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Internal and External Triggers for Action

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Running Head: INTERNALLY GENERATED AND EXTERNALLY TRIGGERED ACTIONS

Internal and External Triggers for Actions

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THESIS

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Abstract

When the self paced preparation of an action is interrupted by a stimulus prompting the same motor response there is an increase in the reaction time to the stimulus as compared to an external or simple reaction time (SRT) condition (Obhi & Haggard, 2004). Previous studies have suggested that this cost is not attributable to perceptual or attentional factors. Therefore, to investigate the source of this RT cost we varied the motor demands of movements in Experiments one and two. Results indicated that the level of motor programming demands did not influence the RT cost in these experiments. While RTs for more demanding movements (i.e., bimanual or serial key presses) were slower than those for simple one finger actions (i.e., single key presses), the RT cost was not significantly different for both response types. That is, the RT cost did not increase as a function of motor programming demands. In a control experiment (experiment three), we assimilated the external and truncation conditions through the creation of the external-subvocal condition, to investigate if the source of the RT cost was reflective of the dual task of subvocalization. The results revealed that although the RT cost was reduced, counting subvocally did not eliminate the RT cost. Simply, the RT cost is not explained by the dual task of subvocalization. The ability to modify planned actions is fundamental to everyday life, thus we investigated the time course of modifying planned actions on the basis of an external cue in experiment four. Reaction times to produce modified actions were significantly greater than those to produce unmodified actions. Additionally, 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. Finally, we conducted two experiments to investigate the time course of cancelling a planned action on the basis of an environmental prompt. It was found that an internally prepared action can be cancelled with 300ms, regardless of the motor demands associated with the prepared action, suggesting that we are cancelling the prospective “when” component of the action.

Keywords: Motor planning, Internally generated actions, Externally triggered actions, Supervisory attentional system, Action modification, Action cancellation, Motor preparation.

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Table of Contents

Abstract.....	i
Keywords.....	ii
Acknowledgements.....	iii
Table of Contents.....	iv
List of Figures.....	vii
General Introduction.....	4
Neuropsychological case studies.....	6
Cognitive theory.....	7
Non-human primate studies.....	8
Neuroimaging studies.....	9
Truncation paradigm.....	10
<i>Purpose for current studies</i>	
Experiments one and two.....	13
Experiment three.....	14
Experiment four.....	14
Experiments five and six.....	15
Experiment one.....	18
Methods.....	22
Results.....	25
Discussion.....	28
Experiment two.....	29
Methods.....	30

Results.....	30
Discussion.....	31
Overall discussion for experiments one and two.....	32
Experiment three.....	37
Methods.....	39
Results.....	41
Discussion.....	43
Experiment four.....	47
Methods.....	50
Results.....	53
Discussion.....	56
Experiment five.....	63
Methods.....	65
Results.....	69
Discussion.....	72
Experiment six.....	72
Methods.....	73
Results.....	74
Discussion.....	77
Overall discussion for experiments five and six.....	77
General Discussion.....	82
Summary of findings from experiments one through three.....	83
Possible neural mechanisms underlying the RT cost of internal preparation.....	84

Summary of findings for modification of actions.....85

Possible neural mechanisms to explain action modification.....86

Summary of cancelling an internally prepared action.....89

Suggested neural correlates of cancelling an internally prepared action.....90

Final conclusion.....91

References.....92

Figure Captions.....100

Figures.....104

List of Figures

Figure 1a

A schematic depiction of the truncation paradigm

Figure 1b

Response times for both unimanual and bimanual responses in the external condition in Experiment 1

Figure 1c

Unimanual and bimanual RT costs of internal preparation in Experiment 1

Figure 1d

Unimanual and bimanual reaction times for both external and truncation conditions in Experiment 1

Figure 1e

Unimanual reaction times for both external and truncation conditions plotted against delivery times of the auditory tones in Experiment 1

Figure 1f

Bimanual reaction times for both external and truncation conditions plotted against delivery times of the auditory tones in Experiment 1

Figure 2a

Single and serial reaction times for both external and truncation conditions in Experiment 2

Figure 2b

Response times for both single and serial responses in the external condition in Experiment 2

Figure 2c

Single and serial RT costs of internal preparation in Experiment 2

Figure 3

Response times for the external, external-subvocal, and truncation conditions in Experiment 3

Figure 4

Single and serial reaction times for the external condition in Experiment 4

Figure 4b

Reaction times from the match and mismatched truncation conditions for single and serial responses in Experiment 4

Figure 5a

A schematic depiction of the external-cancel and truncation-cancel conditions

Figure 5b

Reaction times from external and truncation conditions for all SOAs in Experiment 5

Figure 6a

Single response reaction times from external and truncation conditions for all SOAs in Experiment 6

Figure 6b

Serial response reaction times from external and truncation conditions for all SOAs in Experiment 6

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General Introduction

You get home from work and start thinking of what you need to do that night. You think to yourself I should call my grandparents because I have not talked to them in a while. As you're planning to pick up the phone and call your grandparents the phone rings, essentially requiring you to complete the same action you were planning. Are you faster to answer the phone because you were already preparing to complete that action? Or are you slower because you have to cancel your internally prepared action and then reassemble your response? The present paper addresses these questions with a particular interest in the underlying interacting mechanisms that enable these two modes of action generation.

There are two major influences on a person's actions. The first influence is the environment. People take in the world through their senses such as vision and audition. The second influence is from within themselves. Clearly these two influences interact in that people use their past and current needs to influence their behaviour in the current environment. Thus, everyday life requires a functional balance between actions that are planned from within, (i.e., internally generated actions) and those made in response to external cues (i.e., externally triggered actions). If this balance is lost, as in some individuals with frontal brain damage, actions made in response to external cues can dominate, sometimes in a dysfunctional manner, over the intended actions of the individual.

To be clear, throughout this paper “internally generated” and “externally triggered” actions will be operationalized as two distinct classes of human motor behaviour. However, it is important to acknowledge that in real life it is not very often the case that any one action is entirely internally generated or completely externally triggered. Actions can be thought of as running on a continuum where one extreme is internally generated and the other is externally generated. The key distinction for the purpose of the present work is that internally generated actions are typically made in the absence of any change in the external environment, whereas externally triggered actions are made in response to a change in the environment. An example might be a dog that gets up on its own accord and walks over to its owner, versus the same dog getting up and walking over to its owner because the owner calls for it. Thus, in the former situation there is no change in the environment that prompts the act, whereas in the latter case, the sound of the owner’s call prompts the act. Lastly, depending on how the situation is conceived, all actions can be thought of as containing some degree of “external influence” because we always operate within an environment, and all actions (other than simple reflexes such as the knee jerk) require internal processing. For the sake of simplicity, this paper is referring to actions that are **more** internally generated or **more** externally triggered.

To explore how the mechanisms that govern internally generated and externally triggered actions interact, some case studies will demonstrate dysfunctional behaviour that may result if the ability to balance these two classes of actions is lost. A cognitive framework of how actions are represented will then be discussed followed by some early non-human primate studies that suggest some neural correlates for both modes of action processing.

Some neuroimaging studies involving human participants will add to the primate findings and lead into the creation of the experimental approach used in this thesis, namely the truncation paradigm (Obhi & Haggard, 2004).

Neuropsychological case studies

It is important to illustrate the consequences that may arise if one loses the ability to balance internally generated and externally triggered actions. Some patients who suffer from frontal brain damage can no longer restrain themselves from reacting to exogenous cues, even if it results in inappropriate behaviour. Damage in the medial frontal areas of the brain in these patients often results in a lack of normal interaction between internally generated and externally triggered actions causing cognitive-motor impairments such as utilization behaviour or alien hand syndrome (Della Sala, Marchetti, & Spinner, 1991; Archibald Mateer, & Kerns, 2001; Leube, Knoblich, & Kircher, 2003; Biran & Chatterjee, 2004; Biran, Giovanetti, Buxbaum, & Chatterjee, 2006; Giovanetti, Buxbaum, Biran, & Chatterjee, 2005). For example, patients with utilization behaviour no longer have complete control over their internally generated actions and appear to be “slaves” to their environment because they cannot help but respond to external stimuli, even when such responses are inappropriate (Archibald et al, 2001). In a second example, an alien hand syndrome patient stated 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). In view of the deficits in

such patients, it is very important to understand the way in which the brain balances internally generated and externally triggered actions.

Cognitive theory

Traditionally cognitive models were developed without reference to the brain, although now they are being incorporated into brain function as well. One such concept is that actions are represented as schemas which have been defined as “well-established action[s] or thought[s]” (Burgess, Dumontheil, & Gilbert, 2007). Shallice and colleagues developed one framework, contention scheduling and the supervisory system, that has attempted to explain how internally generated and externally triggered actions are organized in the brain (Norman and Shallice, 1986; Shallice, 1988; Shallice, Burgess, & Robertson 1996). It is believed that simple behavioural routines, such as pressing a button or walking, are represented as action schemas. It is through the process of contention scheduling that these schemas are selected (Cooper & Shallice, 2000). Schemas compete with each other and the most activated schema is selected. It is suggested that schemas can be activated in two qualitatively discrete ways: they can be triggered through one’s environment or through internal mechanisms, such as top-down information by a “supervisory attention system”, associated with the functions of the prefrontal cortex (see also Burgess et al., 2007). Simply put, schemas may be activated by objects in the environment or through top-down processing which provides information about the person’s current needs/goals. Therefore, as schemas are activated by both of the above sources, the most appropriate schema should have the highest activation resulting in the desired behaviour being carried out. The current work attempts to use findings from

primate neurophysiology with the notion of action schemas to shed light on the organization of actions.

Non-human primate studies

Non-human primate studies often provide the underpinnings necessary to conduct future work in human subjects. Thus, it is essential to consider early non-human primate studies before exploring studies involving human participants. There have been several studies that have examined the neural substrates of internally generated and externally triggered actions in both non-human primates and human participants (Passingham, 1987; Petrides, 1982, 1986; Halsband & Freund, 1990; Jahanshahi, Jenkins, Brown, Marsden, Passingham & Brooks, 1995). Passingham (1987) added to the body of research of the motor system and its specification in his early work with monkeys. Particularly, he found that two premotor systems are dissociable in their involvement with respect to internally generated and externally triggered actions. After training monkeys on a visual cue task (i.e., if the cue is blue the handle must be pulled, if the cue is red the handle must be turned), Passingham (1987) lesioned the lateral premotor area in these monkeys. After recovering from this surgery, the monkeys did not relearn the visual cue task easily, although they were able to readily make either movement. In a similar task, six new monkeys were trained to make responses to external cues. After learning the task, three of the monkeys had their supplementary motor area (SMA) lesioned and they were able to perform the task post-surgery, with as few errors as the three control monkeys. These results suggest that the lateral premotor area may mediate visually guided actions. Furthermore, Passingham (1987) taught monkeys to reach out to a specified position that

encompassed an invisible infrared beam. If the monkey interrupted the beam they won a peanut. The SMA was lesioned once the monkeys had learned this task. After recovery, the monkeys had trouble completing the task. However, these monkeys were able to learn a visually cued task as quickly and accurately as the unoperated control monkeys, suggesting that the SMA mediates volitional actions. Taken together, lesion studies in monkeys revealed the medial premotor cortex (supplementary motor area, SMA) to be necessary for self-initiated actions and not for actions that are prompted by visual cues. Conversely, the lateral premotor cortex is involved with externally triggered actions but not with internally generated actions.

Neuroimaging studies

Studies involving humans furthered the neurophysiological evidence providing more support for the specification of the premotor areas. Goldberg (1985) suggested that the fronto-median cortex appears to be involved in self-initiated actions whereas the fronto-lateral cortex is involved in responsive actions. The distinctions of the premotor area have also been demonstrated in electroencephalography (EEG) studies. There are two negative potentials that have been associated with voluntary and involuntary actions. The *bereitschaftspotential* or readiness potential, a slow negative scalp potential which precedes voluntary movement and is found over the SMA, is thought to reflect voluntary self initiated motor preparatory activity (Deecke, Scheid, & Kornhuber, 1969). Whereas the contingent negative variant (CNV) is thought to be elicited in response to an imperative stimulus and task anticipation (Gaillard, 1977).

Recent neuroimaging studies demonstrated that the dissociation found in non-human primates may not be as clear in human participants. Through various imaging studies, it was found that the medial premotor cortex was activated during both classes of action. However, the pre-SMA was activated significantly earlier during self-initiated actions compared to externally triggered action and is thought to reflect motor preparation. Conversely, externally triggered actions activated the caudal SMA more than the internally triggered actions and the caudal SMA is thought to reflect motor execution (Jahanshahi, Jenkins, Brown, Marsden, Passingham, & Brooks, 1995; Jenkins, Jahanshahi, Jueptner, Passingham, & Brooks, 2000; Cunnington, Windischberger, Deecke, & Moser, 2002).

The localization of these movement types goes beyond the scope of the frontal cortex. The cerebellar loop connects strongly to the lateral premotor cortex and the parietal regions and is involved in sensory-motor transformation (i.e., externally triggered actions). By contrast, the basal ganglia loop has high affinity with the SMA and is involved in the initiation and execution of internally generated actions (Ward, 2006; Haggard, 2008).

Truncation paradigm

While internally generated (IG) and externally triggered action (ET) have been studied in isolation, little is known about how they interact. The series of studies proposed here attempts to investigate the issue of switching between IG and ET action generation

modes, and to identify the underlying mechanisms that govern both types of motor action.

What happens when both an internally generated action and an externally triggered action related processes are occurring simultaneously? Consider this situation, you are about to open a door which requires you to internally prepare the action plan to open a door, then there is a knock on the door and you have to react to that external stimulus and effectively complete the *same* action of opening a door. Obhi & Haggard (2004) created a paradigm to investigate how the underlying mechanisms of these two types of actions interact.

The truncation paradigm consists of three conditions: the internally generated action condition, the externally triggered action condition, and the truncation condition. In the internally generated action condition, participants are asked to internally prepare and make an action (i.e., a key press) at a time of their choosing, within a prespecified temporal window. In the externally generated action (or simple reaction time, SRT) condition, participants are asked to respond to an external stimulus (i.e., an auditory tone) that is presented in the same temporal window as the internally generated action condition, as quickly as possible with the same action (i.e., a key press). Finally, the truncation condition is a combination of the previous two conditions. Participants are asked to internally prepare to make an action (i.e., a key press) in the same temporal window, however if an auditory tone is emitted they are to override their internally prepared action and respond to the tone as quickly as possible with the same action (i.e., a

key press). Simply, there are two types of trials that may arise from this condition; truncation-internal trials and truncation-external trials. In internal trials, participants prepare to make a key press and carry out that action. In the external trials, participants prepare to make a key press but before they complete the key press a tone is presented, which requires them to respond to the tone with the same action (refer to Figure 1a for a schematic depiction of the truncation paradigm). So the question is, can the brain utilize this internal preparation and respond to the tone with the same action faster? No, it appears that subjects are at least 50ms slower to respond to the tone in the truncation condition than in the SRT condition (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005).

This time cost was originally termed the RT cost of intention, but in this thesis I will use the less loaded term “the RT cost of internal preparation”. The RT cost was questioned, and an obvious criticism is that the cost has a dual-task/divided attention cause. Astor-Jack & Haggard (2005) addressed this idea in a series of experiments. In these experiments, the authors ruled out that attentional factors or attenuated processing of the external stimulus accounted for the time cost. Briefly, in an event related potential (ERP) study, auditory evoked potentials were constructed in both the simple reaction time condition (SRT) and the truncation conditions. Two key components of the waveform reflecting perceptual processing of the stimulus (N150 and P300) were actually enhanced in the truncation condition involving a stimulus interrupting internal preparation and there were also no latency differences in the peaks of these ERP components that could explain the RT cost observed. Thus, slowed perceptual processing of the stimulus on

account of divided attention in the truncation condition was not found to account for the RT cost of internal preparation. In a second study, the RT cost of internal preparation was found not to be due to differences in attentional allocation. Astor-Jack and Haggard (2005) suggest that this RT cost is the consequence of a fundamental incompatibility between the mental processes involved in producing a reaction to an external stimulus and the assembly of an internally generated action, even when the actions to be completed are the same.

Experiments one and two

If the RT cost does not reflect attentional allocation or attenuated processing of the imperative stimulus, as suggested by Astor-Jack and Haggard (2005), then the question remains, what is the source of the RT cost? The first two experiments of this thesis attempt to address this question. Specifically, these two experiments were designed to establish whether the RT cost can be localized to motor stages of processing. This was done by varying the motor demands of the response (i.e., unimanual compared to bimanual responses and single compared to serial responses). We hypothesized that if the source of the RT cost is motoric in nature, then the RT cost should increase with more motorically demanding responses. Alternatively, if the RT cost is not related to motor demands, there should not be a corresponding increase in the RT cost for responses with greater motor processing demands and thus we suggest the RT cost would be related to a higher cognitive function.

