

Modification of planned actions

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Abstract To elucidate the time course and processes underlying pre-movement modification of planned actions, participants prepared to make an action at a time of their own choosing within a specified temporal window. In some conditions, participants prepared to make a single right index finger key press, whereas in others, they prepared to make a sequence of two key presses consisting of a right index finger key press followed by a right middle finger key press. On a proportion of trials, their internal preparation was interrupted by an auditory tone, in response to which they made either: the same action as they were intending, a different action requiring an additional effector (i.e. switch from preparing a single right index finger key press to executing a right index, middle finger sequence), or a different action requiring one less effector (i.e. switch from preparing a right index, middle finger sequence to executing a right index finger key press). For unmodified actions, switching from an internally generated to an externally triggered mode of response production produced a significant reaction time cost (RT cost) for both single and sequential actions, with the cost for single actions being significantly greater than that for sequential actions. Given that the RT cost did not increase as the complexity of the actions increased it is unlikely that the source of the cost is related

to motor execution processes, and it is suggested that it may arise at a higher level cognitive stage of processing. In addition, reaction times to produce modified actions were significantly greater than those to produce unmodified actions. Finally, it took significantly longer to produce modified actions requiring one *less* effector than to produce modified actions requiring one *more* effector. We suggest that two time-consuming processes are involved in switching between internally generated and externally triggered actions that are modified or unmodified: a trigger switch cost when the same action has to be produced in response to an external trigger as opposed to an internal trigger, and a switch cost reflecting changes in the pattern of executed motor commands when modification is necessary. It is suggested that such processes may be mediated by regions of the frontal lobes.

Keywords Motor planning · Internally generated actions · Externally triggered actions · Supervisory attentional system · Task switching · Action modification · Action cancellation · Motor preparation

Introduction

A cyclist is going to work and as they near their destination, they begin to slow their pedalling rate and prepare to squeeze the rear brake lever so they can come to a safe stop. However, a child suddenly runs into the road, and the cyclist slams on both brakes in a desperate effort to avoid an accident. Now consider two basketball players who have just finished an amazing alioop dunk manoeuvre. As they rush toward each other to celebrate, the dunker raises two hands to give an enthusiastic double high five to his team mate. However, at the last second he realizes that his team

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mate has only raised one hand for a single handed high five. To avoid hitting his team mate in the face, the dunker has to somehow stop his planned two handed high five and produce instead a safer single handed high five. In both these examples, executive control over action is needed for functional behaviour to emerge. First, in response to an external cue, the cyclist must rapidly assemble and execute extra motor commands in addition to those originally prepared. Second, the basketball dunker must rapidly inhibit a prepared sub-set of motor commands, in response to an external cue. This ability to efficiently and rapidly change ongoing behaviour on the basis of *both* external cues *and* internal plans is fundamental to daily life.

The importance of maintaining appropriate coordination between internally generated actions and reactions to external events is perhaps best highlighted in individuals with neurological conditions such as alien hand syndrome and utilization behaviour. These individuals, usually as a result of damage to medial frontal areas of the brain, lack the normal interplay between internally and externally driven actions, such that their capacity for inhibiting inappropriate reactive movements is impaired. Thus they suffer from reduced endogenous control, and tend to make many unwilling, but seemingly purposeful movements toward (and upon) objects in the environment (e.g. Archibald et al. 2001; Leube et al. 2003; Biran and Chatterjee 2004; Biran et al. 2006; Giovannetti et al. 2005). In one example, an alien hand syndrome patient remarked that she would not drink the tea given to her by an experimenter because it was too hot. Despite the fact that she had just uttered these words, her alien hand reached out to pick up the tea-cup, and she had to restrain it with her “good” hand which was still under volitional control (Della Sala et al. 1991).

Even though one of the cognitive system’s most important functions is to maintain this functional interplay between internally and externally driven action control processes, surprisingly little is known about the mechanisms responsible for this. In particular, when altering internally prepared, self paced action plans on the basis of external cues, what is the time course of modification both when the altered action plan requires an increase in the number of descending motor commands, and when it requires a reduced number of descending motor commands? Second, what does this time course suggest about the potential cognitive mechanisms involved in such motor modification? This paper reports an experiment addressing these questions.

