite being given this additional time to implement endogenous control over the new mappings, these subjects showed a switch cost of the same magnitude as the one reported in the main experiment (a cost of around 175 msec in both cases). Consistent with studies of task switching utilizing other response modalities (Meiran, 1996; Rogers & Monsell, 1996), eye movement latency costs appear to be insensitive to long intertrial intervals following a task change.

Another way of assessing the role of endogenous control processes in switch costs is by examining response latencies on the first trial of the experimental block, before any task changes have occurred (the initial run of trials in each block was always excluded from the analyses of switch costs). Calculating the mean latency across subjects in this manner revealed that the first response latency was always increased relative to the second trial in the block. This “restart cost” (Allport & Wylie, 2000) could be interpreted as indicating that switch costs are due to the initiation of a new task, rather than reflecting an interference effect from the preceding run of trials. However, restart costs were found in all the experiments reported here, independent of the magnitude of the latency increase following task changes. Even in the case of pro saccades, a large restart cost was observed, suggesting that the switch and restart effects rely on different mechanisms (Table 1).

There is also currently debate about whether switch costs can be explained by processes operating during response selection or by the retrieval of arbitrary stimulus–response mappings from long-term memory (e.g., Allport & Wylie, 2000; De Jong, Berendsen, & Cools,

1999; Meiran, 1996; Rogers & Monsell, 1995). It is true that performing the tasks described in this article necessitates retrieval of task parameters from memory. But memory retrieval can itself be viewed as a competitive process, similar to that proposed to operate in the selection of visual objects for action (Desimone, 1999; Duncan, 1999). According to this view, the onset of a new stimulus initiates competitive interactions between conflicting task memory traces, which continue until they are resolved through selection of one or another behavioral response. It makes little sense to characterize this process as one that is exclusively response versus memory based, or even motor versus perceptually based (Tipper, 2001; Newell, 1973). Interactions at the task level occur in parallel at multiple processing levels within the brain.

Recent neurophysiological evidence is also consistent with the existence of competitive interactions in task based control (Miller & Cohen, 2001; Miller, 1999; Asaad, Rainer, & Miller, 1998). Neurons in the prefrontal cortex have been found to represent particular combinations of cue color and saccade direction that have been subject to reinforcing feedback (Murray, Bussey, & Wise, 2000). When the contingencies among a visual cue, saccade direction, and reward are reversed, firing of cells that were tuned to the old stimulus–response mappings is inhibited, and different cell populations encoding the new rule mapping become active.

Evidence from neuropsychological studies indicate that similar mechanisms operate within human frontal cortex. Husain et al. (2003) report a patient with localized damage to an area of dorsomedial frontal cortex, corresponding to the location of the supplementary eye fields. This patient was found to make a greatly increased rate of saccade errors on the first trial after a task switch in the symbolically cued switching task described in Experiment 2. However, this patient's lesion did not impair his ability to monitor and correct these errors such that his rate of perseverative errors (for which an error feedback was received) did not differ significantly to controls. In contrast, patients with lateral frontal lobe damage also show greatly increased

number of saccade errors, but fail to correct their mistakes and consequently make actual errors for several trials following a change in task mappings (Hodgson & Golding, 2003).

Experiments 2 and 3 also indicate that saccadic response selection is modulated by affective factors. Eye movement responses were found to be subject to an inhibition of return effect following a punishing feedback (Figure 4). This effect is consistent with the proposal that humans associate objects, locations, and behaviors within their environment with endogenous autonomic responses (Bechara et al., 1997; Damasio, 1996). Monitoring these “somatic markers” enables the brain to carry out rapid and efficient decision making in complex social and natural environments and this process appears to be disrupted following ventromedial frontal lobe damage in man (Hodgson et al., 2002; Bechara, Damasio, Damasio, & Anderson, 1994).

Conclusions

The main conclusion of this study is that there are two systems subserving eye movement control that differ in their characteristics following a task switch. Tasks involving reflexive responding and a single arbitrary mapping are not susceptible to switch costs, as long as sufficient time is given for subjects to reset themselves for the new task. However, whenever two tasks involve switching between symbolic stimulus–saccade mappings, large switch costs are always observed. Switch costs occur when two arbitrary stimulus–saccade associations have to be coordinated within on-line/“working” memory.

METHODS

Experiment 1

Subjects

Twelve subjects took part in Experiment 1 (6 men, 6 women). The mean age of the subjects was 27 years (range 20–36). All subjects who took part in the experiments described in this article were naïve concerning the purpose and background to the experiments.