Experiment three

The third experiment in this thesis is a control experiment to assimilate the external and truncation conditions as closely as possible. During debriefing of the previous experiments (1-6), participants disclosed that they used the strategy of counting subvocally to plan when their internally prepared action was going to be executed in both the internal trials and the truncation trials. Consequently, a new condition (i.e., external-subvocal) was created that required participants to use the same strategy in the external condition as that used in the truncation condition. Specifically, participants were instructed to respond to an auditory tone as quickly as possible, while counting subvocally. Thus, the only difference remaining between the truncation condition and the external-subvocal condition was that the counting had the purpose of planning when the action would be executed in the truncation condition compared to passive counting with no purpose in the external-subvocal condition. If the RT cost is eliminated when comparing the reaction times from the external-subvocal condition to the truncation condition it might be suggested that the RT cost is simply reflective of the dual task of subvocalization. Conversely, if the RT cost remains it might be suggested that it reflects another process, perhaps a higher cognitive function or another form of incompatibility between the preparation for internally generated and externally triggered actions.

Experiment four

The above experiments, as well as past studies involving the truncation paradigm (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005), all dissected the time course of planning and executing the same action. Specifically, they all inspected a situation where

participants prepared to make a single finger key press or a two-finger key press, and occasionally their internally prepared action was interrupted by an auditory tone, to which they responded with the same action (i.e., a single finger key press or a two-finger key press, respectively). Moreover, many studies have explored the time course in which participants switch between actions depending on the stimulus presented, such as stop-signal and antisaccade paradigms (Curtis, Cole, Rao & D'Esposito, 2005; and Munoz & Everling, 2004, respectively). Nevertheless, there seems to be a lack of research investigating the time course for modification of a planned action. This situation would involve some but not all of the prepared motor commands to have access to the appropriate peripheral musculature. Thus, there may be similarities between the processes of action cancellation and action modification, however they are not the same.

Experiment four, used the truncation paradigm to investigate the processes of action modification. Specifically, this experiment was designed to shed light on the time course of adding or inhibiting part of a movement to an internally prepared movement. The ability to modify a planned action is necessary for flexible and adaptive behaviour. It is important to be able to change internal plans (sometimes just partially) in the light of incoming sensory information.

Experiments five and six

An important aspect of action cancellation has been neglected in the literature: cancelling an internally generated action plan or a mental process of preparing to act. There have been many studies that have investigated the time course of cancelling an action made in response to an external stimulus, such as stop signal paradigms (Rubia, Overmeyer,

Brammer, Bullmore, Sharma, Simmons, Williams, Giampietro, Andrew, & Taylor, 2001). A typical stop signal paradigm consists of a go signal instructing participants to respond as quickly as possible. On approximately 50% of the trials a stop signal is presented after the go signal, indicating to the participant to cancel their action. The SOA between the go signal and the stop signal is varied to examine the time course of cancelling an action made in response to an external stimulus. Nonetheless, there is little research that has investigated the time course of cancelling an internally planned action. Experiment five and six altered the original truncation paradigm (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005) to include two new conditions, external-cancel and truncation-cancel conditions. The key difference to these conditions is the addition of a cancellation tone (i.e., a lower frequency tone) before the high tone that requires a response. Specifically, the present experiment attempts to discover at what point the reaction times in the truncation condition are no longer different to the reaction times in the external condition. This would suggest that at that point (i.e., when the RT cost is eliminated), an internally prepared action or a mental process has been cancelled.

Experiment 1 and 2: Switching between Internal and External Triggers for Action

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Author Contributions:

The study was designed by Dr. S.S. Obhi and Shannon Matkovich. Shannon Matkovich programmed the experiment, collected and analyzed all data. Shannon Matkovich wrote the paper with assistance from Dr. S.S. Obhi.

Experiment 1 - Unimanual versus Bimanual Responses

The ability to balance actions made from within (internally generated actions) with those made in response to external stimuli (externally triggered actions) is fundamental to everyday life. What happens when an internally generated action is competing with an externally triggered action? Specifically, does the internal preparation for a specific action facilitate performance of an identical action made in response to an intervening stimulus?

Previous work suggests that internal preparation delays a reaction requiring the same movement by approximately 50 ms (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005). In their paper, Obhi and Haggard (2004) introduced the ‘truncation’ paradigm as a useful experimental approach to examining the relationship between the systems involved in preparing internally generated and externally triggered actions. Briefly, there are two critical conditions in this paradigm: In the simple reaction time condition (SRT) or external condition, subjects are given a warning stimulus (WS) and told to react as quickly as possible to a tone that can occur at unpredictable times within a certain time window after the WS (e.g., 3-10 seconds after the WS). Reaction times (RTs) are recorded as the dependent measure. The other critical condition is the ‘truncation’ condition. In this condition, subjects are again given a WS, but this time they are instructed to make an internally generated key press at a random time of their own choosing again within a particular time window after the WS. The critical manipulation is the occurrence of a tone, on a proportion of trials, in response to which subjects are instructed to make the very same key press as quickly as possible. Hence, a situation is

set up in which the subject is internally preparing to press the key at a particular time, but must then press the key as quickly as possible if a tone occurs, in so doing, overriding their internal plans. On approximately half the trials the subject actually makes the internally generated key press prior to the tone and this terminates the trial. By comparing the RTs in the SRT condition to the RTs in the truncation trials where a tone interrupted the ongoing internal preparation, it is possible to elucidate the potential relationship between the systems underlying internally generated and externally triggered actions. The robust result is that the presence of an internal preparation to make a key press makes subjects slower (by approximately 50 ms) than SRT levels when they have to respond to a tone with the same key press. Thus, there is a “RT cost of internal preparation” (c.f., Obhi & Haggard, 2004).

One potential explanation for the RT cost is that in the situation where a participant prepares to make a self paced action and is interrupted by an intervening stimulus prompting the same action, they are dividing their attention over two processes (internal preparation, and monitoring for an external stimulus). This may have the effect of delaying perceptual processing of the intervening stimulus, thus increasing RT. However, Astor-Jack and Haggard (2005) ruled out this possibility in two experiments. First, in an experiment where participants were instructed to prioritize the processing of the external stimulus (i.e., direct attention to the stimulus) the RT cost of internal preparation remained suggesting that simple division of attention does not account for the observed cost. Second, in an electroencephalography (EEG) experiment, event related potentials in the SRT and the truncation conditions, showed that two key components of the

waveform, reflecting perceptual processing of the stimulus (N150 and P300) were actually enhanced in the condition involving a stimulus interrupting internal preparation. Additionally, there were no latency differences in these components of the ERP waveform that could explain the RT cost observed. Hence impaired perceptual processing of the stimulus on account of divided attention in the truncation condition was not found to account for the RT cost of internal preparation.

Hence the RT cost of internal preparation remains to be explained. The current experiments were designed to determine if the RT cost of internal preparation is localized to the motor programming stage of processing. We investigated this by varying the motor programming demands of the actions required from participants. We defined more demanding motor responses as bimanual or serial responses, and less demanding responses as unimanual. It is important to be clear about what is meant by programming demands in this context. We operationalize this term to mean the degree of motor programming underlying a particular movement task. Hence, we suggest that a bimanual task requiring simultaneous flexions of both index fingers places greater demands on motor programming than either of the unimanual constituent movements made alone. The same logic is applied to the case of serial responses versus single responses. This idea gains support from previous studies that have compared bimanual versus unimanual reaction times and serial versus single action reaction times and shown increased RTs for bimanual and serial responses compared to unimanual responses (e.g., Shen & Franz, 2005; Hughes & Franz, 2007; Sternberg, Monsell, Knoll, & Wright, 1978).

In Experiment 1, the original “truncation” paradigm (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005) was employed and the RT cost for unimanual responses were compared to the RT cost of bimanual responses. Again, in the original paradigm, the key conditions are an SRT (also called “external”) condition and a truncation condition. In SRT conditions participants simply respond with a key press to an unpredictable tone that occurred within a 3-10 second window post trial onset. In truncation conditions, participants prepare to make an index finger key press at a time of their own choosing within a 3-10 second window post trial onset, but are interrupted by a tone on approximately 50% of trials. In such cases, participants are required to respond to the tone with exactly the same action that they were preparing internally, as fast as possible. Reaction times from this condition (termed “truncated RTs”) are compared with those from the SRT condition, and are found to be consistently longer. The difference in truncated RT and SRT is termed the RT cost of internal preparation. In the present experiments, it was reasoned that if the RT cost increases for actions that are motorically more demanding, then the RT cost of internal preparation is linked to central motor programming processes. Conversely, if the RT cost does not increase as motor programming demands increase this would support the idea that the RT cost is unrelated to motor programming processes.

Finally, in the present paradigm, participants are asked to switch from an internally generated to an externally triggered mode of response production. They are specifically asked to make the **same** response they were internally preparing, if interrupted by the tone. Of course, as Bernstein (1967) famously noted, no two movements are ever exactly

identical. Hence, when we refer to “same” movements in the present study, we mean that the movements that are switched between are best considered as motorically similar, functionally equivalent and intentionally identical. To be clear, this operationalization allows for the variability inherent in repeated movements, the fact that the same goal of pressing the key(s) is being achieved, and the fact that participants are intending to make the same action within an experimental condition.

Method

Participants: 16 healthy subjects (20 ± 3 years, 5 males, 11 females) took part in an experiment for monetary compensation or course credit. The experiment was carried out in accordance with local ethics guidelines and informed consent was obtained from all participants.

Procedure: Participants performed unimanual and bimanual key presses either in response to an external cue or under their own volition during three- to ten-second intervals. In all conditions, subjects sat at a computer with their right index finger placed lightly on the “/” key and their right middle finger placed lightly on the “Z” key. The experiment comprised six conditions: two external (SRT) conditions, two internal conditions, and two truncation conditions. In the external conditions, participants responded as quickly as possible to an auditory tone, which was presented at unpredictable times within a 3-10 second temporal window. The presentation of the auditory tones was 3000ms-9650ms increasing with 350ms increments. In the internal conditions, participants were instructed to internally prepare and execute a key press

within the same temporal window. The data from the internal trials were not included in the analysis as they served mainly to provide participants with experience for making self-paced movements. Lastly, in the truncation condition, participants were instructed to internally prepare to make a key press within the same 3-10 second temporal window. However, in this condition, on some trials participants executed their internally prepared key press which terminated the trial, whereas on other trials their internal preparation was interrupted by an auditory tone, which required the participants to respond with the same movement they were internally preparing. The auditory tones were presented at unpredictable times within the same 3-10 second temporal window. Specifically, we had a pool of 20 different tone times within the 3-10 window and a computer program randomly selected from this pool for each trial of the experiment. The number of trials in the truncation condition was twice that of the SRT condition, due to the expectation that, approximately half the time, participants would make their action prior to delivery of a tone, and would be interrupted by the tone on the other half of trials. The conditions were blocked and in some blocks participants responded with a unimanual key press (right index finger) on the “/” key whereas in others they responded with a bimanual key press: right index finger on the “/” key and the left index finger on the “z” key.

Participants were told at the beginning of the external blocks that sometime between 3-10seconds a tone will sound; respond to the tone as fast as possible. For the internal blocks, participants were instructed to make an internally prepared key press sometime between 3-10seconds. Randomly vary the time of your key press for each trial and try and use the whole temporal window. Finally, participants were instructed to internally

prepare to make a key press sometime between 3-10seconds and vary the time of their internally prepared key press. However, on occasion they may hear a tone before they make their internally prepared key press, respond to the tone as fast as you can.

The order of the conditions was such that the participants completed an internal, external and truncation condition which they responded with one movement type (i.e., unimanual response) and then completed an internal, external and truncation condition which they responded with the remaining movement type (i.e., bimanual response). The order of response type was counterbalanced across subjects. The internal and external blocks were randomized using DirectRT software and were always the first and second block out of three. The truncation condition was always last as it encompassed details of both the internal and external conditions. That is, in the present study we chose to run the most complex condition last, and only counterbalanced the first two conditions. Comparing the results of the present experiment to other experiments from our lab in which we fully randomized or counter-balanced the order of internal, external and truncation conditions reveals no differences in the overall pattern of results observed, so we are quite sure the ordering of conditions in the present study would not present any problems for interpretation of the data. In all other ways, the general procedure is the same to that employed in previous studies (Obhi & Haggard, 2004, Obhi et al, 2009).

Key presses were recorded with a precision of 1ms using DirectRT software and customized hardware. In accordance with previous studies (Astor-Jack & Haggard, 2005) a 100 ms 1 kHz auditory tone was presented in all conditions which required a reaction.

There were 40 trials in each of the external and internal blocks and 80 trials in each of the truncation blocks with the expectation that 40 trials would result in internal trials and 40 trials would result in truncation-external trials. Only external trials and truncation-external trials were used in the analysis. Lastly, only reaction times from the right index finger press were compared across conditions.

Results

In accordance with previous studies (Obhi & Haggard, 2004 and Obhi, Matkovich & Gilbert, 2009), reaction times were trimmed at 75ms and 1000ms as they represent anticipated and missed trials respectively. This resulted in a total loss of 1.09% of trials. This trimming criterion was used to maximize comparability across studies, especially a very recent study (Obhi et al, 2009) which also used the same lower and upper boundaries on RT, even though RT measures were not obtained using EMG.

Additionally, only the reaction times from the right index finger were compared across conditions. That is, in bimanual trials, the RT measure was the RT of the right index finger. This ensures that we were always comparing RTs from physically similar actions. The remaining external and truncation-external trials for unimanual and bimanual responses were entered into a 2 x 2 repeated measures ANOVA (condition: external, truncation external; response type: unimanual, bimanual).

Breakdown of data

For unimanual responses, the percentage of truncation-external trials versus truncation-internal trials was 41% compared to 58% respectively. The percentage of truncation-external trials versus truncation-internal trials for bimanual responses was 38% compared to 61% respectively.

Main effects and interaction

There was a main effect of the condition factor indicating that reaction times from the truncation external trials were on average significantly longer than reaction times in external trials ($F_{1,15} = 32.895$, $p < .0001$), replicating the RT cost of internal preparation that has been found in previous studies (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005). There was also a main effect of response type where bimanual movements on average took longer to produce than unimanual responses ($F_{1,15} = 5.378$, $p < .035$). Crucially, it appears the RT cost of internal preparation is not significantly different for unimanual and bimanual responses as there was no condition x response type interaction ($F_{1,15} = 2.496$, $p = .135$).

Planned paired t-tests

Three planned paired t-tests were performed to further examine the main effects. The first test comparing unimanual external trials with bimanual external trials, confirmed that bimanual responses are significantly more motor demanding than unimanual response ($t(15) = 3.249$, $p = .005$). Figure 1b illustrates the significant differences between the unimanual and bimanual response types in the external condition. The second test

confirmed that for both unimanual and bimanual responses, reaction times increased significantly in truncation-external trials compared to external trials ($t(15) = 6.003$, $p < .0001$ and $t(15) = 4.727$, $p < .0001$, respectively). Critically, as suggested by the non-significant interaction of condition \times response type, the RT cost of internal preparation was not significantly different for unimanual responses compared to bimanual responses ($t(15) = -1.594$, $p = .132$), suggesting that the RT cost of internal preparation does not arise in relation to the motor demands of the task. Figure 1c depicts this similar RT cost for unimanual and bimanual responses. The reaction times from unimanual SRT and unimanual truncation as well as bimanual SRT and bimanual truncation conditions are depicted in Figure 1d.

Figures 1e and 1f display the reaction times of each condition versus binned (four tone onsets per bin) auditory tone onset (tone onsets ranged from 3000ms-9650ms, and increased by 350ms increments), illustrating increased reaction times in the truncation condition compared to the external condition for the first three binned groups for unimanual responses and for the first four groups for bimanual responses (all tests, $p < .05$). Hence, there was an RT cost of internal preparation for earlier auditory tone onsets and it appears the RT cost dissipates for auditory tone onsets later in the foreperiod.

It might be thought that the ordering of conditions in this experiment affected the results. However, we point out that previous studies have counterbalanced the three conditions (internal, external and truncation) and found statistically similar results (for one finger

movements) to those reported here (Obhi & Haggard, 2004). Hence we are quite sure that running the truncation condition last did not contribute to our observed effects. Again, the rationale for running this condition last in the present experiment was because it consists of elements of both the internal and external conditions, and participants therefore has ample experience in the “constituent” conditions prior to doing the “hybrid” truncation condition.