Although many studies have investigated the ability to stop actions, the majority of these have used stop-signal and countermanding paradigms (Logan and Cowan 1984; Corneil and Elsley 2005; Ito et al. 2003; Coxon et al. 2006). Such paradigms estimate the time course of stopping an eye or limb movement by presenting a stop stimulus at various

times after a go signal. Typically they consider the process of stopping an action as a race between activity underlying ‘go’ processes and ‘stop’ processes (e.g. Curtis et al. 2005). In addition, many studies have investigated the processes involved in switching between two or more stimulus–response mappings, i.e. replacing one action with another, for example when one has to switch between executing saccades towards versus away from a stimulus in the antisaccade paradigm (Munoz and Everling 2004). These studies have demonstrated the importance of frontal lobe regions, particularly lateral prefrontal cortex, in this process (e.g. Ford et al. 2005; Nyffeler et al. 2007). By contrast, other studies implicate posterior parietal regions in rapid alteration of behaviour, for example when the target of a reaching action switches from one location to another (Pisella et al. 2000).

Whilst these approaches has proved useful in determining how much time is needed to stop an action, or to replace one action with another, they have not revealed as much about the processes involved in *modifying* internally prepared actions via the addition of extra movement components or the inhibition of a prepared movement component. The latter situation is one in which not all the motor commands in a prepared set need to be inhibited. Thus, some commands must be allowed access to the peripheral musculature, whilst others must be selectively inhibited. The process of action modification then, is not the same (although some mechanisms may be shared) as the process of action cancellation. To shed light on action *modification* processes, experiments are required in which participants switch between actions that are internally prepared and those that are externally cued, in situations where the “switched to” actions are similar or dissimilar to the actions originally planned.

In the present experiment, participants were required to internally prepare for the self-paced execution of a one-finger (i.e. single) or two-finger (i.e. sequential) key press, within a pre-specified time window after the start of a trial. Specifically, one finger movement conditions consisted of the execution of a right index finger key press, and two finger movement conditions consisted of a sequential right index finger followed by right middle finger key press. In one condition, participants’ preparation was interrupted at random times by an auditory tone in response to which they had to make the very same action they were internally preparing. Thus, if participants were preparing to make a self-paced one finger action, and an auditory tone was presented before their overt action occurred, they had to override their internal preparation to move at self-determined time and make the very same right index finger key press immediately. The same was true for the sequential finger movement condition. These conditions require a switch from an internal process of self paced motor preparation to a more

externally triggered, reactive process. This situation is theoretically interesting because the switch is between triggers for action (internal to external), but the required action is identical (single or sequential key presses). This (single key press) condition has been termed the “truncation” condition in previous studies and it produces two types of trial: those in which the participants’ internal process of preparation unfolds to execution of the action prior to the occurrence of the auditory tone, and those in which their internal preparation to move at a time of their choice is interrupted by the tone and a switch from an internal trigger to an external trigger is required (Obhi and Haggard 2004; Astor-Jack and Haggard 2005). The typical finding in these truncation experiments is that participants are (approximately 50 ms) slower to respond to the tone in truncation trials compared to baseline simple reaction time trials in which they are not preparing a self paced action and simply have to respond to a randomly presented tone.

In the present study, in a “modified truncation” condition, participants prepared to make an internally generated, self paced right index-finger key press but were instructed to produce a two-finger sequential response consisting of sequential right index and middle finger key presses, if a tone interrupted their internal preparation. Hence the internally prepared and externally triggered actions mismatched, such that an extra set of motor commands were necessary, if the tone interrupted the internal preparatory process. In another scenario, the opposite situation was created in which subjects prepared to produce a sequential movement, but had to produce just the first movement of the sequence if interrupted by a tone. Again, this condition produces a mismatch between internally generated and externally prompted actions, but this time, the requirement is to reduce the number of descending motor commands in response to the tone. By comparing the reaction times between the conditions it was possible to determine the time required for switching between different modes of response production, both when the switch did not require a change in the internally prepared action plan, and when it did require a change in the intended action plan. Specifically, using the paradigm described, we were able to determine the time course of switching from internal to external generation of action for movements involving an increased or decreased number of motor commands (i.e. effectors).

Method

Twelve healthy subjects (23 ± 4 years, nine females, three males) took part in the experiment for monetary compensation. The experiment was carried out in accordance with local ethics guidelines and informed consent was obtained from all participants. In all conditions, subjects sat at a

computer with their right index finger placed lightly on the “B” key and their right middle finger placed lightly on the “N” key. The experiment consisted of three conditions which were arranged in blocks and randomly arranged across participants to avoid order effects. Specifically, participants completed two *internally generated action* blocks, two *simple reaction time* blocks, two *truncation matched* blocks, and two *truncation mismatched* blocks. In internally generated blocks, participants simply prepared and executed a self paced action (one finger, or two finger sequential key press(es)) within a 3–10 s window post trial onset. These conditions served mainly to give participants experience in making self paced motor actions and data from these conditions were not included in the main analysis. In the simple reaction time condition, participants responded with one right index finger response or a right index right middle finger sequence when an auditory tone was presented. The presentation of the tone was randomly varied across times throughout a 3–10 s window post trial onset.