Design and Procedure

Three boxes, outlined in black on a gray-colored background, were presented in the center and 9° to the left and right of the center of a 22-in. color monitor. Each box subtended 3° of visual angle. The general procedure was as follows. Each trial started with the presentation of a white spot (0.5° diameter) in the center of the central box. After 500 msec, the spot was extinguished and simultaneously reappeared in either the left or the right box. Subjects then executed the appropriate eye movement toward one of the response boxes. Once either the left or right location had been fixated for a period longer

Table 1. Restart and Switch Costs across Tasks and Experiments

<i>Experiment-task</i>	<i>Restart cost</i>	<i>Switch cost</i>
1 - Pro saccades	139*	–10
2 - Centrally cued saccades	127	162*
4 - Vertical saccades	139	118*
5 - Vertical saccades	103*	28

Restart costs refer to the mean increase in latency on the first relative to the second saccade executed at the start of experimental block (before the occurrence) of the first task switch). Switch costs are defined as the average difference in latency between the first and second trials after a task change (* = significant costs).

than 800 msec, feedback was given to indicate that a correct or incorrect movement had been executed (feedbacks were either a high-pitched tone or low-pitched “buzz” sound accompanied by a happy or sad face presented at the response location for 500 msec). Following a delay of a further 1500 msec, the next trial could commence contingent upon the subject having made a return saccade to fixate the central location for a further 800 msec (Figure 1A).

Subjects were presented with separate practice blocks comprised of 60 pro saccades and 60 anti saccades. The order of the practice blocks was counterbalanced across subject. Each subject then completed two experimental blocks in which the two tasks were alternated. We chose not to interleave uniform blocks with switching blocks to ensure that subjects were well practiced on both tasks before commencing the switching blocks. Each block started with the subject executing pro saccades. After a random number of trials (between 9 and 13), the task would then change. The subjects were instructed in advance that the computer would change the task unexpectedly at several points during the test. Task changes were cued by the occurrence of unexpected error feedbacks (see above). A total of nine task changes occurred in each block of 100 trials and subjects completed two blocks in total.

Eye Movement Recording

Eye movements were recorded using an EyeLink system (Sensorimotoric Systems/SR Research), a video-based pupil tracker, with head movement compensation system sampling at 250 Hz. Subjects were seated at a comfortable viewing distance in front of the display monitor approximately 60 cm from the computer screen. Pupil position was monitored via two miniature infrared CCD video cameras mounted on an adjustable headband. Subjects were instructed to keep head movements to a minimum and no active restraint of head movements was required to obtain sufficiently accurate gaze position recordings. Eye movements were visualized off-line, saccades were identified, and artifacts removed using custom software programs developed within the LabVIEW visual programming environment.

Experiment 2

Subjects

Twelve subjects took part in Experiment 2 (6 men, 6 women). The mean age of the subjects was 28 years (range 21–36).

Design and Procedure

The design and procedure were identical to that used in Experiment 1, with the exception that each trial commenced with the presentation of a colored shape at

fixation. For half the subjects, a rule linked the color of the shape with a correct eye movement response to the left or the right. For the other six subjects, it was the shape of the central cue that was the discriminating dimension (circle vs. square). Subjects were told in advance which was the critical stimulus dimension. All subjects performed a practice block of 60 trials for which the stimulus response mappings remained constant. They then completed two switching blocks of 100 trials each in which the mappings between central cue and response could reverse. The first run of 9–13 trials in the switching block used the same rule that they had practiced in the initial practice block. In all other respects, the task was identical to Experiment 1 with reversals in the stimulus response mappings being cued by the occurrence of unexpected errors (Figure 1B).

Experiment 3

Subjects

Eight young control subjects took part in Experiment 3 (3 men, 5 women). The mean age of the subjects was 23 years (range 21–26).

Design and Procedure

The design and procedure were identical to Experiment 2 with the exception that instead of positive and negative feedbacks instructing subjects whether to maintain or switch tasks, the words “hold” or “switch” were presented at the response locations at the end of each trial. Auditory feedback was also presented to subjects. Hold feedbacks used the same high pitched tone that indicated correct responses in Experiments 1 and 2. Switch feedbacks were accompanied by a high pitched buzz. Unforced response errors were followed by the same error feedback used in Experiments 1 and 2.

Experiment 4

Subjects

Eight subjects took part in Experiment 4 (5 men, 3 women). The mean age of the subjects was 28 years (range 19–34).

Design and Procedure

The design and procedure was the same as in Experiment 1 with the exception that in addition to the two locations positioned to the left and right of central fixation, two more boxes were displayed 6° above and below the fixation point (Figure 6). Subjects were given a block of 60 practice trials in which they learned the arbitrary association between movement of the target stimulus to the left and right and eye movements to fixate the upper and lower response boxes, respectively. Again, feedbacks were displayed in the relevant response box at the end

of each trial. Each experimental block commenced with subjects being instructed to perform the vertical saccade task. As in the earlier experiments, the occurrence of an unexpected error instructed the subject to switch from the vertical saccade task to the antisaccade task. The computer then continued to switch between these tasks after runs of between 9 and 13 response trials throughout the block of 100 trials.

Experiment 5

Eight subjects participated in Experiment 5 (5 men, 3 women). The mean age of the subjects was 30 years (range 23–34). Otherwise, the methods were identical to Experiment 4 except that prosaccades rather than antisaccades were alternated with the vertical saccade task.

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