Discussion

The present results confirm the RT cost of internal preparation found in previous studies (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005). That is, slowed reaction times were found in the truncation condition comparatively to the external condition for both unimanual and bimanual responses. Interestingly, the RT cost was not statistically different for unimanual and bimanual responses, even though the more motorically demanding responses (i.e., bimanual responses) took significantly longer to complete than the simple responses (i.e., unimanual) in the external condition. This is in accordance with past studies (Shen & Franz, 2005), that report that bimanual reaction times are typically greater than unimanual reaction times.

The finding that the RT costs are statistically indifferent suggests that this cost may not be reflective of motor processing because if it were then the changes in motor demands would most likely affect the RT costs. To be clear this was not observed in the present results, suggesting the RT cost may reflect a high order cognitive function. Such a time consuming cognitive process may be switching between internal triggers and external

triggers for the same action which may be reflected in the RT cost of internal preparation (Burgess, Dumontheil & Gilbert, 2007).

Experiment 2 – Single versus Serial Responses

We performed a second experiment to confirm the result of the first experiment, that the source of the RT cost is not related to motor programming stages of processing.

However, in this experiment we modified our manipulation of motor programming demands by requiring a single index finger key press (a single finger response) in one condition, and a right index finger key press followed by a right middle finger key press (a serial finger response) in the second condition. This approach incorporates the fact that the reaction time for the first element in a multi-element movement sequence is greater than the reaction time of the same element when performed alone or in a shorter sequence (e.g., Sternberg et al., 1978). Through a series of studies involving tapping or typing, Sternberg et al., (1978) proposed the subprogram retrieval model. It assumes that an action sequence is programmed entirely before sequence execution. Later, during sequence execution, participants serially search their planned sequence for the first unit to be executed and then complete this serial search for all subsequent units. These authors argue that as the action sequence increases this search processes is more time consuming, thus there is an observed increase in reaction time that corresponds to increased sequence length. Hence, a multi-element sequence can be considered to be more demanding in motor programming processes than a single element sequence, and if the RT cost is a function of programming demands, then it should differ across the two conditions.

Method

A partial replication of Experiment 1 was completed where 12 healthy subjects (22±3 years, 2 males, 10 females) took part in an experiment with the following changes: participants made a single key press on “B” and a serial key press with the right index finger pressing “B” followed by the right middle finger pressing “N”. In all conditions, subjects sat at a computer with their right index finger placed lightly on the “B” key for single responses and their right index finger placed lightly on the “B” key with their right middle finger placed lightly on the “N” key for serial responses. The experiment consisted of the same six conditions as employed in experiment one, however they were quasi randomly arranged across participants to avoid order effects.

Results

Breakdown of Data

For single responses, the percentage of truncation external trials versus truncation internal trials was 50% compared to 50% respectively. The percentage of truncation external trials versus truncation internal trials for serial responses was 48% compared to 52% respectively.

Main effects and interaction

The same exclusion criteria used in Experiment one were used in this experiment to preprocess the data resulting in a loss of less than 1% of trials. A 2 x 2 repeated measures ANOVA with the factors response (single and serial responses) and condition (external and truncation conditions) was again run on the RT data. There was a main effect of

response type, as well as condition, ($F_{1,11}=14.23$, $p=.003$ and $F_{1,11}=27.241$, $p<.001$ respectively). The reaction times from single SRT and single truncation, as well as serial SRT and serial truncation conditions are depicted in Figure 2a.

Planned paired t-tests

With further analysis through planned paired t-tests, it was found that serial action external trials took significantly longer to initiate than single action external trials ($t(11) = 4.816$, $p=.001$) as depicted in Figure 2b. In addition, both single finger and serial finger responses resulted in an RT cost of internal preparation when comparing external trials to truncation-external trials ($t(11) = 5.216$, $p<.001$ and $t(11) = 4.299$, $p=.001$, respectively). Of particular interest, Figure 2c illustrates that the RT cost for single finger responses is not statistically different from the RT cost for serial finger responses ($t(11) = -1.666$, $p=.124$), thus replicating the results from Experiment one and suggesting that the source of the RT cost cannot be isolated to the motor programming stage of processing.

Discussion

The present findings confirm the results found in the previous experiment. Briefly, the more motorically demanding responses (i.e., serial response) had greater reaction times in the external condition comparatively to the simpler responses (i.e., single response) and the RT cost of internal preparation was present for both single and serial responses. Additionally, the RT cost was not statistically different between the single and serial responses suggesting that the RT cost does not reflect motor processing.

Furthermore, the RT cost found in the first experiment, does not appear to reflect order effects, as the RT cost remained present in the second experiment even though the three conditions (external, internal, and truncation) were quasi randomized.

Overall Discussion for Experiments One and Two

In two experiments, 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. The findings from these experiments confirm previous results (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005; Obhi et al., 2009) suggesting that internal preparation for the self paced production of a specific action does not facilitate performance of a motorically similar, functionally equivalent action made in response to an intervening stimulus. In both experiments we observed slowed reaction times in a truncation condition (i.e., when subjects were preparing an action internally and had to override this preparation and respond with the same movement to an intervening stimulus) compared to an external condition (i.e., when subjects are responding to an auditory tone as quickly as possible).

A closer look at the Figures 1e & 1f depicting the reaction times for the binned auditory onsets and condition, it appears that the RTs actually decrease as the duration of the preparatory period increases, however RTs appear to be evenly distributed throughout the preparatory period in the external condition. It is hard to say anything concrete about this pattern of RTs without knowing the participant's intended time of key press on each trial. However, we have carried out other experiments (in preparation) in which the intended

time of action is known, that suggest that the RT cost diminishes as time of intended key press approaches. Such a pattern of results is inconsistent with an account of the RT cost that invokes ideas related to dismantling internal preparation prior to being able to react (e.g., Astor-Jack & Haggard, 2005), as these accounts predict an increasing RT cost as intended time of movement approaches. Furthermore, this notion is also in line with the central tenet of the present two experiments, which is that, increases in motor programming demands, do not affect the time required to switch between an internal and external mode of action production. So a mechanism for the switch cost that involves dismantling of “additional motor preparation” prior to a reaction seems unlikely, given that the amount of dismantling would be greater (and hence predict a greater RT cost) for more demanding movements; a result which we do not observe.

This RT cost has been observed previously and suggests that internally generated actions and externally triggered actions do not involve fully independent preparatory mechanisms (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005, Obhi et al., 2009). This is because if these two classes of action could be prepared fully independently, there would be no cost associated with engaging in internally driven and externally cued action preparation processes simultaneously. Early lesion studies involving primates suggest that there is a sharp dichotomy between the motor preparation systems that mediate internally generated and externally triggered actions (Passingham, 1987). In contrast, 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 such as the pre-

supplementary motor area (Pre-SMA, Cunnington, Windischberger, Deecke, & Moser, 2002; Lee et al, 1999; Deiber, Honda, Ibanez, Sadato, & Hallett, 1999).

The present results extend previous findings in that we found that the RT cost is not significantly different for conditions involving a simple movement (a unimanual or single key press) compared to those requiring a more motorically demanding movement (a bimanual or serial key press, respectively). Again, bimanual responses and serial responses are more demanding because they require additional motor programming compared to unimanual actions. This increase in motor programming demands is reflected in greater RTs. Critically, the cost of switching between an internal and an external mode (in response to presentation of the auditory tone) was not affected by these additional demands. It is interesting that there is a trend towards a larger RT cost for the simple movements compared to the more motorically demanding movements. This result is difficult to explain, but is robust, as we have carried out another experiment using a three element sequence in which the same pattern is observed. There may be something unique about one finger actions, but at present, we cannot explain why the trend is for the cost to be smaller for more complex movement types. However, this pattern confirms that the cost is not a function of increasing motor programming demands. Thus the pattern of RT cost suggests that the cost of switching may be independent of specifically motor preparatory processing and thus does not relate directly to motor programming processes.

There are at least two potential mechanisms that could account for the results in the present study. First, we suggest that a higher cognitive process may involve a mechanism

that switches access to motor output between an internal and an external trigger. There is evidence that the rostral prefrontal cortex (BA 10) might be involved in switching between external and internal sources of information (Gilbert, Frith & Burgess, 2005). In particular, these authors used functional magnetic resonance imaging (fMRI) and engaged participants in a task which required them to process externally provided information in some phases of the experiment, and to do the same task using internally generated information in other phases. These authors found a transient increase in lateral rostral prefrontal cortex activation when participants switched from doing the task using external information to doing the task using internal information. Our contention is that the “high level” cognitive switch between internal triggers and external triggers for the same action, perhaps mediated by the rPFC is a time consuming process, accounting for the observed RT cost (Burgess, Dumontheil & Gilbert, 2007). A second possibility which doesn’t necessarily invoke rPFC relates to the role of the pre-SMA in action generation. It is known that the pre-SMA is involved in internally generated action preparation (through its role in the basal ganglia-thalamo-cortical circuit) and also in the inhibition of action (e.g., Chen et al, 2009). Thus, another potential mechanism is that, during self-paced preparation to act, the pre-SMA is involved in inhibiting all motor output to avoid premature movement. Production of a movement prompted by an external stimulus within this period of inhibition would be subject to time costs involved with removing the inhibition, and this could manifest as the RT cost of internal preparation. However, further experiments, possibly employing the application of transcranial magnetic stimulation over the pre-supplementary area and measuring the effects on the RT cost are needed to address this possibility.

In summary, we found that production of action is delayed when self-paced preparation for the same action is interrupted by a temporally unpredictable external cue, but the magnitude of this delay is not influenced by the motor programming demands of the action. We therefore suggest two potential accounts for the RT cost of internal preparation. First, the cost could reflect a time consuming trigger switch cost between internal and external triggers for action and, on the basis of mounting imaging evidence, this switching process may depend on the lateral rostral prefrontal cortex. Second, the cost could reflect the time required for the removal or dissipation of inhibition applied to motor output structures during the preparatory period. Future studies employing the truncation paradigm and using fMRI and TMS are needed to confirm these suggestions.

Experiment 3 – Subvocal Truncation

The effects found in the truncation paradigm are interesting, although based on debriefing there is the potential problem referring to dual task effects of subvocalization that may be a confound in this paradigm. Dual-tasks are used in the literature to investigate if two tasks share cognitive processes. For example, it is rather easy to pat your head and read aloud simultaneously, thus suggesting these two tasks share little cognitive mechanisms. Moreover, it is very easy to rub you stomach or pat your head separately, however it is rather difficult to do both simultaneously. In the latter example, there is a decrement in performance associated with patting your head and rubbing your stomach simultaneously, suggesting that these two movements share cognitive processes a concept termed dual-task interference.

A commonly used dual task paradigm is the dichotic listening task. A typical dichotic listening task requires participants to wear headphones and they receive different messages to each ear. After asking participants to attend to the message in one ear, they can remember almost nothing about the message sent to the unattended ear, not even the language spoken (Broadbent, 1952), thus suggesting dual-task interference as evident from the decrement in performance of the unattended ear.

The dichotic listening task was varied slightly by Allport, Antonis & Reynolds (1972), in such a way that participants were asked to shadow an auditory message while simultaneously being presented with visual or non-verbal images (i.e., words or pictures). These authors found that recognition of the visual words was affected greatly by the

divided attention condition. However, recognition of the pictures during the divided attention task was much less affected. This would suggest more shared cognitive processes between the shadowed auditory message and with the visual words than the non-verbal images resulting in larger interference effects seen with the visual words condition.

As a control, the present experiment was conducted to assimilate the external and truncation condition. During debriefing of previous studies (Experiments 1-6), many participants reported using the strategy of counting subvocally to plan when their internally prepared key press was going to occur in both the internal condition (participants always made a key press at a time of their own choosing) and the truncation condition. Consequently, the present study created a new condition, external-subvocal condition, in addition to the original truncation paradigm (Obhi & Haggard, 2004). Participants were instructed to respond to an auditory tone as quickly as possible, while counting subvocally, in this new condition. As a result, the only difference between the truncation condition and the external-subvocal condition was the fact that the passive counting had a purpose in the truncation condition (i.e., it was used as a strategy in planning an internal action) compared to a simple dual task in the external-subvocal condition (i.e., there was not a purpose to counting subvocally). Therefore, if the RT cost is simply the result of a dual task effect due to counting it should be eliminated when comparing the reaction times from the truncation condition to the reaction times from the external-subvocal condition. Conversely, if the RT cost is not eliminated, then RT cost may reflect a qualitatively different process, perhaps at a higher order cognitive stage of

processing, or an incompatibility between the preparation of internally generated and externally triggered actions.

Method

Participants: 12 healthy subjects (23 ± 9 years, 5 males, 7 females) took part in an experiment for monetary compensation or course credit. The experiment was carried out in accordance with local ethics guidelines and informed consent was obtained from all participants.

Procedure: The experimenters employed four conditions which were arranged into four blocks and quasi randomly arranged across participants to avoid order effects. In all conditions, subjects sat at a computer with their right index finger placed lightly on the “B” key. Specifically, participants completed one external condition, one external – subvocal condition, one internal condition, and one truncation condition. In the external conditions, participants responded to an auditory tone, which was presented within a one- to six-second temporal window, as quickly as possible. The presentation of the auditory tones was 1250ms-5750ms increasing with 350ms increments. In the external – subvocal condition, participants were told to respond to the auditory tone, which was presented within a one- to six-second temporal window, while counting subvocally to themselves during the trial. In the internal conditions, participants internally prepared and executed a key press within the same temporal window. The data from the internal trials were not included in the analysis as they served mainly to provide participants with experience for making self paced movements. Lastly, in the truncation condition, participants internally

prepared to make a key press within the same temporal window. However, in this condition, on some trials participants executed their internally prepared key press which terminated the trial, whereas on other trials their internal preparation was interrupted by an auditory tone, which required the participants to override their internal preparation and respond with the same movement they were internally preparing. In view of this, the number of trials in the truncation condition was twice that of the external and external-subvocal conditions. The conditions were blocked and in all conditions participants made a right index finger key press on the “B” key.

Participants were told at the beginning of the external blocks that sometime between 1-6seconds a tone will sound; respond to the tone as fast as possible. Participants were instructed to respond to the tone as quickly as possible while counting passively. For the internal blocks, participants were instructed to make an internally prepared key press sometime between 3-10seconds using the strategy of counting subvocally. Randomly vary the time of your key press for each trial and try and use the whole temporal window. Finally, participants were instructed to internally prepare to make a key press sometime between 1-6seconds and vary the time of their internally prepared key press using the strategy of counting subvocally. However, on occasion they may hear a tone before they make their internally prepared key press, respond to the tone as fast as you can.

In accordance with a previous study (Astor-Jack & Haggard, 2005) there were 20 trials in each of the external blocks and the internal block. There were 40 trials in the truncation - block, with 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 the participants' internal preparations prompting a response.

Furthermore, we did not match the foreperiods between external blocks and truncation block (Astor-Jack & Haggard, 2005; Obhi et al., 2009) as this does not appear to impact the RT costs. During debriefing participants revealed that although they were merely counting passively during the external – subvocal condition, they reported knowing when the auditory tone was presented with respect to their counting.

Additionally, participants completed six practice truncation trials. Participants were welcome to repeat the practice trials until they felt comfortable with the task and the experimenter agreed they were executing the task correctly. In all conditions involving a reaction, a 100ms 1 kHz auditory tone served as the tone. All stimuli and reaction times were recorded using DirectRT and custom response hardware, which provided timing precision of 1ms.

Results

In accordance with Obhi and Haggard (2004), reaction times were trimmed at 75 ms and 1000 ms as they represent anticipated and missed trials respectively. This resulted in a total loss of 1.17% of trials. These trimming criteria were used for reaction times to facilitate comparison of the present study to earlier studies using the truncation paradigm

(Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005; Obhi et al., 2009). The remaining external and truncation-external trials were entered into a one factor (condition: external, external – subvocal, and truncation) repeated measures ANOVA.

Breakdown of data

The percentage of truncation external trials versus truncation internal trials was 50% compared to 50% respectively.

Main effect

There was a main effect of the condition factor indicating that reaction times from the truncation external trials were on average significantly longer than reaction times in both types of external trials ($F_{2,10} = 4.518$, $p = .040$), replicating the RT cost of internal preparation that has been found in previous studies (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005).

Planned paired t-tests

Three planned paired t-tests were performed to further examine this main effect. The first test revealed that reaction times in external-subvocal trials were on average longer than external trials ($t(11) = 2.833$, $p = 0.016$). As suggested by the main effect, truncation external trials were significantly slower than external trials ($t(11) = 3.096$, $p = .010$). Interestingly, truncation external trials yielded on average significantly longer reaction times than external-subvocal trials ($t(11) = 2.833$, $p = .016$) suggesting that the RT cost is

not the result of a dual task (i.e., due to the additional load of a subvocal counting process). Refer to Figure 3 for a depiction of the reaction times from all three conditions.