In addition, there were four “truncation” conditions, two comprising “matched truncation” and two comprising “mismatched truncation”. In one of the matched conditions participants prepared to make a self paced right index finger movement and were asked to respond as quickly as possible with *exactly the same movement* if their internal preparation was interrupted by an auditory tone (one finger matched condition). A second truncation condition was identical except that participants internally prepared to make a self paced two finger sequence (right index followed by right middle finger movement) and to respond with the identical sequence if a tone interrupted their preparation (two finger matched condition). As in previous studies, the reaction times from the truncation trials involving a reaction to a tone were compared to those from the simple reaction time condition to assess the reaction time cost of internal preparation (previously reported by Obhi and Haggard 2004; Astor-Jack and Haggard 2005). Furthermore, to ensure that differences in foreperiods between simple reaction time trials and reactive trials from truncation matched conditions did not contribute to any differences in the reaction times from these trials, the foreperiods from each participant’s truncation condition were used as the foreperiods for the next participant’s simple reaction time condition. Hence, the foreperiods were precisely matched at the group level for these comparisons. Lastly, only reaction times from the right index finger key press were compared across conditions.

In the two mismatched truncation conditions, participants either prepared to make a single right index finger key press but made a sequential (right index followed by right middle finger) response if the tone interrupted their preparation (add a movement condition), or, they prepared to

make a sequential (right index followed by right middle finger) key press but made a single right index finger response if the tone interrupted their preparation (inhibit a movement condition). We then compared the reaction times from all four truncation conditions to determine the relative costs of switching between triggers for action when the “switched to” movements were the same or partially different from the internally prepared actions.

In all conditions involving a reaction, a 100 ms 1 kHz auditory tone served as the stimulus and only reaction times of the right index finger were compared. In accordance with a previous study (Astor-Jack and Haggard 2005) there were 20 trials in the simple reaction time condition and the internally generated action condition, and 40 trials in the truncation conditions, based on the expectation that, in truncation conditions, approximately half the trials would be classified as internally generated trials in which the participant made their internally prepared, self paced key press prior to the occurrence of the tone, and the other half would be trials in which the tone interrupted participants’ internal preparations prompting them to respond with the pre-instructed movement. All stimuli and reaction times were recorded using DirectRT and custom response hardware, which provided timing precision of 1 ms.

Results

In accordance with a previous study (Obhi and Haggard 2004) reaction times that were less than 75 ms or greater than 1,000 ms were excluded from the analysis because they represent anticipations and missed trials, respectively. To be clear, these trimming criteria were used for reaction times to facilitate comparison of the present study to earlier studies using the truncation paradigm (Obhi and Haggard 2004; Astor-Jack and Haggard 2005). This procedure, in addition to removal of trials in which participants failed to follow instructions, resulted in loss of less than 1% of trials across all subjects. To ensure that reaction time measures were meaningful, we only ever compared the reaction time of the right index finger response between conditions.

One finger versus two finger simple reaction times

A 2×2 ANOVA was performed to assess the effects of movement type (single, sequential) and condition (simple reaction time, truncation) on reaction times. This test revealed a statistically significant main effect of the movement type factor ($F_{1,11} = 22.861$, $P = 0.001$). As Fig. 1 illustrates, right index finger reaction times from the sequential movements (right index finger followed by right middle finger key press) were significantly greater than right index finger reaction times when they were performed

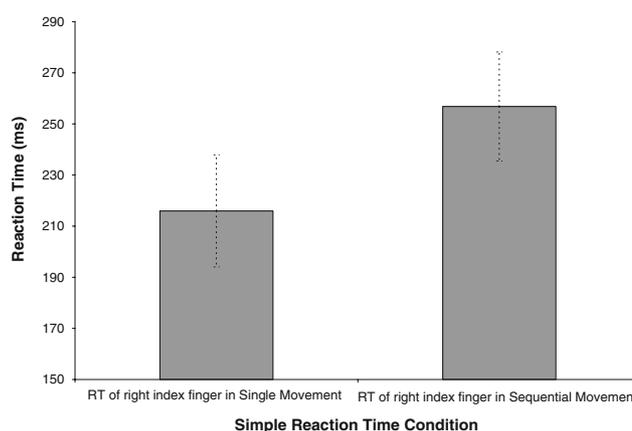


Fig. 1 Single and sequential simple reaction times of the right index finger (RT). Note that right index finger RT in sequential actions was significantly greater than the right index finger RT in single actions, reflecting greater processing demands for sequential versus single actions. Error bars are SEM

alone (mean right index finger RT (single) = 216 ± 76 ms, mean right index finger RT (sequence) = 257 ± 74 ms). A planned t-test confirmed that this result was also statistically significant ($t = -5.350$, $df = 11$, $P < 0.0001$).

Truncation conditions

Figure 2a shows distributions of the auditory tone in all four truncation conditions and Fig. 2b shows reaction time distributions in each of the four truncation conditions. In matched truncation conditions the percentage of truncation trials in which participants responded to a tone was 48% for the single response condition and 46.5% for the sequential response condition. In mismatched truncation conditions the percentage of truncation trials in which participants responded to a tone was 45.2% for the condition in which an extra movement was added in response to the tone and 45% for the condition in which a movement was inhibited in response to the tone.

Comparison of truncation matched conditions to simple reaction time conditions

The 2×2 ANOVA also revealed a significant main effect of condition confirming that reaction times in the truncation conditions were reliably greater than those in the simple reaction time conditions ($F_{1,11} = 26.573$, $P < 0.0001$). In addition there was a significant movement type \times condition interaction ($F_{1,11} = 13.539$, $P = 0.004$). On the basis of previous results (Obhi and Haggard 2004; Astor-Jack and Haggard 2005), a planned paired samples *t* test was conducted to determine the difference in reaction time between the single right index finger movement simple reaction times and the single right index finger movements in the