A planned paired t-test confirmed that the RT cost found when comparing the external reaction times and truncation reaction times was significantly larger than the RT cost found when comparing the external-subvocal condition reaction times to the truncation reaction times ($t(11) = 2.833, p=.016$).

Discussion:

The presence of the RT cost of internal preparation found in the present experiment confirms previous research (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005; Obhi et al., 2009). Concisely, participants were preparing to make a key press on their own volition, if this preparation was interrupted by an intervening stimulus to which they had to respond with the same action, they were slower to respond to that stimulus than in a simple reaction time condition where they were simply responding to the same stimulus as quickly as possible.

Interestingly, through the addition of the external-subvocal condition, we were able to assimilate the strategies used in the external and truncation condition. The RT cost was smaller when comparing the external-subvocal reaction times to the reaction times from the truncation condition than the RT cost found when comparing the external reaction times to the truncation reaction times. However, the RT cost was present in both conditions. These results suggest that that the RT cost of internal preparation does not

completely reflect the demands of the secondary task of counting subvocally. If this were the case, the RT cost should have been eliminated when comparing the reaction times from the external-subvocal condition and the reaction times from the truncation condition because the dual-task interference should have been equal in both conditions. To be clear, this was not the case; the RT cost remained even in the presence of a dual task (i.e., due to the additional load of a subvocal counting process).

These results further support the notion that some, but not all, of the underlying processes of internally-prepared actions are common to the processes underlying externally triggered actions, at the very least when the same motor output is required. Similar to the argument of dual task interference, if these two modes of action (i.e., internally generated and externally triggered actions) were fully independent, then one would not expect to see a cost associated with engaging both internally generated and externally triggered action preparation processes simultaneously. Although early primate studies suggest there is a sharp dichotomy between the motor preparation systems underlying these two modes of action (Passingham, 1987), more recent neuroimaging studies involving human subjects suggest a similar network of brain structures may mediate the production of both modes of action preparation (Cunnington et al., 2002).

In sum, the present results suggest that the RT cost of internal preparation does not reflect the dual task of counting subvocally (a strategy commonly used in the truncation condition to plan the internally prepared action) as evident from the presence of the

residual RT cost when comparing the reaction times from the external-subvocal condition to the reaction times of the truncation condition.

Experiment 4: Modification of Planned Actions

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Experiment 4 – Modification of Planned Action

All of the previous studies using the truncation paradigm (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005; Experiments 1-3) have investigated the time course associated with changing from internally generated actions to externally triggered actions involving the **same** movement. Thus, it is necessary to examine the time course associated with modifying an action on the basis of an external prompt. Consider the following scenario: a cyclist is going to work and as they near their destination, they begin to slow their pedaling 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 maneuver. 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 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.

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 & Cowan, 1984; Corneil & Elsley, 2005; Ito, Stuphorn, Brown & Schall, 2003; Coxon, Stinear & Byblow, 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, Cole, Rao & D'Esposito, 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 & Everling, 2004). These studies have demonstrated the importance of frontal lobe regions, particularly lateral prefrontal cortex, in this process (e.g. Ford, Goltz, Brown & Everling, 2005; Nyffeler, Müri, Bucher-Ottiger, Pierrot-

Deseilligny, Gaymard, & Rivaud-Pechoux, 2007). In contrast, other studies implicate posterior parietal regions in rapid alteration of behavior, for example when the target of a reaching action switches from one location to another (Pisella, Gréa, Tilikete, Vighetto, Desmurget, Rode, Boisson, Rossetti, 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 study, the original truncation paradigm was employed with the addition of a modified truncation condition (please refer to the introduction, page 9, for the original truncation paradigm). 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

Participants: 12 healthy subjects (23±4 years, 9 females, 3 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.

Procedure: 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 8 conditions which were arranged in blocks and quasi randomly arranged across participants to avoid order effects. Specifically, participants completed two internally generated action blocks, two external 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 serial key press(es)) within a 3-10 second 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 external 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 second window post trial onset (3000ms-9650ms increasing with 350ms increments).

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 & Haggard, 2004; Astor-Jack & 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 serial (right index followed by right middle finger) response if the tone interrupted their preparation (add a movement condition), or, they prepared to make a serial (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.

Participants were told at the beginning of the external blocks that sometime between 3-10seconds a tone will sound; respond to the tone as fast as possible. For the internal blocks, participants were instructed to make an internally prepared key press sometime

between 3-10seconds. Randomly vary the time of your key press for each trial and try and use the whole temporal window. Finally, participants were instructed to internally prepare to make a key press sometime between 3-10seconds and vary the time of their internally prepared key press. However, on occasion they may hear a tone before they make their internally prepared key press, respond to the tone as fast as you can.

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 & 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 1ms.

Results

In accordance with a previous study (Obhi & Haggard, 2004) reaction times that were less than 75 ms or greater than 1000 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 & Haggard, 2004; Astor-Jack & 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 external reaction times

As Figure 4a illustrates, a planned paired samples t-test revealed that right index finger reaction times from the serial movements (right index finger followed by right middle finger key press) were significantly greater than right index finger reaction times when they were performed alone (mean right index finger RT (single) = 216 ± 76 ms, mean right index finger RT (sequence) = 257 ± 74 ms, $t(11) = 5.350$, $p < .0001$).

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 serial 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 external conditions

On the basis of previous results (Obhi & Haggard, 2004; Astor-Jack & 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 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 external condition ($t(11) = 5.766$, $p < .0001$). This was also true for the condition in which a right index followed by right a middle finger sequential movement was internally prepared and executed in response to a tone compared to the external condition involving the serial response ($t(11) = 4.117$, $p = .002$). Interestingly, 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 serial responses ($t(11) = 3.763$, $p = .003$; single response cost = 98 ± 59 ms, serial response cost = 65 ± 55 ms). 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).

Comparison between the 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 X 2 ANOVA was performed with the factors of “Type of Movement Planned” (single, serial) and “Type of Movement Executed” (single, serial). This test revealed a main effect for the type of movement planned and the type of movement executed factors ($F_{1,11} = 11.768, p=.006$ and $F_{1,11} = 15.126, p=.003$ respectively). There was also a significant Type of Movement Planned X Type of Movement Executed interaction ($F_{1,11} = 14.661, p=.003$). 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; $t(11) = -3.886, p=.003$). The Type of movement planned X Type of movement executed interaction is shown in Figure 4b.

Discussion

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 & Haggard, 2004; Obhi & 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. 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.

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 & 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, Windischberger, Deecke, & Moser, 2002; Lee et al, 1999; Deiber, Honda, Ibanez, Sadato, & Hallett, 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).

Compared to a simple reaction time condition, extra time is required to produce a motor response, even when that response is identical to one being internally planned. 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 & Haggard, 2004; Astor-Jack & 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, Styles & Hsieh, 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 & 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 & 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, Frith, and Burgess (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.

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.

Experiment 5 – Cancelling an Internally Planned Action

It would be maladaptive to go through life only doing what you want to do and never considering the environment surrounding us. Thus, cancelling an internally prepared action on the basis of environmental cues is necessary for adaptive behaviour. Following is an example that considers such a situation. A driver is driving along the highway. He is aware his exit is coming up shortly and begins to internally prepare a lane change. Before he makes his lane change he decides to check his blind spot and sees a car right beside him. He has to cancel his internally prepared lane change. It is crucial that he cancels his internally prepared action because if it is not cancelled an accident may result.

Despite the vast number of studies that have investigated the phenomenon of stopping or cancelling an action, they have mainly focused on cancelling an action that is made in response to an external stimulus such as in a stop-signal paradigm (Rubia et al., 2001). A stop-signal paradigm investigates the time course of cancelling a limb or eye movement, made in response to an external stimulus, by presenting a stop stimulus at various stimulus onset asynchronies (SOAs) after a go stimulus. Nevertheless, little research has attempted to determine the time course of stopping an internally prepared action (i.e., an intention). The ability to cancel an internally prepared action is fundamental to everyday life. There are many times in a day when one might plan an action which is then interrupted by an unexpected environmental cue that requires immediate action.

The present experiment uses the truncation paradigm created by Obhi and Haggard (2004) with two additional conditions to investigate the time course of cancelling an

internally prepared action (refer to the introduction, page 9, for more details on the truncation paradigm). To be clear, the original external condition is going to be referred to as the external-original condition and the original truncation condition is going to be referred to as the truncation-original condition. The two new conditions are the external-cancel and truncation-cancel conditions. The external-cancel condition consisted of a warning stimulus (WS) stimulus followed by a low frequency auditory tone followed by a high frequency auditory tone. Participants were instructed to ignore the low tone and respond to the high auditory tone as quickly as possible. The high auditory tone is the same tone that participants respond to in all other conditions. The low tone was presented at various stimulus onset asynchronies (SOAs: 50ms, 150ms, 300ms and 500ms) prior to the presentation of the high tone. This condition was necessary to account for any perceptual differences that may arise as a result of hearing two auditory tones compared to one auditory tone. Furthermore, participants were instructed to prepare to make a key press at a time of their choosing in the truncation-cancel condition. The important distinction of this new condition was the presentation of a low tone (with the same SOAs as the external-cancel condition) before the high tone in the truncation condition. Participants were instructed to cancel their internally prepared key press in response to the low tone and then react as quickly as possible to the high tone. Simply, a truncation-cancel trial could terminate as a result of an internally prepared key press after the presentation of a WS or as a reaction to the high tone. In the reaction trials, the WS would be presented, participants would then begin to internally prepare their key press, however this internal preparation would be interrupted by a low tone (requiring them to cancel all internal preparation) and a high tone would be presented at various SOAs to which the

participants had to respond as quickly as possible (refer to Figure 5a for a schematic depiction of the external-cancel and truncation-cancel conditions).

The objective of this study was to examine the time course of cancelling an internally prepared key press (i.e., a mental process). We did this by comparing the RTs from the truncation conditions to their respective RTs from the external conditions to see at what, if any, SOA the RT cost of internal preparation was eliminated.

Methods

Participants: 12 healthy subjects (17 ± 0.4 years, 6 females, 6 males) took part in the experiment for monetary or course credit compensation. The experiment was carried out in accordance with local ethics guidelines and informed consent was obtained from all participants.

Procedure: The experiment consisted of five conditions which were arranged into nine blocks and quasi randomly arranged across participants to avoid order effects. In all conditions, subjects sat at a computer with their right index finger placed lightly on the “B” key. Specifically, participants completed one internally generated action block, three external or simple reaction time (SRT) blocks, and five truncation blocks. In internally generated blocks, participants simply prepared and executed a self paced action (right index finger key press on the “B” key) within a 1-6 second 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. There

were two sub-conditions within the external condition: external-original and external-cancel. In the external-original condition participants were required to respond with a right index finger response (“B” key) as quickly as possible in response to a high auditory tone (no SOA). The presentation of the auditory tones was 1250ms-5750ms increasing with 350ms increments. In the external - cancel condition participants were required to ignore the low tone and respond with a right index finger response (“B” key) as quickly as possible in response to a high auditory tone. The difference between the external – cancel and the external original condition was that there was a low auditory tone presented at various SOAs (50ms, 150ms, 300ms and 500ms) prior to the high tone in the external – cancel condition. This condition was necessary to account for any perceptual differences that may arise as a result of hearing two auditory tones compared to one auditory tone. For all SRT trials, the presentation of the low tone was randomly varied across times throughout a 1-6 second window post trial onset.

The truncation conditions were divided into two sub-conditions: truncation – original and truncation – cancel. In the truncation – original condition, participants were required to prepare a self paced movement (a right index finger key press on the “B” key) within a 1-6 second post trial onset. There are two types of trials that may arise from this condition: truncation internal trials and truncation external trials. In the truncation internal trials, participants execute their self paced movement and continue onto the next trial. In the truncation external trials, participants prepare their self paced movement, but this internal preparation is interrupted by a high auditory tone which requires participants to respond with the exact same movement (a right index finger key press on the “B” key) to the tone

as quickly as possible. The difference between the truncation – cancel and the truncation - original condition was that there was a low auditory tone presented at various times (no SOA, 50ms, 150ms, 300ms and 500ms) prior to the high tone in the truncation – cancel condition. In the truncation – cancel condition, participants were instructed to cancel any form of internal preparation they had made for their self-paced movement upon presentation of the low tone and to respond to the high tone as quickly as possible with the same action they were preparing originally. In all conditions participants were preparing and executing a right index finger key press on the “B” key.

Participants were told at the beginning of the external blocks that sometime between 1-6seconds a tone will sound; respond to the tone as fast as possible. Participants were instructed to ignore the presentation of the low frequency tone and respond to the high frequency tone as quickly as possible in the external-cancel condition. For the internal blocks, participants were instructed to make an internally prepared key press sometime between 1-6seconds. Randomly vary the time of your key press for each trial and try and use the whole temporal window. Finally, participants were instructed to internally prepare to make a key press sometime between 1-6seconds and vary the time of their internally prepared key press. However, on occasion they may hear a tone before they make their internally prepared key press, respond to the tone as fast as you can. In the truncation-cancel condition, participants were instructed to prepare to make their internally prepared key. However, on the trials where their internal preparation was interrupted by a low frequency tone, they were instructed to cancel any internal preparation and then respond to the high frequency tone as quickly as possible.

In accordance with a previous study (Astor-Jack & Haggard, 2005) there was one block of 20 trials for the internally generated action condition and the external conditions. There were two blocks of 40 trials for the external – cancel condition to provide a total of 20 trials for each of the various SOAs. There were 40 trials in the truncation - original conditions, with 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. There were four blocks of 40 trials for the truncation – cancel condition to provide us with approximately 20 truncation external trials for each of the various SOAs assuming the same expectation as believed in the truncation – original trials. Both the external-original condition and truncation – original condition were blocked separately to eliminate any choice that might occur. Precisely, we did not want participants to have to decide if the auditory tone they heard was a low or high tone before responding. In both the external – cancel and truncation – cancel conditions participants knew that a low tone would always be followed by a high tone so there should not have been any ambiguity as to which auditory tone they were responding to (i.e., they always responded to the high tone throughout all conditions). We randomized the SOAs within both the external – cancel blocks as well as all four of the truncation – cancel blocks to eliminate any predictions of when the high tone will be presented.

Furthermore, we did not match the foreperiods between simple reaction time trials and truncation external trials (as noted in a previous study: Astor-Jack & Haggard, 2005). We wanted to guarantee that the same number of trials for each SOA were present in each of the external – cancel blocks. There was no way to make sure that the same number of trials were present in each external – cancel block if we matched the foreperiod and order of the truncation – cancel external trials because there were four truncation – cancel blocks and only two external – cancel blocks.

Additionally, participants completed 13 practice truncation trials comprised of 5 trials for the truncation – original condition and 8 trials for the truncation – cancel conditions. Participants were welcome to repeat the practice trials until they felt comfortable with the task and the experimenter agreed they were executing the task correctly.

In all conditions involving a reaction, a 100ms 1 kHz auditory tone served as the high tone. All stimuli and reaction times were recorded using DirectRT and custom response hardware, which provided timing precision of 1ms.

Results

In accordance with previous studies (Obhi & Haggard, 2004) reaction times that were less than 75 ms and 1000ms were excluded from the analysis because they represent anticipated and missed trials respectively. These trimming criteria were used for reaction times to facilitate comparison of the present study to earlier studies using the truncation paradigm (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005; Obhi et al., 2009). This

procedure, in addition to removal of trials in which participants failed to follow instructions, resulted in loss of 2.47% of trials across all subjects. The remaining external and truncation external trials were entered into a 2 x 5 repeated measures ANOVA (condition: external, truncation; SOA: no SOA, 50ms SOA, 150ms SOA, 300ms SOA, 500ms SOA).

Breakdown of Data

In the truncation – original condition (i.e., no SOA), 54.8% of the trials resulted in truncation external trials. Participants responded to 52.7% of the truncation – cancel trials for the SOA of 50ms. For the remaining truncation – cancel trials, participants responded to 50.6%, 50.8%, and 51% of the trials for 150ms SOA, 300ms SOA and 500ms SOA, respectively.

Comparison between two truncation conditions

To determine a time frame for canceling an intention or mental process of preparing to act a 2 x 5 repeated measures ANOVA with the factors condition (external, truncation) and SOA (0, 50, 150, 300, & 500 ms SOAs) was performed. A significant main effect was found for both condition and SOA ($F_{1,11} = 13.532, p=.004$ and $F_{4,8} = 4.403, p=.036$, respectfully). Additionally, the test revealed a significant interaction between condition and SOA ($F_{4,8} = 10.204, p=.003$).