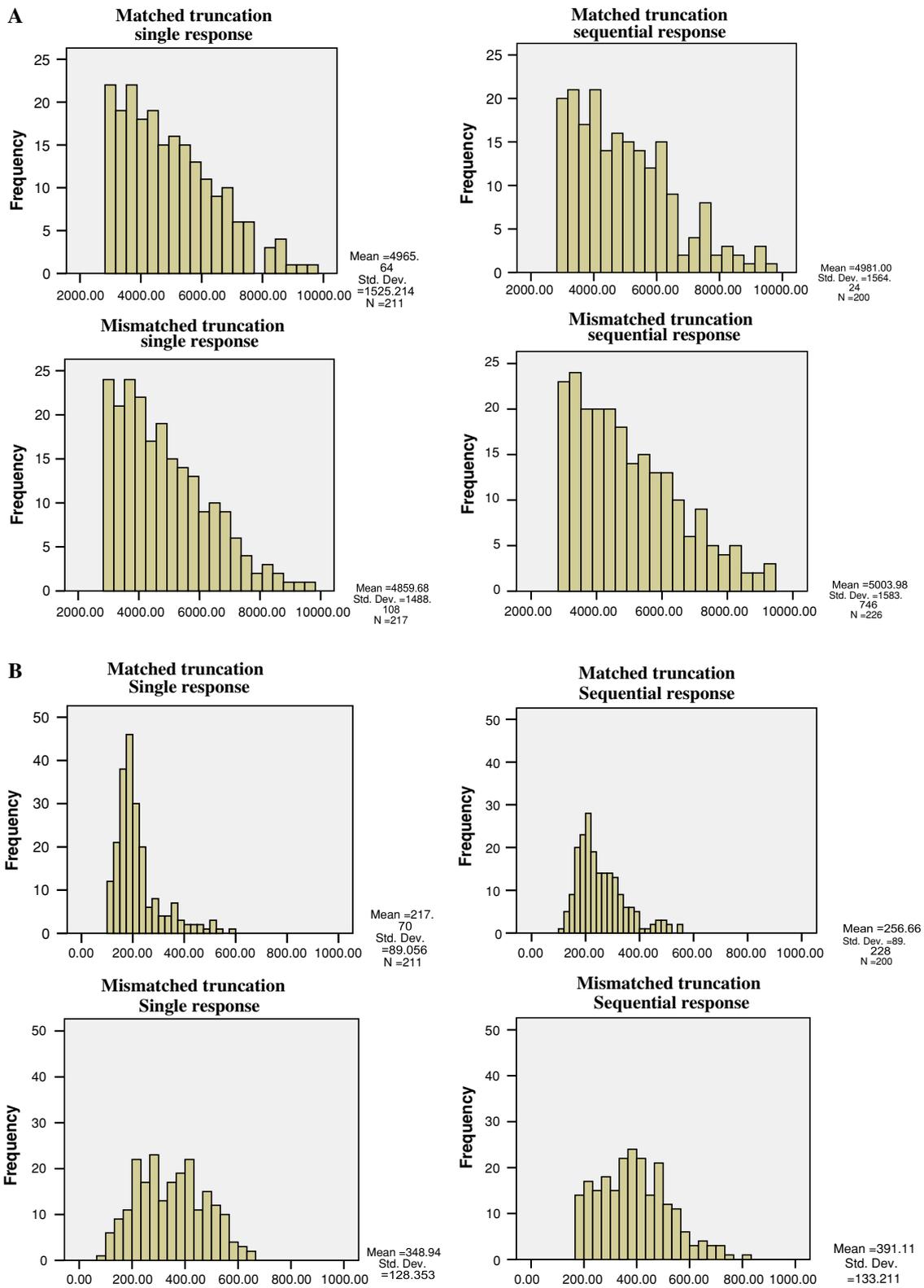


Fig. 2 **a** Distributions of tone presentation times in four truncation conditions. **b** Distributions of Reaction times in four truncation conditions

matched truncation condition. Importantly, the foreperiods in the simple reaction time and matched truncation conditions were matched at the group level. Thus, we compare reaction times across blocks in which both the *time* and *order* of tone presentation are the same. This test revealed that, when a single right index finger movement was internally prepared and made in response to a tone, reaction times were significantly greater than in the simple reaction time condition (314 ± 85 vs. 216 ± 76 ms, $t = -5.766$, $df = 11$, $P < 0.0001$). This was also true for the condition in which right index followed by right middle finger sequential movements were internally prepared and executed in response to a tone compared to the simple reaction time condition involving the sequential response (322 ± 79 vs. 257 ± 74 ms, $t = -4.117$, $df = 11$, $P = 0.002$). In line with the interaction, the average cost of switching from an internal to an external mode of response production, when the response required was the same as the internally prepared response, was greater for single finger responses compared to sequential responses (single response cost = 98 ± 59 ms, sequential response cost = 65 ± 55 ms, $t = 3.763$, $df = 11$, $P = 0.003$). Hence the reaction time cost of switching between internal and external action triggers does not increase as the computational difficulty of the response set increases (i.e. moves from a single movement to a two movement sequence).

Variability of reaction times in simple reaction time and truncation conditions

To assess the effects of movement type (single, sequential) and condition (simple reaction time, truncation) on the variability of reaction times, a 2×2 ANOVA was conducted. Specifically, the standard deviation from each subject for each experimental condition was entered into the analysis which revealed no main effect of movement type ($F_{1,11} = 1.335$, $P = 0.272$), a significant main effect of condition ($F_{1,11} = 18.312$, $P = 0.001$) and no interaction ($F_{1,11} = .028$, $P = 0.871$). Bonferroni corrected follow-up t tests showed that the variability of truncation conditions was greater than that in simple reaction time conditions both for single ($t = -3.779$, $df = 11$, $P = 0.003$) and sequential responses ($t = -3.145$, $df = 11$, $P = 0.009$).

Comparison between four truncation (matched and mismatched) conditions

To determine whether there were any differences in the reaction time to execute an action that matched or mismatched the action being internally prepared, a 2×2 ANOVA was performed with the factors of “Type of Movement Planned” (single, sequential) and “Type of Movement Executed” (single, sequential). This test

revealed a main effect for the type of movement planned and the type of movement executed factors ($F_{1,11} = 11.768$, $P = 0.006$ and $F_{1,11} = 15.126$, $P = 0.003$, respectively). There was also a significant Type of Movement Planned \times Type of Movement Executed interaction ($F_{1,11} = 14.661$, $P = 0.003$). A Bonferroni corrected pairwise comparison revealed that reaction times in the add a movement condition were significantly greater than those in the condition in which a single movement was planned and executed on the tone (RT (add) = 353 ± 108 ms versus RT (make same single response) = 314 ± 85 ms, $t = -2.880$, $df = 11$, $P = 0.015$). An additional Bonferroni corrected pairwise comparison revealed that the same was true for the inhibit a movement condition versus the condition in which a sequential movement was planned and executed on the tone (RT (inhibit) = 391 ± 106 versus RT (make same sequential response) = 322 ± 79 ms, $t = -4.442$, $df = 11$, $P = 0.001$). A planned comparison revealed that the reaction time cost of inhibiting a movement from an internally prepared action plan was significantly greater than the cost of adding a movement to an internally prepared action plan—(average reaction time cost of inhibiting a movement = 69 ± 54 ms, average reaction time cost of adding a motorically identical movement = 40 ± 48 ms; $t(11) = -3.886$, $P = 0.003$). The Type of movement planned \times Type of movement executed interaction is shown in Fig. 3.

Variability of reaction times in matched and mismatched truncation conditions

To assess the effects of the factors of movement type (single, sequential) and condition (matched truncation, mismatched truncation) on the variability of reaction times, a 2×2 ANOVA was conducted. Specifically, each participant’s

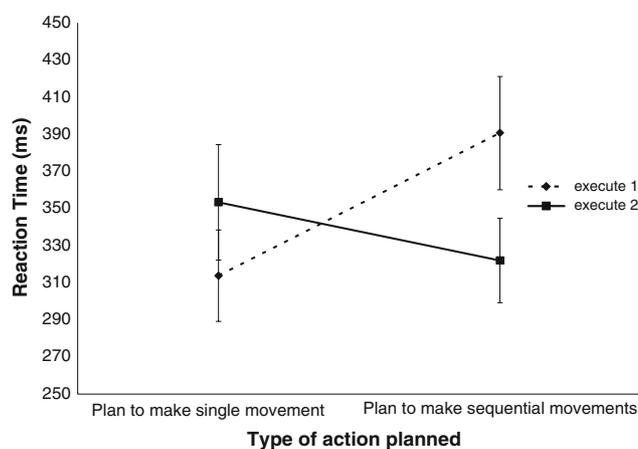


Fig. 3 Interaction plot depicting the reaction times in single and sequential matched truncation and mismatched truncation conditions (plan single, execute single; plan sequential, execute sequential; plan single, execute sequential; plan sequential, execute single). Error bars are SEM

standard deviation from each experimental condition was entered into the analysis which revealed no statistically reliable differences in variability between the matched and mismatched truncation conditions. Specifically, there was no main effect of movement type ($F_{1,11} = 1.027, P = 0.333$), no main effect of condition ($F_{1,11} = 4.007, P = 0.071$) and no interaction ($F_{1,11} = 0.096, P = 0.762$). It is interesting to note that even though non-significant, there is a trend towards reaction times in the mismatched conditions being more variable than those in the matched conditions.

Discussion

In daily life humans often have to modify the actions that they are planning internally (i.e. in an endogenously driven, self paced manner) on the basis of imperative environmental cues. Indeed, such flexibility to modify planned actions is critical for functional and adaptive behaviour. There are at least two theoretical features that define such situations. First, there is a *switch* from an internally prepared, self paced preparatory process, to a more exogenously driven process—this can be considered a switch from an internal to an external trigger for action. Second, there is a change in the action that is executed such that the appropriate action (based on the cue) is produced. This can be considered a change in the pattern of executed motor commands, from those that were initially intended. Of course, the change in the required action in response to the tone could reflect a rapid assembly of extra motor commands (or the inhibition of a sub-set of motor commands), or it could reflect a switch between one prepared action plan and another. This second possibility is based on previous research from partial precueing experiment which suggests that more than one response can be prepared in parallel (e.g. Jentzsch et al. 2004). Hence, it is possible that, in truncation conditions involving the possibility of making a different action in response to the tone, participants actually prepare two action plans ahead of time and simply switch from one to another. However, whatever the specific strategy that the brain uses, the general notion that there are *at least* two processes (internal–external trigger switch, and change in pattern of executed motor commands) governing modification of intended action holds. The present study sought to determine the time course of these two components of the action modification process, in a simple laboratory task.

To investigate the time required to switch between internal and external triggers for action, we determined reaction times in a “matched truncation” condition in which participants prepared to make an action at a time of their own choosing but had to override this preparatory process and make the same action immediately if presented with an auditory tone. We compared these reaction times (matched

truncation reaction times) to reaction times from a simple reaction time condition (with identical foreperiods to the matched truncation condition) in which participants simply waited for and responded to an identical auditory tone. This comparison was made for two actions; a single right index finger key press and a sequential right index followed by right middle finger key press. To investigate the time required to modify an intended action, we also determined the reaction time to produce an action that differed by one more or one less movement than the action being internally prepared (mismatched truncation conditions).