Comparison of truncation conditions to external conditions

On the basis of previous results (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005), five planned paired samples t-tests were conducted to determine if there is a difference in reaction time between each of the external conditions and their respective truncation condition, thus resulting in an average RT cost. The first test revealed that participants were significantly slower to respond to the truncation – original trials than to external-original trials ($t(11) = 3.027$, $p=.012$). Participants were also slower to respond to truncation external trials with a 50ms SOA and 150ms SOA than their respective external trials ($t(11) = 4.760$, $p=.001$; $t(11) = 3.253$, $p=.008$, respectively). Interestingly, there was not a significant difference in reaction times for truncation trials with a 300ms SOA or a 500ms compared to their respective external trials ($t(11) = 1.266$, $p=.232$; $t(11) = .970$, $p=.353$, respectively) suggesting that participants were able to successively cancel their internal preparation (i.e., a mental process) sometime between 150ms and 300ms (refer to figure 5b for a depiction of the reaction times in both conditions).

Comparison of the three RT costs

Surprisingly, there was no difference in the average RT cost of switching from an internal to an external mode of response production, for no SOA and 50ms SOA ($t(11) = .466$, $p=.651$). Nevertheless, the average RT cost for the 50ms SOA was greater than the average RT cost for the 150ms SOA ($t(11) = 3.078$, $p=.011$).

Discussion

The present results suggest that it takes sometime between 150ms and 300ms to cancel an internally prepared action on the basis of a change in the environment. This is evident by the diminished RT cost of internal preparation at the 300ms SOA. Since there are no other studies to our knowledge that have looked at the time course of cancelling an internally prepared action, we conducted a second experiment (Experiment 6) to confirm the present findings and to extend them by determining if the time to cancel an internally prepared action is extended for actions that are more motorically complex.

Experiment 6 – Cancelling a Single versus Serial Response

As illustrated in Experiment five, the RT cost of internal preparation appears to be abolished sometime between 150ms and 300ms. This suggests that a mental process can be cancelled within 300ms of presentation of a cancellation tone. As suggested from Experiments one and two as well as past research, the effects of preparing a more demanding motor response are reflected as increased reaction times in simple reaction time conditions (e.g., Shen & Franz, 2005; Hughes & Franz, 2007). In the context of the present experiment, we investigated whether the time taken to cancel a more complex action (i.e., a two finger serial response) would be greater than the time taken to cancel a simple one finger key press.

The present experiment examines the time course of a more motorically demanding response (i.e., a two finger serial response) compared to a more simplistic motor response (i.e., a single finger response) to determine if cancellation time for an internally prepared

action is influenced by the complexity of the action being planned. In brief, do serial responses take longer to cancel than single finger responses? If so, this would tell us that “response specific” preparation is being ramped down during cancellation. In contrast, if cancellation time is independent of the specific response being prepared, then it might suggest that what is being cancelled is related to more general preparation.

Methods

A partial replication of Experiment 5 was completed where 12 healthy subjects (± 2.86 years, 10 females, 2 males) took part in an experiment with the following changes: participants made a single key press on “B” and a serial key press with the right index finger pressing “B” followed by the right middle finger pressing “N”. In all conditions, subjects sat at a computer with their right index finger placed lightly on the “B” key for single responses and their right index finger placed lightly on the “B” key with their right middle finger placed lightly on the “N” key for the serial responses. The same five conditions were employed; there were 5 blocks where participants made a single key press and 5 blocks with identical instructions in which participants made a serial response. Also, because there was not a significant difference in the RT cost for the no SOA compared to the 50ms SOA, the 50ms SOA was not used in the present study. To be clear, in the present study 150ms, 300ms, and 500ms SOAs were used in the external-cancel and truncation-cancel conditions. Additionally, there were two blocks of 20 trials for the external-original condition. There were two blocks of 60 trials for the external – cancel condition to provide a total of 20 trials for each of the various SOAs. There were 40 trials in the truncation - original conditions and there were four blocks of 60 trials for

the truncation – cancel condition to provide a total of 20 trials for each of the various SOAs with the expectation that in the truncation conditions half of the trials would result in truncation – internal trials and half of the trials would result in truncation – external trials. Lastly, only reaction times from the right index finger key press were compared across conditions.

Results

The same exclusion criteria used in all experiments were used in this experiment to preprocess the data. This procedure, in addition to removal of trials in which participants failed to follow instructions, resulted in loss of 1.4% of trials across all subjects. The remaining external and truncation external trials were entered into a 2 x 2 x 4 repeated measures ANOVA (response: one, serial; condition: external, truncation; SOA: no SOA, 150ms SOA, 300ms SOA, and 500ms SOA).

Breakdown of Data

In the truncation – original condition (i.e., no SOA), 47.9% of the trials resulted in truncation external trials for a single response. For the remaining truncation – cancel trials with a single response, participants responded to 48.3%, 52.9%, and 54.4% of the trials for 150ms SOA, 300ms SOA and 500ms SOA, respectively. When participants completed a serial response 48.8%, 50.4%, 51.3% and 54.4% of the truncation trials resulted in truncation external trials for no SOA, 150ms SOA, 300ms SOA, and 500ms SOA, respectively.

Comparison between four truncation conditions

To determine a time frame for canceling an intention or mental process a 2 x 2 x 4 repeated measures ANOVA with the factors response (single, serial), condition (external, truncation) and SOA (no SOA, 150ms SOA, 300ms SOA, and 500ms SOA) was performed. There was a main effect for all factors: response, condition, and SOA ($F_{1,11} = 39.582, p < .001$; $F_{1,11} = 35.404, p < .001$ and $F_{3,9} = 26.308, p < .001$, respectfully). Additionally, the test revealed a significant interaction between condition and SOA ($F_{3,9} = 40.221, p < .001$).

One finger versus two finger external reaction times

Four planned paired samples t-tests were conducted to determine if there were any differences in reaction times for single responses compared to serial responses. For all SOAs, right index finger external reaction times from the serial movements (right index finger followed by right middle finger key press) were significantly greater than right index finger external reaction times when they were performed alone (No SOA: $t(11) = 5.746, p < .001$; 150ms SOA: $t(11) = 6.819, p < .001$; 300ms SOA: $t(11) = 5.096, p < .001$; and 500ms SOA: $t(11) = 4.135, p = .002$).

Comparison of truncation conditions to external conditions

On the basis of previous results (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005), five planned paired samples t-tests were conducted to determine if there is a difference in reaction time between each of the external conditions and their respective truncation condition, thus resulting in an average RT cost. The first test revealed that participants

were significantly slower to respond on the truncation – original trials (i.e., no SOA; when a participant was internally preparing a key press but a high auditory tone interrupted their internal preparation and they respond with the exact same movement to the high tone) than on external trials where participants were simply responding to a high tone as quickly as possible for both single responses and serial responses ($t(11) = 4.863$, $p < .001$ and $t(11) = 4.294$, $p = .001$, respectively). Participants were also slower to respond to truncation external trials with a 150ms SOA compared to external trials for both single and serial responses ($t(11) = 6.882$, $p < .001$ and $t(11) = 3.889$, $p = .003$). Interestingly, there was no difference in reaction times for truncation trials with a 300ms SOA or a 500ms SOA compared to their respective external trials for single responses ($t(11) = 1.562$, $p = .147$ and $t(11) = 1.184$, $p = .261$, respectively) or serial responses ($t(11) = 1.346$, $p = .205$ and $t(11) = .383$, $p = .709$, respectively). These results suggest that participants were able to successively cancel their internal preparation (i.e., a mental process of preparing to act) for both single responses and serial responses sometime between 150ms and 300ms (refer to Figure 6a and b for the reaction times from both conditions for single and serial responses).

Comparison of the two RT costs

Surprisingly, there was no difference in the average RT cost of switching from an internal to an external mode of response production, for no SOA for single responses compared to serial responses ($t(11) = 1.435$, $p = .179$) or for 150ms SOA ($t(11) = 1.865$, $p = .089$), which is in accordance with Experiments one (unimanual RT cost = 74 ± 49 ; bimanual RT cost =

60±50), two (single RT cost = 106±70; bimanual RT cost = 80±64) and four (single RT cost = 98±59; serial RT cost = 65±55).

Discussion

The present results confirm the findings found in Experiment five, that an internally prepared action can be cancelled sometime between 150ms and 300ms on the basis of a change in the environment. Furthermore, the present results add to this finding, that a more motorically demanding response (i.e., a serial response) can be cancelled in the same temporal window of 150ms to 300ms as a single finger response. This suggests that we are cancelling a prospective time of action independent of what the action itself is.

Overall Discussion for Experiments Five and Six

In two experiments, participants were instructed to prepare to make an internally generated key press at the time of their choosing. Occasionally, a low auditory tone was presented instructing the participant to cancel their internal planning. This low tone was followed a high tone, at various SOAs, instructing the participants to respond to the high tone as quickly as possible. For no SOA (only the high tone presented) and for small SOAs (50ms and 150ms) the results confirmed that of previous studies (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005, Obhi, et al., 2009), suggesting that internal preparation for a self-paced movement does not facilitate performance for a functionally equivalent action made in response to an intervening stimulus. In both experiments we observed slowed reaction times in the truncation-original and truncation-cancel conditions (i.e., when subjects were preparing an action internally and had to override

this preparation and respond with the same movement to an intervening stimulus or had to cancel their internal preparation and respond to the high tone, respectively) compared to the external-original and external-cancel conditions (i.e., when subjects are responding to an auditory tone as quickly as possible), respectively, for no SOAs and small SOAs (50ms and 150ms). Simply, for no SOA and small SOAs, the RT cost of internal preparation remained present.

Interestingly, for larger SOAs (300ms and 500ms), the RT cost was abolished. Specifically, there was no statistical difference between the reaction times for the truncation-cancel condition compared to their respective external-cancel condition for 300ms and 500ms SOAs. These results suggest that an internally prepared action (i.e., a mental process of preparing to act) can be cancelled sometime between 150ms and 300ms after an instruction to do so. Moreover, a more motorically demanding action (i.e., a serial response) can be cancelled within approximately the same temporal window (150-300ms) as a less motorically demanding action (i.e., a single response).

These results are consistent with a past study that suggests (at least for reaching responses) an action can be prepared within 300ms of post trial onset and held for later execution (Deubel & Schneider, 2003). It is interesting to note that it appears to take the same amount of time to prepare an action as it does to cancel an internally prepared action. In addition, Walsh & Haggard (2007) completed a study investigating the time course of cancelling an action based on the detection of a shock. Using a go/no-go paradigm, participants planned an action and had to inform the experimenter if he/she

detected of a weak shock. They compared to a condition where the participant knew if they were going to move or not move at the beginning of each trial. They found that the detection of the shock was significantly lower in the no-go trials than all other trials. It was suggested from these results that when a prepared movement is inhibited the dismantling of the sensory consequences of the motor command takes at least 200ms. This is consistent with the present results, suggesting that a mental process can be cancelled sometime between 150ms-300ms. They suggest that motor preparation contributes to sensory attenuation, in such a way that merely preparing a movement gates sensory input. Peripheral feedback cannot have played a role in this attenuation, since there was no actual movement. They suggest that until the time of the no-go signal, the movement is held in preparation and the sensory system is suppressed correspondingly.

Furthermore, Brass & Haggard (2008) developed the what, when, whether model of intentional actions to help explain the mixed results regarding self-initiated actions. These authors suggest these mixed results are due to the fact that intentions have been thought of as a unitary concept when they feel it is a multidimensional concept. In their model, the “what” component reflects the decision of which action to make and is often compared to stimulus-response tasks (Lau et al., 2004b). The “when” component considers when to execute the action and has led to questions about free will (Libet et al., 1983). Finally the “whether” component reflects the decision of whether to execute the action or not (Brass & Haggard, 2007). In our experiment, the fact that participants know at the beginning of each trial which action (a serial or single response) they are going to prepare and execute, suggests that participants are not cancelling the “what” component

of the action on the tone. Furthermore, an auditory tone signifies that the internal action should be cancelled, suggesting that participants do not have to decide whether to complete the action or not, at least on their own initiative. Additionally, the fact that the motor demands did not influence the time course of cancelling an internally prepared action suggests that participants are potentially cancelling the “when” component of the intention to act. Participants may be cancelling the prospective when of the action which may be independent of the action itself.

Go/no-go and stop signal tasks have not only shed light on the time course of cancelling an action made in response to an external stimulus but also on potential brain regions that may be involved in cancelling actions. An fMRI study (Rubia et al., 2001) using go/no-go and stop signal paradigms, was implemented to study the underlying brain regions that correspond with cancelling an action. It appears that the mesial, middle, and inferior frontal and inferior parietal lobes mediate performance of tasks which require inhibition of motor responses. The authors suggest that the supplementary motor area is involved in both the initiation and suppression of voluntary motor acts.

As proposed from previous studies (Rubia et al, 2001; Aron, Fletcher Bullmore, Sahakian, & Robbins, 2003) the frontal lobes have been suggested to be involved in inhibition of responses to exogenous cues. Using fMRI and a paradigm similar to Libet et al., (1983)’s study of ‘free won’t’, Brass & Haggard (2007) instructed participants to prepare to make a key press at a time of their own choosing while watching a rotating clock and then reported the time of their key press. On some

inhibition trials they were told to inhibit their prepared key press at the last second(s) prior to movement. Contrasting the activation of action and inhibition trials yielded greater activation in dorsal frontomedian cortex (dFMC). They argue that their results suggest that a specific top-down control signal gates the neural pathways of intention to action, which is supported by the negative correlation between the dFMC activation and the primary motor cortex activation. Taken together, they propose that the dFMC may be one of the areas that reflects self-control, at least for situations where one is controlling their behaviour on their own volition. However, future studies involving fMRI and TMS and the truncation cancelling paradigm are needed to investigate the neural correlates of the slightly different task of cancelling an intention on the basis of an environmental cue.

In summary, the present experiments propose that a mental process of preparing to act can be cancelled within 300ms. This appears to hold true regardless of the motor demands affiliated with the action that is being prepared, at least in simple finger movement tasks. Simply, regardless of whether the action was a two finger serial response or a single finger response, the internally prepared action was cancelled sometime between 150-300ms temporal window. The time taken to cancel an internally prepared action plan in this experiment may involve cancelling the prospective when component of the intention to act.

General Discussion

This thesis began with the suggestion that the systems mediating internally generated and externally triggered actions are not mutually exclusive, which was corroborated by the finding of the RT cost of internal preparation (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005). Simply, when a participant is internally preparing to make an action and this internal preparation is interrupted by an intervening stimulus which requires the same action; participants are slower to respond to this stimulus compared to a simple reaction time condition where participants are responding to a tone as quickly as possible with an equivalent action. This finding (i.e., the presence of the RT cost) was supported by all six experiments conducted for this thesis. Therefore, internally-prepared actions and externally triggered actions do in fact appear to be mediated by some common processes. If the two modes of action were prepared fully independently, then there would not be cost associated with engaging simultaneously in internally driven and externally cued action preparation processes. Early primate studies demonstrate a sharp dichotomy between the motor preparatory systems that underlie internally generated and externally triggered actions; in such a way that the supplementary motor area appears to mediate internally generated actions whereas the lateral premotor area appears to mediate externally triggered actions (Passingham, 1987). However this dissociation has not been as strongly supported in neuroimaging methods involving human participants (Jahanshahi et al., 1995; Jenkins et al., 2000; Cunnington et al., 2002). Instead, several studies have suggested that a similar network of brain structures is involved in the production of both modes of action, with perhaps some differences in the extent and timing of activation in the medial premotor structures (particularly the pre-SMA) in the case of internally

prepared actions (Cunnington et al., 2002; Deiber et al., 1999). The present results are in accordance with these latter findings as there is a cost associated with engaging both action systems simultaneously.

Summary of findings from Experiments one through three

Previous studies conducted by Astor-Jack & Haggard (2005), ruled out attentional and perceptual factors as the source of the RT cost of internal preparation. Experiments one and two further investigated the source of the RT cost. These studies extended previous findings in such a way that the RT cost was not significantly different for conditions involving a simple response (i.e., a unimanual or single key press) compared to conditions involving more motorically demanding responses (i.e., bimanual or serial key presses, respectively). Concisely, through the manipulation of motor demands it appears the RT cost does not reflect motor processing.

Experiment three, acted as a control and examined the role of subvocal counting on reaction time. Specifically, a new condition was created, external-subvocal, that required participants to count subvocally while responding to the auditory tone as quickly as possible. In our previous debriefing sessions we learned that counting subvocally was a strategy used by most participants for planning their internally prepared key press, hence this new condition was created to assess whether the RT cost might simply be due to the dual task of counting in truncation conditions. If the RT cost of truncation was identical to the RT cost in the external-subvocal condition, it would support the idea that the cost is simply due to subvocal counting. Regardless of whether participants were counting

subvocally or not in the external conditions, the RT cost remained present in the truncation condition, suggesting that the RT cost in truncation conditions is not due to subvocal counting.