The main results were as follows. First, as has been found previously, relative to simple reaction time, there was a significant cost of producing an externally-triggered action that is identical to an action being internally prepared (see Astor-Jack and Haggard 2005; Obhi and Haggard 2004 for similar results). Second, the first new finding of the current study is that this cost was greater for conditions involving a single response compared to those requiring a sequential response (reaction times from right index finger movement only compared). This was true even though, in simple reaction time conditions, the reaction time of the right index finger movement in the sequential action was significantly greater than the reaction time of the same movement in the single action condition. That is, even though the sequential movement was computationally more demanding than the single movement, the cost of switching between an internal and an external trigger was smaller than for the single movement condition. This result is somewhat surprising and difficult to explain, but we have observed it in at least two other experiments (unpublished studies). It may be that there is some form of ceiling effect which precludes the cost from increasing as movement complexity increases, or it could be that there is something different about single responses compared to multi-movement responses. It remains for future studies to address this issue in more detail. Possibly the most important results come from the comparison of matched truncation conditions (those in which the switched to movement is identical to the internally prepared movement) with mismatched truncation conditions (those in which the switched to movement partially differs from the internally prepared movement). Specifically, the reaction time to produce a partially different action to that being planned was significantly greater than the reaction time to produce an identical action to the one being planned (mismatched truncation condition versus matched truncation condition). Finally, the reaction time to produce an action containing one less movement than the action being planned was significantly greater than the reaction time to produce an action containing one more movement than the action being planned (inhibit a movement condition versus add a movement condition comparison). Thus, inhibiting part of a prepared action plan in

response to a tone was more time consuming than adding a motorically identical movement to an intended action plan.

An obvious criticism of the first set of results in which truncation matched conditions are compared to simple reaction time conditions is that the former conditions contain two processes to which participants are allocating their attention; an internal preparatory process and a cue monitoring process. Thus the cost associated with reacting to the cue in matched truncation could be due to an attenuated perceptual processing of the auditory stimulus due to divided attention. However, this is not thought to be the case, and evidence for this comes from a study in which auditory evoked potentials were recorded in a simple reaction time condition and a truncation condition (Astor-Jack and Haggard 2005). The amplitude of N150 and N300 components of the waveform were actually greater in the truncation condition suggesting enhanced and not attenuated processing of the tone in truncation conditions. There was a small increase in the latency of the N150 component in the truncation condition (8 ms later than in the simple reaction time condition) but this difference is far too small to explain the reaction time costs found in the present study. Furthermore, the reaction time cost found in the present study is likely not due to a 'divided attention effect' as previous studies have found that, as long as there is at least 300 ms allowed for preparing a manual aiming movement, such movements can be executed concurrently with a perceptual discrimination judgment made about a target at a different spatial location (Deubel and Schneider 2003). Since the present study allowed at least 3,000 ms prior to the possibility of an auditory stimulus, and the movements required were button presses compared to target directed aiming movements, it seems unlikely that divided attention explanations can account for the reaction time costs observed in the present study. In addition, a previous study using the truncation paradigm manipulated attention (attend to internal preparatory process or attend to beep) and found that attentional effects are too small to account for the RT costs observed (Astor-Jack and Haggard 2005). Another objection to the comparison made between simple reaction time and matched truncation conditions is that differences in foreperiods between the two conditions could contribute to the observed differences in reaction time. However, in the present study foreperiods were identical at the group level because we used the preceding participants' foreperiods from the matched truncation conditions as the foreperiods for the simple reaction time condition of the next participant. Hence, we are confident that the reaction time cost of switching between modes of response production found in the present study is real and reflects the time taken to switch from an endogenous action generation process to a more exogenously cued action production process.

Previous studies have shown that internally-prepared and externally-cued actions are supported by at least partially separable processes, even when subjects are attempting to produce the same motor response in the two conditions (Obhi and Haggard 2004). The present study extends these results by showing that there is an additional cost when the actions constituting the internally-prepared and externally-triggered responses differ. In other words, although there is a significant reaction time cost when internally-prepared and externally-triggered actions match, this cost is substantially less than the cost incurred when internally-prepared and externally-triggered actions differ. This implies that some, but not all, of the processes underlying internally-prepared and externally-triggered actions are common to the two conditions, at least when the two types of action require the same motor output. If internally-prepared and externally-triggered actions depended on entirely separate processes, it would not matter whether the actions required in these conditions match. The suggestion that internally and externally generated action systems may be mediated by partially overlapping processes fits with neuroimaging data on these classes of action. For example, in contrast to some early lesion work on non-human primates which suggested a sharp dichotomy between the motor preparatory systems mediating internally and externally generated actions, more recent neuroimaging studies have supported the idea that internally generated and externally triggered actions share many neural substrates, albeit with some differences in the extent and timing of activations, especially in medial frontal areas (e.g. Passingham 1987; Jahanshahi et al. 1995; Cunnington et al. 2002; Lee et al. 1999; Deiber et al. 1999).