Further, it is interesting to note that the source of the RT cost does not appear to be the result of incomplete preparation of the internally prepared action. As noted by Deubel & Schneider (2003), an action (at least for reaching responses) can be prepared within 300ms of post trial onset and held for later execution. All of the above experiments instructed participants to prepare to make an action within either a three to ten second or one to six second temporal window. Even in the latter case, there is at least triple the amount of time needed to fully internally prepare a key press. Thus, inadequate preparation of the internal key press does not appear to be the source of the RT cost either.

Possible neural mechanism underlying the RT cost of internal preparation

Taken together, if the source of the RT cost is not perceptual or attentional in nature, is not related to motor demands or a simple dual task or the result of inadequate preparation of an internal action, then it must be reflective of a higher level cognitive function. Two alternative mechanisms have been proposed to explain the present findings. The first is a possible mechanism that switches between internal triggers and external triggers for actions. Gilbert et al., (2005) used fMRI to investigate the neural correlates that are involved in switching between attention towards externally triggered and internally generated information. They found a transient increase in the lateral rostral prefrontal

cortex (BA 10) when participants switched from doing the task with exogenous information to completing the task with endogenous information. Consequently, the RT cost of internal preparation may reflect the time consuming process of switching between internal triggers and external triggers for the same action which may be mediated by the rPFC (Burgess et al., 2007). The second potential explanation relates to the notion of inhibition. The pre-SMA has been implicated in both internally generated action preparation (through its role in the basal ganglia-thalamo-cortical circuit) and also in the inhibition of action (e.g., Chen et al, 2009). Therefore, we suggest that the pre-SMA may be involved in inhibiting all motor output to avoid premature movement. Any exogenous cue prompting a movement during this inhibition period will result in a delayed response. This delayed response or RT cost would then reflect the time taken to remove the inhibition. However, it is not possible to make a clear distinction as to which of the two explanations, if any, is correct. Thus, further experiments, possibly employing fMRI and transcranial magnetic stimulation (TMS) are necessary to provide some clarity of the neural underpinnings.

Summary of findings for modification of actions

All of the previous studies that have employed the truncation paradigm thus far (Obhi & Haggard, 2004; Astor-Jack & Haggard, 2005; this thesis Experiments 1-3) have investigated the time course when an internally planned action is interrupted by an intervening stimulus requiring the **same** response. For that reason, Experiment four examined the course associated with modifying an internally prepared action (i.e., either adding an action to an internally prepared movement or inhibiting part of an internally

prepared action). Recall the previous example, your teammate shoots a basket and you plan to give him a single high five. He comes over to you and has two hands ready, thus you have to add your second hand to your internally planned action to complete a double high five. Conversely, you may have prepared for the double high five and your teammate comes over with one hand ready. Consequently, you have to inhibit your second hand in order to achieve a single high five. Specifically, Experiment four was interested in the time course of action modification and not switching between two different actions.

Experiment four confirmed the results of Experiments one and two, suggesting that the RT cost does not have a locus of motor processing. It extended these findings in such a way that switching between triggers for action (i.e., internal to external triggers) results in a larger RT cost when the internally planned action is modified. Interestingly, the RT cost of internal preparation was larger when one has to inhibit part of an internally planned action (i.e., planning for a double high five but complete a single high five) compared to adding a movement to a planned action (i.e., planning a single high five but completely a double high five). Hence, inhibition of action appears to be more costly than addition of an equivalent action to a prepared motor set.

Possible neural mechanisms to explain action modification

The increased RT cost associated with action modification may be accounted for in the previous two neural explanations that were proposed as the source of the RT cost. First, if the RT cost is the result of switching between triggers for action (i.e., internal and

external triggers) which may be mediated by the rPFC (Burgess et al., 2007), the increased RT cost found for modified actions may be a two step process. Specifically, not only would there be the time consuming process of switching between internal and external triggers for the action (Burgess et al., 2007), there would also be a time consuming process of switching from one schema to the another schema because in action modification the actions differ and therefore would be represented by separate schemas.

Alternatively, it is important consider the notion that the pre-SMA is implicated in inhibiting all motor output, as it has been associated in the inhibition of action (e.g., Chen et al, 2009; Xue, Aron & Poldrack, 2008). Additionally, Coxon, Stinear, & Byblow (2008) have suggested that the right prefrontal cortex (PFC) especially the right inferior frontal gyrus (IFG) plays a crucial role in the prevention of volitional movements. Specifically, fMRI was used with an anticipatory task, where participants had to simultaneously extend both their right index finger and right middle finger for most trials, while preventing one or both finger movements on the remaining trials on the basis of visual indicators. They found the right IFG to be activated when part of the movement had to be inhibited as well as when both movements had to be inhibited, with an overlap in activation in the inferior frontal cortex and middle frontal gyrus. Interestingly, the medial frontal cortex was activated when part of the movement (i.e., one finger) had to be inhibited. This result fits nicely with the present results, where participants are modifying part of an action on the basis of an external cue (i.e., an auditory), suggesting both the SMA and the IFG may be crucial in the prevention of premature movements. However

future studies are necessary to determine the neural correlates for inhibition of premature movements.

Furthermore, if there is a universal inhibition of motor output, there would be delayed responses to exogenous cues presented during this inhibition because the inhibition has to be removed before the response can be completed. Previous studies employing transcranial magnetic stimulation (TMS) to the motor cortex provide evidence for this universal inhibition of motor output (Hasbroucq, Kaneko, Akamatsu, & Possamaï, 1997; Hasbroucq, Osman, Possamaï, Burle, Carron, Dépy, Latour, & Mouret, 1999). These authors used TMS to elicit motor evoked potentials (MEPs) in the effector of interest (i.e., prime mover), which resulted in a progressive decrease in cortico-spinal excitability during the foreperiod of a simple reaction time (SRT) task. It is important to note, that participants were able to accurately determine the time elapsed in the foreperiod thus able to engage in effective temporal preparation which corresponds with the current study, where participants were clearly able to discern the time left until movement because this time was self-determined. Incorporating the present action modification results, it may be suggested that in addition to this general inhibition, there is additional inhibition placed upon all movements that differ from the planned action, thus accounting for the increased RT cost connected to action modification.

However, at this time it is not possible to tease apart which explanation is more accurate. Thus, future studies involving fMRI and TMS may shed light on this issue. Specifically, fMRI may be useful to provide information about the neural correlates of the observed

RT costs. Additionally, repetitive TMS (rTMS) to the pre-SMA and IFG would act as a temporary lesion of these areas and thus provide insight into the role of the pre-SMA and IFG in general inhibition of motor output, when used in experimental designs similar to the ones reported in this thesis. Ultimately, it is important to conduct further experiments employing the truncation paradigm with fMRI and TMS to improve clarity on potential causes.

Summary of cancelling an internally prepared action

Experiment four illustrated that the RT cost was largest when part of an internally prepared action had to be cancelled, which provided the motive to investigate the time course of cancelling an entire internally prepared action? Through the addition of an exogenous cue prompting the cancelling of the internally prepared action in the truncation condition, it was found that an internally prepared action can be cancelled sometime between 150ms and 300ms temporal window, regardless of the motor demands associated with the planned action, at least in the context of simple finger responses. This is similar to the time course of cancelling a response, which occurs around 200ms (Walsh & Haggard, 2007).

Moreover, a closer look at Brass and Haggard's (2008) what, when, whether model of intentional action suggests that the time course of cancelling an internally prepared action (i.e., 150-300ms) may involve cancelling the prospective "when" component of the action.

Suggested neural correlates of cancelling an internally prepared action

The frontal lobes, specifically the mesial, middle and inferior frontal lobes as well as the inferior parietal lobes, have been suggested to mediate inhibition of responses to external cues in previous studies (Rubia et al, 2001; Aron et al., 2003). Additionally, Brass and Haggard (2007) propose that the dorsal frontomedian cortex (dFMC) is a neural correlate of self-initiated cancellation of an internally prepared action. Moreover, Xue et al., (2008), used fMRI and a stop-signal paradigm to examine the neural correlates of verbal response control and manual motor control. Subjects had to either verbally respond or physically respond with a key press to the visually presented stimuli on go trials, and inhibit responses when presented with a stop signal. They found that both the right inferior frontal cortex (IFC) and the pre-supplementary motor area (pre-SMA) were activated by successful inhibition of both verbal and motor responses. Thus, these authors suggest that manual responses and speech acts share a common inhibitory mechanisms localized in the right IFC and the pre-SMA. Taken together, it is speculated that the supplementary motor area may be implicated in the inhibition of the internally prepared action seen in the present study. Moreover, because the internally prepared action is cancelled due to the presentation of an external cue, the inferior frontal cortex may also be activated as they have been implicated in inhibition processes of responses.

It would be of interest to conduct a future study employing this new version of the truncation paradigm (i.e., the addition of an auditory tone prompting the cancellation of the internally prepared action) with fMRI to explore the neural correlates of cancelling an internally prepared action due to a change in the environment.

Final Conclusion

In conclusion, flexible behaviours, the ability to switch back and forth between internally generated actions and externally triggered actions, are necessary for adaptive behaviour.

Future studies employing fMRI and TMS may prove useful in identifying the neural correlates of the underlying mechanisms for both internally driven and externally triggered actions and how these mechanisms interact as a function of flexible, adaptive behaviour.

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Figure Captions

Figure 1a: A schematic depiction of the truncation conditions (external or simple reaction time (SRT) condition, internal condition, & truncation condition). WS = warning stimulus, IS = imperative stimulus.

Figure 1b: Unimanual and bimanual reaction times from external trials of the participants' right index finger. Notice that bimanual RTs are significantly longer than unimanual RTs, illustrating the increase in motor demands for bimanual versus unimanual responses. Error bars are SEM.

Figure 1c: Unimanual and bimanual RT cost of internal preparation. Notice these two RT costs are statistically indifferent, suggesting the source of the RT cost of internal preparation is non-motor in nature. Error bars are SEM.

Figure 1d: Unimanual and bimanual reaction times for external trials and truncation external trials of the participants' right index finger. Notice that although bimanual RTs for the SRT condition are significantly longer than the unimanual RTs their RTs are not significantly different for truncation external trials. Error bars are SEM.

Figure 1e: Unimanual reaction times are plotted against the delivery times of the auditory tones binned into five groups in the external condition and truncation condition. Reaction times were slowed in the truncation condition compared to the external condition confirming the presence of the RT cost of internal preparation (the difference

between each pair of bars). Note the RT cost diminished for the last two binned groups. Error bars are SEM

Figure 1f: Bimanual reactions times are plotted against the delivery times of the auditory tones binned into five groups in the external condition and truncation condition.

Reactions times were slowed in the truncation condition compared to the external condition confirming the presence of the RT cost of internal preparation (the difference between each pair of bars). Note the RT cost diminished for the last binned groups. Error bars are SEM.

Figure 2a: Single and serial reaction times for external trials and truncation external trials of the participants' right index finger. Notice that although serial RTs for the SRT condition are significantly longer than the single RTs their RTs are not significantly different for truncation external trials. Error bars are SEM.

Figure 2b: Single and serial reaction times from external trials of the participants' right index finger. Notice that serial RTs are significantly longer than single RTs, illustrating the increase in motor programming demands for serial versus single responses. Error bars are SEM.

Figure 2c: Single and serial RT cost of internal preparation. Notice these two RT costs are not statistically different, suggesting the source of the RT cost of internal preparation is not affected by increasing motor programming demands. Error bars are SEM.

Figure 3: Reactions times for the external (SRT), external-subvocal (SRT-subvocal), and truncation condition. Note that the RT cost remains present even when participants are counting subvocally, proposing that the RT cost does not simply reflect the dual task of counting subvocally (a task that has been reported as a strategy for planning an internal action in the truncation condition). Error bars are SEM.

Figure 4a: Single and serial external reaction times of the right index finger (RT). Note that right index finger RT in serial actions was significantly greater than the right index finger RT in single actions, reflecting greater processing demands for serial versus single actions. Error bars are SEM.

Figure 4b. Interaction plot depicting the reaction times in single and serial matched truncation and mismatched truncation conditions (plan single, execute single; plan serial, execute serial; plan single, execute serial; plan serial, execute single). Error bars are SEM.

Figure 5a: A schematic representation of the two addition conditions that were used in conjunction with the truncation paradigm to investigate the time course of cancelling an internally planned action (external-cancel and truncation-cancel). WS = warning stimulus.

Figure 5b: Reaction times in both SRT and truncation conditions for each SOA. Note that the RT cost disappears sometime between 150ms and 300ms SOA, suggesting that an

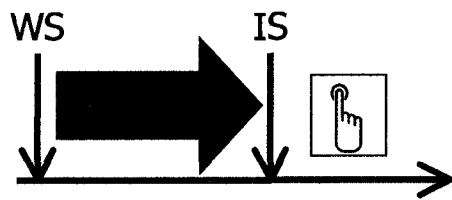
internally prepared action takes approximately 150-300ms to be cancelled. Error bars are SEM.

Figure 6a: Single finger reaction times in both SRT and truncation conditions for each SOA. Note that the RT cost disappears sometime between 150ms and 300ms SOA, suggesting that an internally prepared action takes approximately 150-300ms to be cancelled. Error bars are SEM.

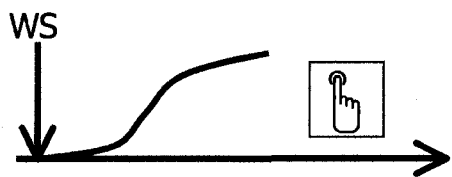
Figure 6b: Serial finger reaction times in both SRT and truncation conditions for each SOA. Note that the RT cost disappears sometime between 150ms and 300ms SOA, suggesting that even a more motorically demanding internally prepared action can be cancelled in 150-300ms. Error bars are SEM.