Perhaps the most important result in the present paper, however, is that inhibition of a part of a movement requires more processing time than addition of a motorically identical movement. To our knowledge, this emphasis on partial cancellation of a response represents a new line of inquiry that has not been studied in previous research (which has tended to focus on complete cancellation of movements).

For a given motor action, reaction times are increased compared to SRT when internal preparation is interrupted by an auditory tone prompting the same action. Hence it appears that the brain cannot take advantage of pre-existing levels of internal preparation for an action when prompted to make the same action by an external cue. In the current study this cost was around 98 ms for single index finger responses and 65 ms for sequential finger key presses. Similar results (for single responses) have been reported before and have been suggested to reflect the difficulty of engaging in endogenous and exogenous processing at the same time (Obhi and Haggard 2004; Astor-Jack and Haggard 2005). A new finding of the present work is that, although sequential actions produced significantly greater simple RTs of the

right index finger than single right index finger actions, the reaction time cost of switching from an internally driven to an externally triggered process was actually significantly greater for single right index finger actions compared to sequential actions. This suggests that the cost of switching does not relate directly to motor execution processes since this would predict a greater cost for more computationally demanding (i.e. sequential) actions compared to less computationally demanding (i.e. single) actions. Instead, it seems likely that the source of the cost is at a higher level “cognitive” stage of processing. This result is reminiscent of previous findings that switching to an easier task may be associated with a greater reaction time cost than switching to a more difficult task (Allport et al. 1994).

One framework that could potentially account for these results is the contention scheduling/supervisory system framework developed by Shallice and colleagues (Norman and Shallice 1986; Shallice 1988; Shallice and Burgess 1996). According to this framework, simple behavioural routines, such as pressing a button or reading a word, are under control of action “schemas”. Schemas are selected in a process of “contention scheduling”, in which they compete with each other and the most active schema is selected (Cooper and Shallice 2000). According to this framework, schemas can become activated in two qualitatively distinct ways: they can be directly triggered by events in one’s environment or they can be triggered internally by a “supervisory attention system”, associated with the functions of the prefrontal cortex (see also Burgess et al. 2007). The contention scheduling/supervisory system framework could potentially account for both the truncation cost, when internally-prepared and externally-triggered actions match, and also the additional cost when they differ. In the case where internally-prepared and externally-cued actions match, the same schema may be involved in producing both actions. Hence, the observed cost (relative to simple RT) would result from the necessity to switch between internal and external triggers for this schema (see Burgess et al. 2007, for discussion of this process). However, in the case where internally-prepared and externally-triggered actions do not match, it would be necessary to switch not only from an internal to an external trigger, but also from one schema, or set of schemas, to another (commanding single versus sequential actions). This could account for the extra time cost observed in the present study in cases where subjects switched between internally generated and externally driven actions that were different rather than identical.

Consistent with this behavioural data, recent neuroimaging evidence suggests that different parts of the prefrontal cortex may support a) switching between internal versus external triggering of schemas, and b) switching activation from one schema (or set of schemas) to another (see Burgess et al. 2007). For instance, Gilbert et al. (2005)

investigated the process of switching between attention towards externally-provided versus internally generated information. They suggested that this switching process is supported particularly by the rostral prefrontal cortex, approximating Brodmann Area 10, whereas switching between various stimulus-response rules (i.e. between different schemas) may be supported by other regions within the frontal lobes, such as the dorsolateral prefrontal cortex (Braver et al. 2003).

In summary, the present results point towards two operations involved in modifying internally planned actions on the basis of incoming perceptual information. First, an operation whereby the *trigger* for action is switched from internally-oriented to externally-cued processes; second, an operation whereby prepared action plans are updated in light of new information. These results indicate that *both* operations are associated with a time cost. In combination, these processes may play a crucial role in producing safe, efficient, and flexible behaviour.

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