Figures

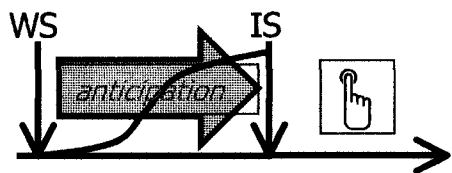
Figure 1a



External (SRT) Condition



Internal Condition



Truncation Condition

Figure 1b

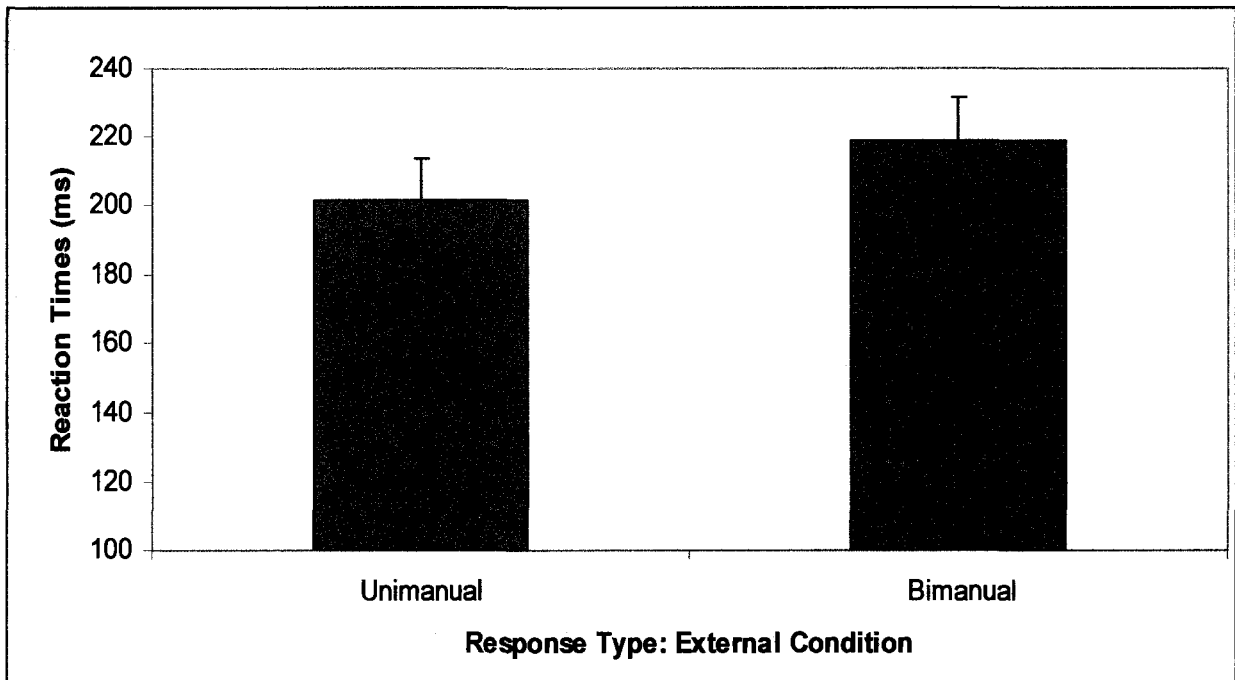


Figure 1c

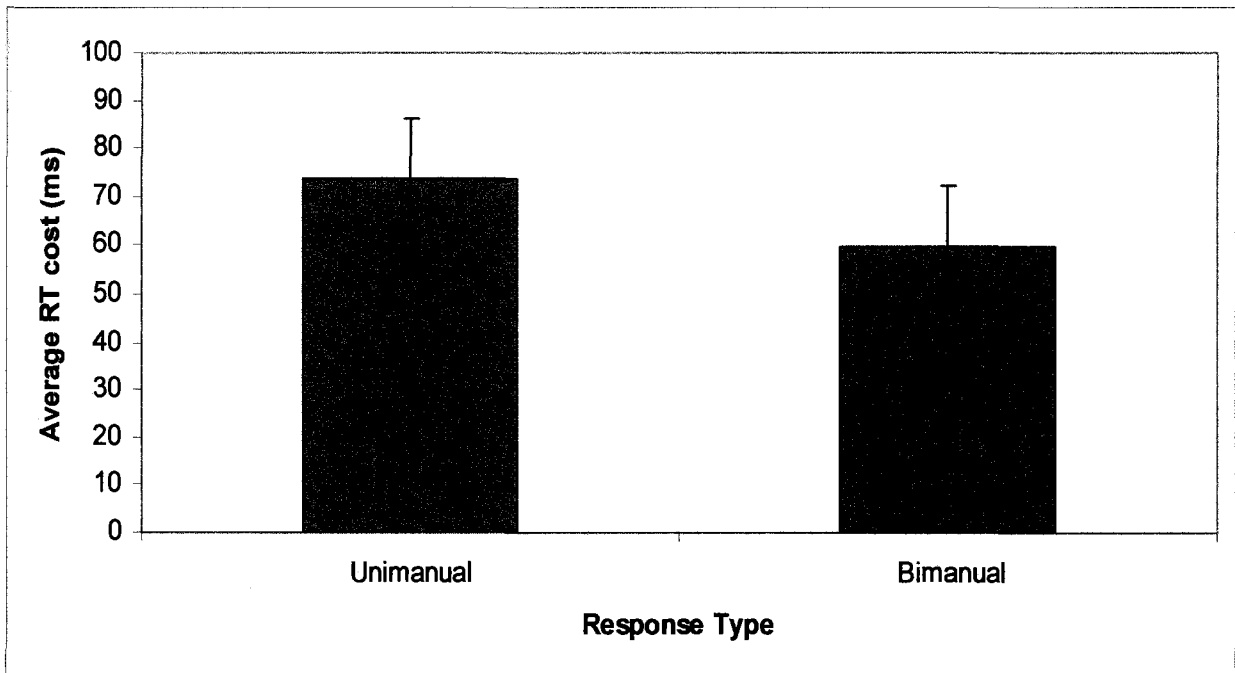


Figure 1d

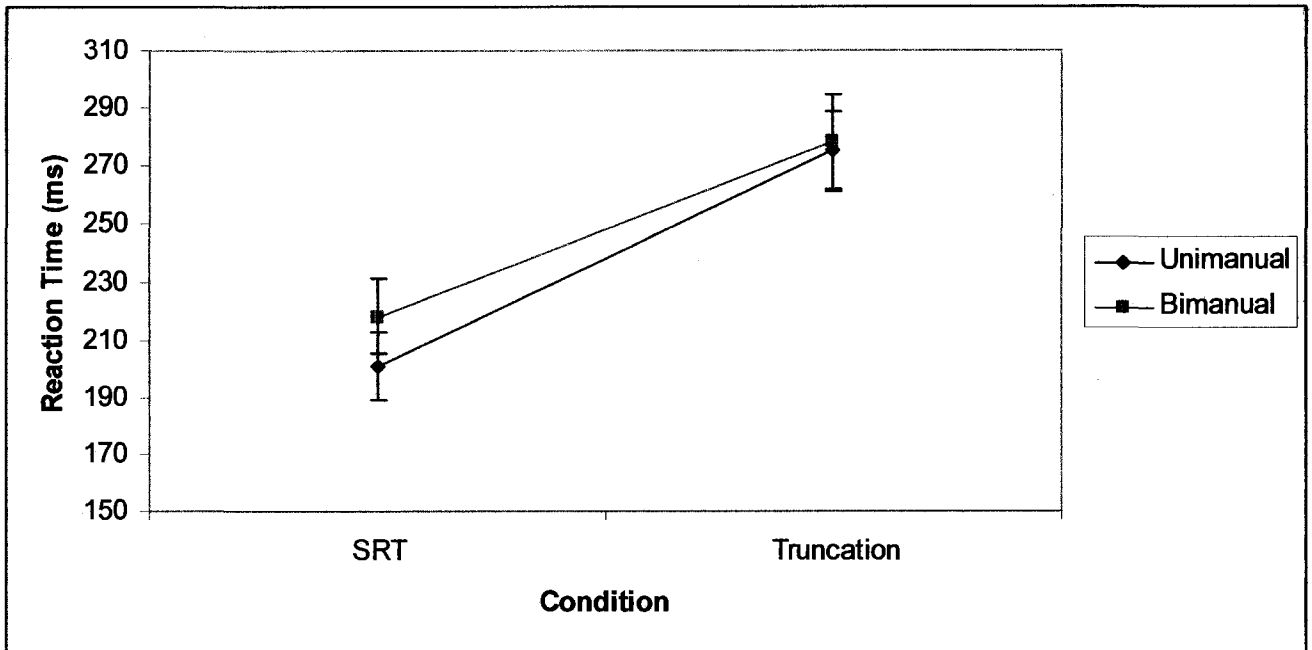


Figure 1e

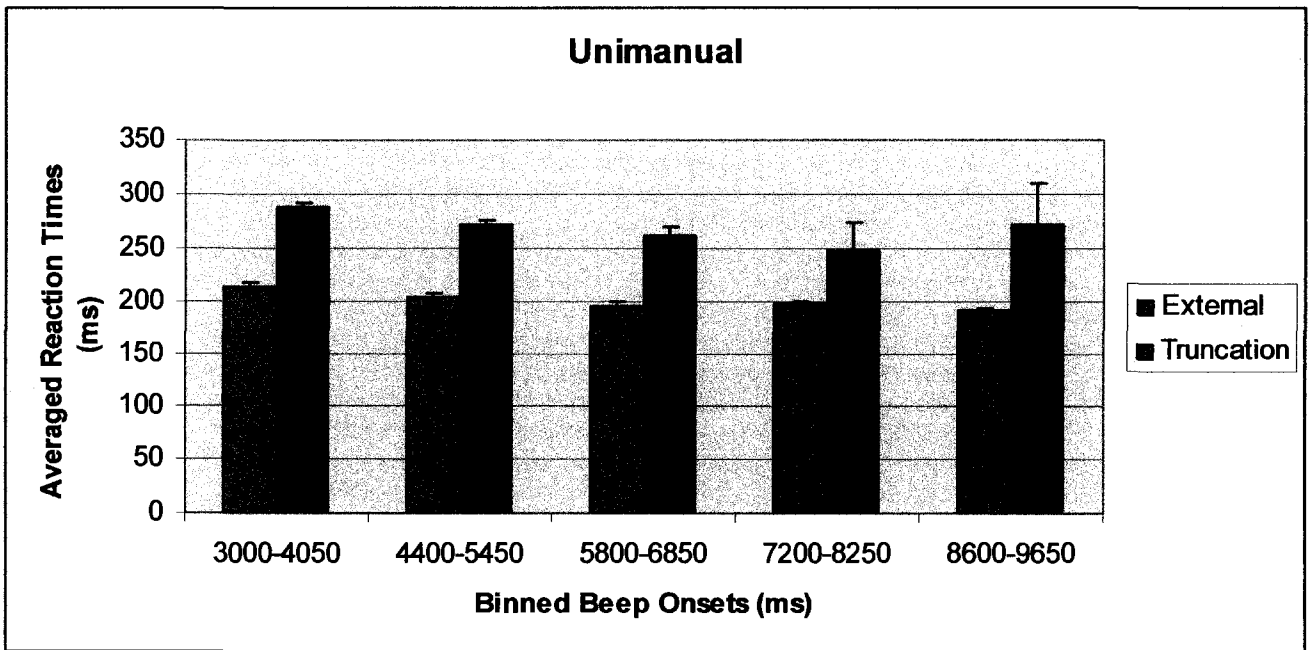


Figure 1f

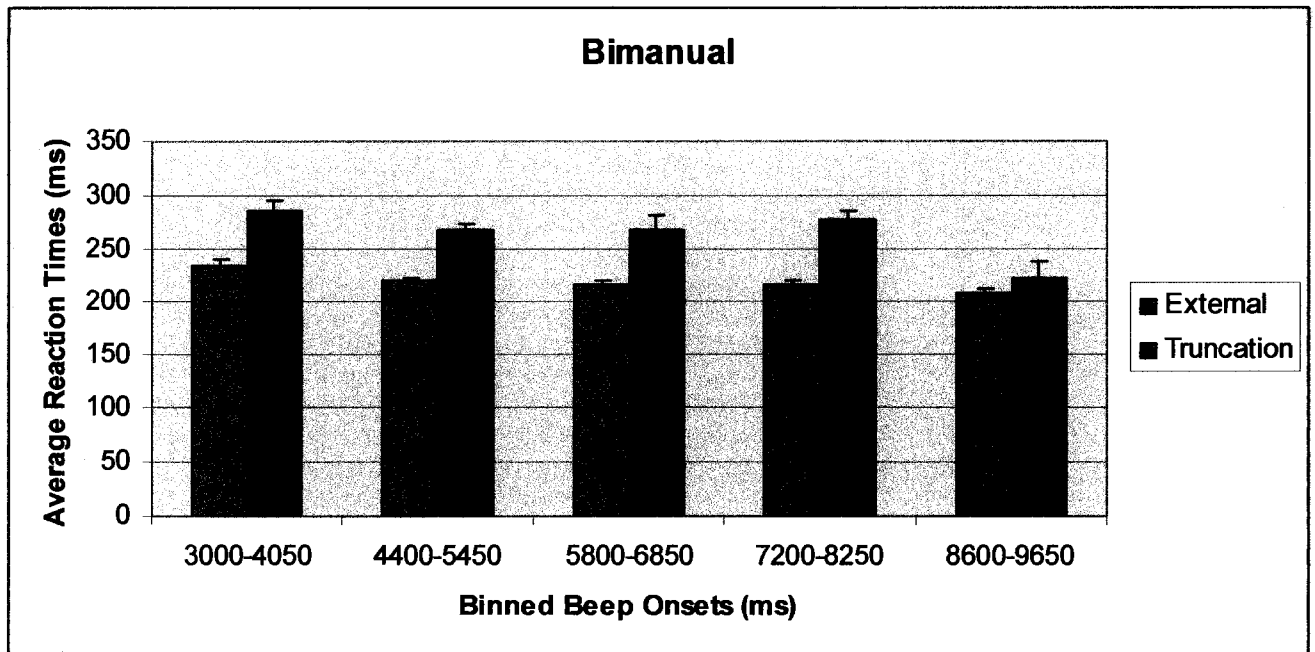


Figure 2a

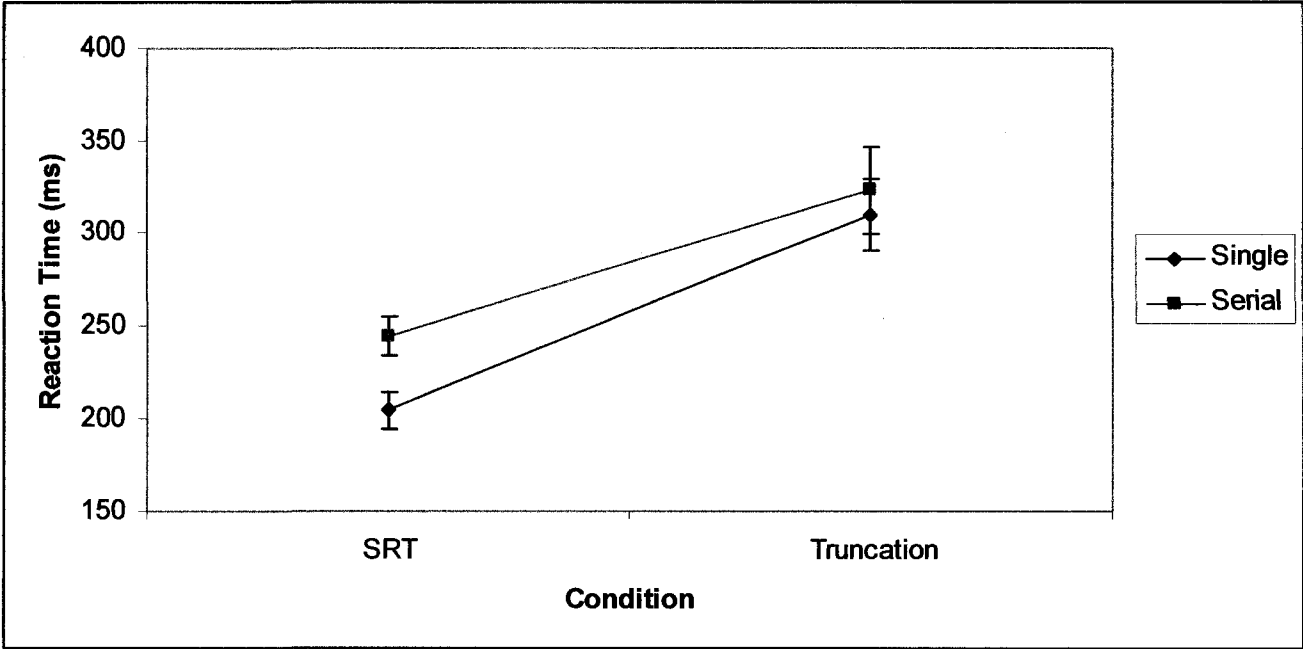


Figure 2b

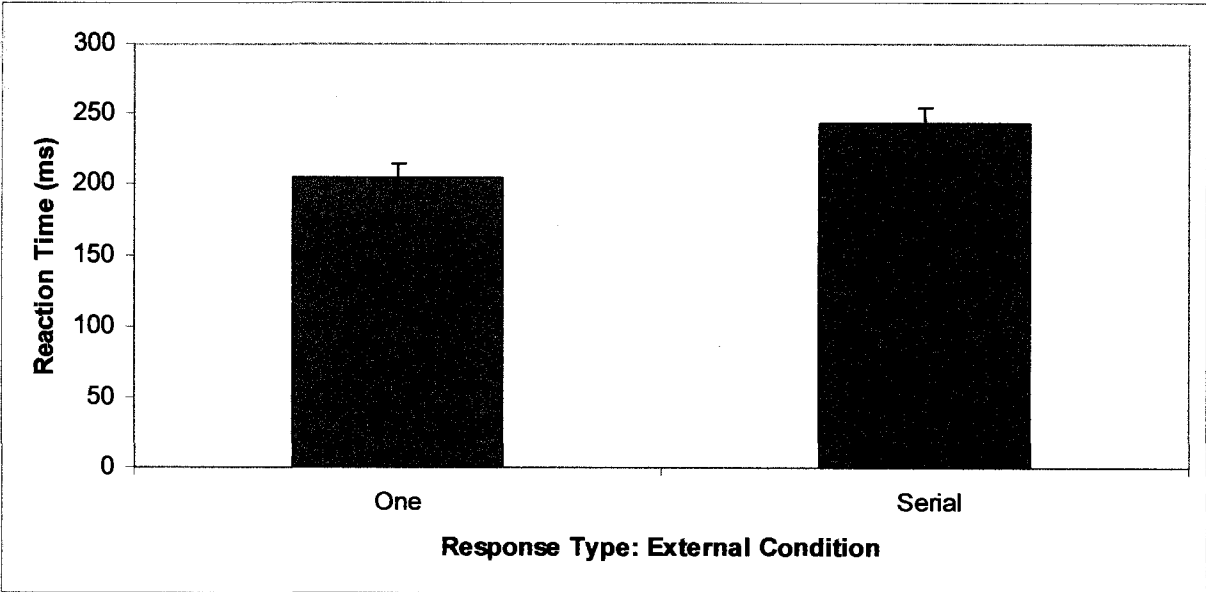


Figure 2c

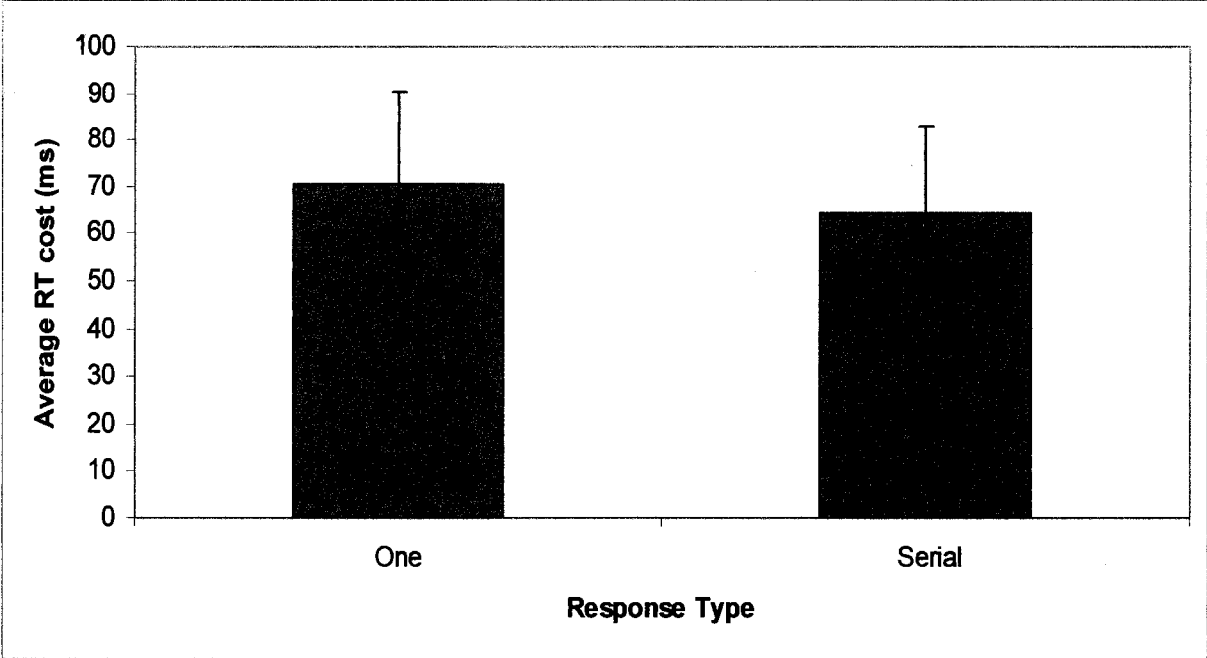


Figure 3

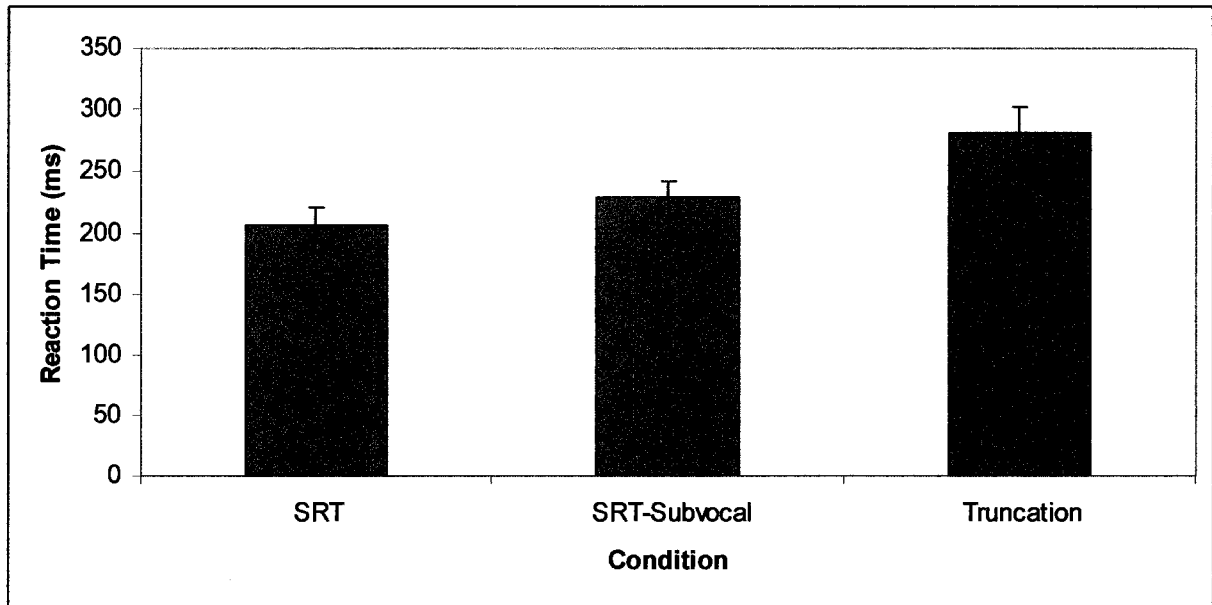


Figure 4a

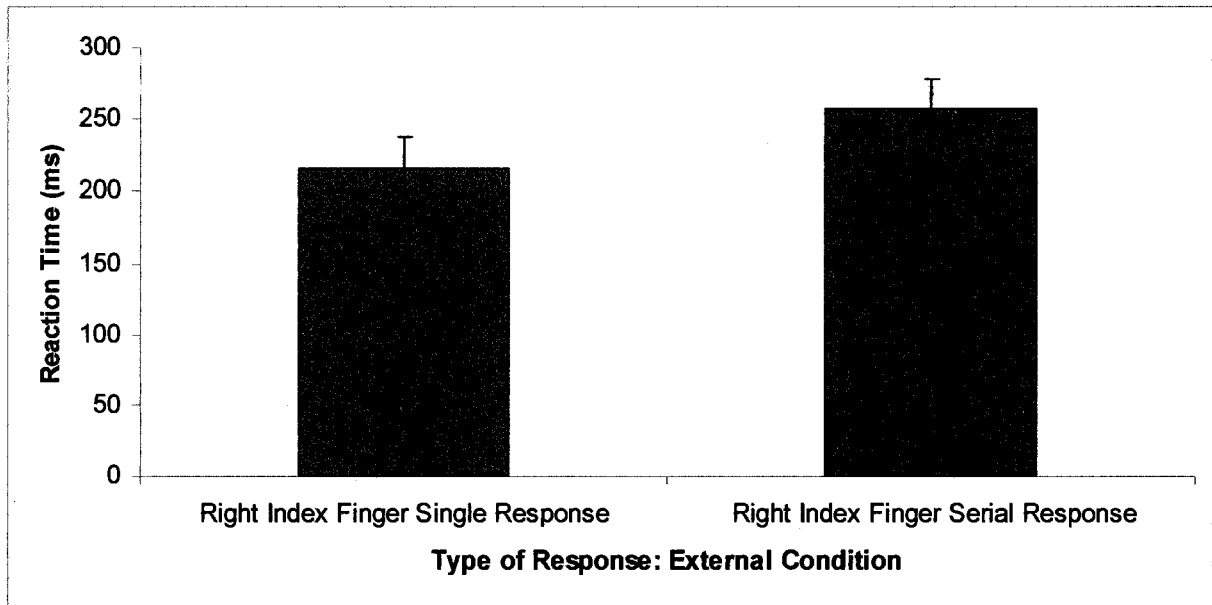


Figure 4b

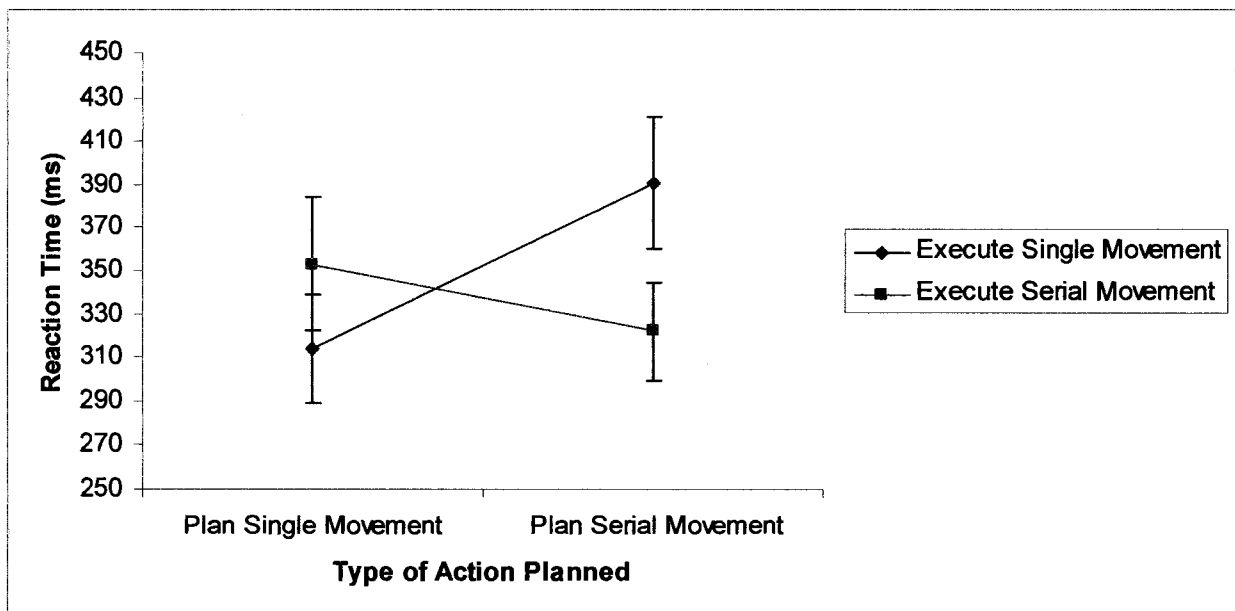


Figure 5a

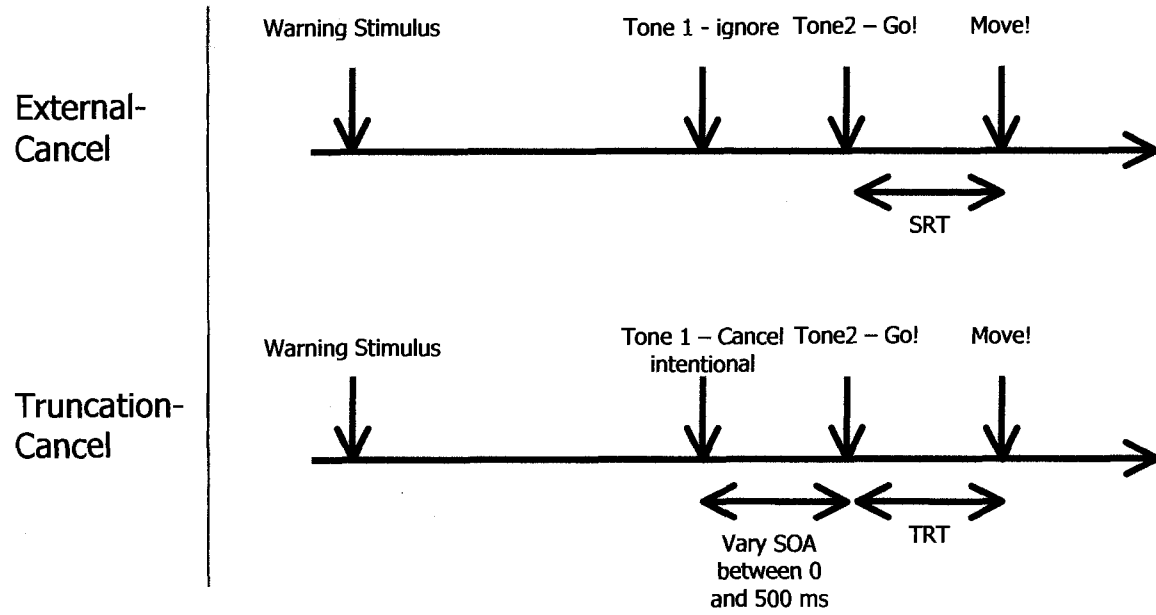


Figure 5b

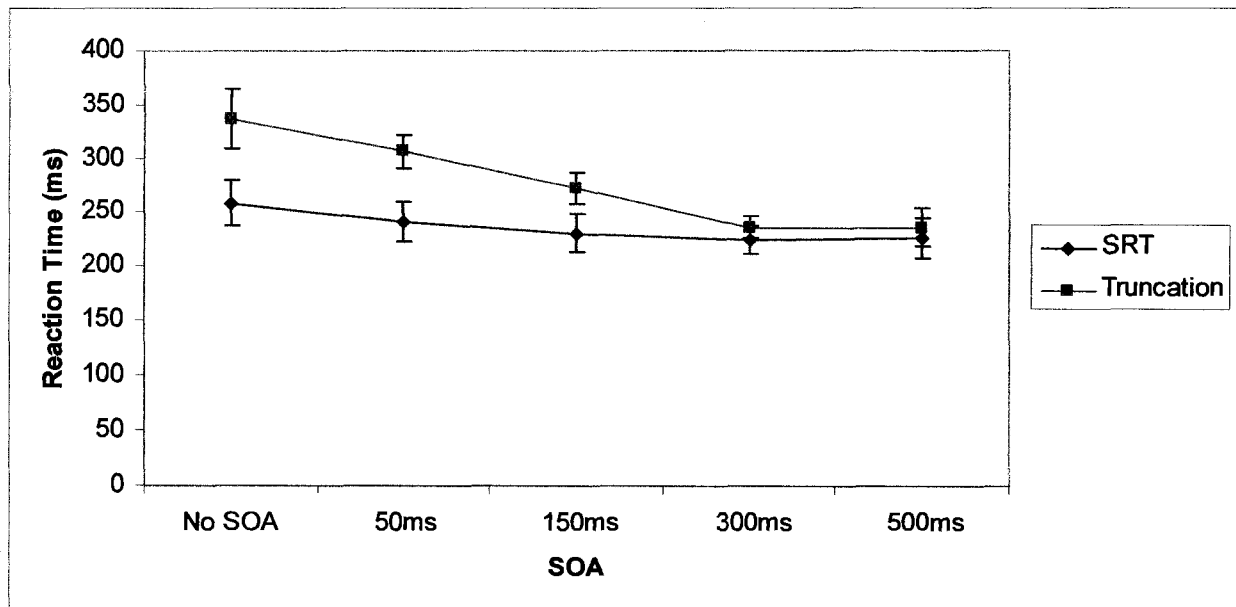


Figure 6a

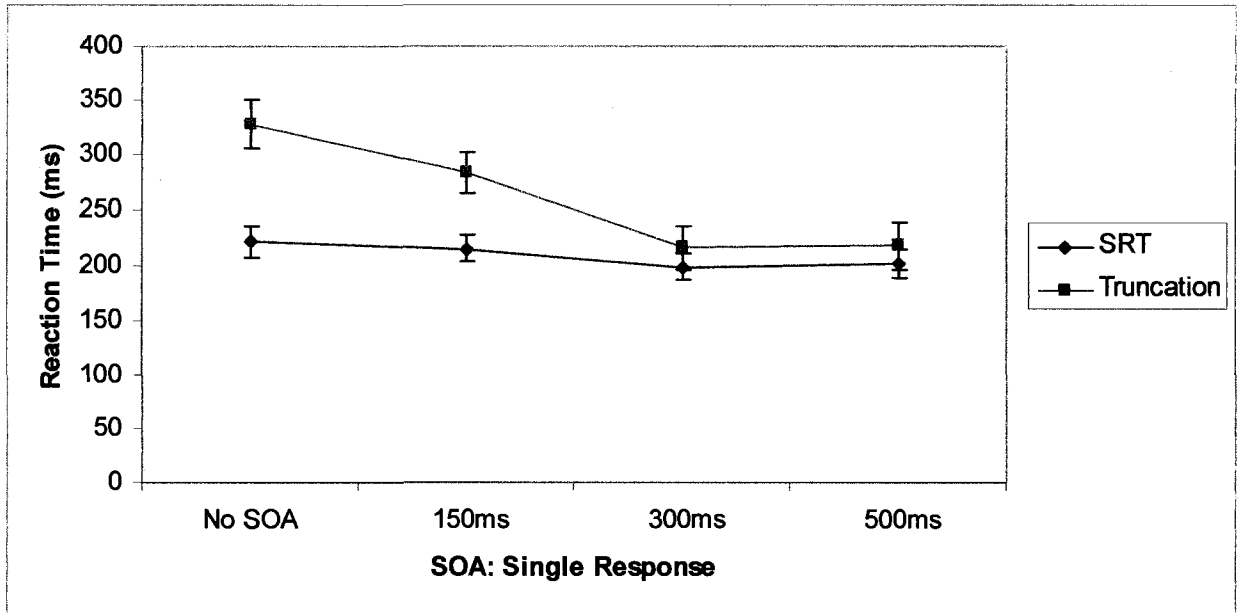


Figure 6b

