AUDITORY STARTLE RESPONSE AND REACTION TIME

By

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Abstract

Recent experiments involving the use of a startling acoustic stimulus during a simple reaction time (RT) task have shown that premotor RT (PMT) can be significantly reduced when participants are startled (Valls-Solé et al., 1999; Carlsen et al., in press). This effect is not produced by an early startle reflex adding on to a later voluntary response, as EMG profiles remain largely unmodified. Further, the lack of an effect of the startle on final position and aiming accuracy suggests that the response produced is indeed the prepared response. These findings suggest that a startle stimulus may act to trigger a prepared movement earlier in comparison to voluntary initiation (Carlsen et al., 2000).

It has been shown that individuals habituate to a startling stimulus at different rates depending on the required activity level of the participant in the task (Brown et al., 1991a; Siegmund et al., 2001). The aim of the first study of this thesis was to determine the rate at which participants habituate to a startle during the completion of a RT task. Participants performed a targeted wrist extension in a Simple RT task. An auditory startle stimulus (124 dB) replaced the imperative stimulus in some of the trials. For the duration of the experiment, startle response electromyographic (EMG) activity continued to be produced, but not on every startle trial, indicting habituation was not complete after 20 startle trials. PMT in the startle (ST) condition was significantly shorter than control PMT however, within the ST condition, when a measurable EMG burst in the SCM was present, PMT was significantly shorter than when no SCM burst was present.

It has been suggested that a startling stimulus activates structures in the lower CNS that are common to both the startle and voluntary response pathways, acting to

trigger a preprogrammed movement (Valls-Solé et al. 1999). In a Choice RT paradigm, however, it is thought that cortical processing must occur before a response can be prepared, since the appropriate response is not known in advance (Schluter et al., 1998 Schluter et al., 2001). The second experiment of the thesis addressed the issue of response preparation through the use of a Choice RT paradigm. Participants performed targeted wrist flexion / extension movements involving 1, 2, or 4 Stimulus-response (S-R) alternatives. Results showed that while in the Simple RT situation PMT was significantly shorter when participants were startled, that no difference in PMT was observed when participants were startled in the Choice RT situations. Furthermore, more errors occurred when participants were startled during the Choice RT conditions suggesting that the startle may actually interfere with ongoing cortical processes. These results support the hypothesis that a startle acts to trigger a prepared response, rather than only increasing systemic activation.

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General Introduction

The startle reflex is a generalized and diffuse protective response consisting of a characteristic set of muscle actions initiated by a sudden, intense stimulus (Davis, 1984; Yeomans and Frankland, 1996). More specifically, in response to a sudden, unexpected, acoustic, tactile or vestibular stimulus (Scott, Frankland, Li, & Yeomans, 1999; Yeomans and Frankland, 1996), a generalized flexion response is observed in mammals. The startle response consists of a characteristic pattern of muscle flexion (although extension has also been observed; see Brown, Rothwell, Thompson, Britton, Day, and Marsden, 1991a), as well as an increase in central nervous system and autonomic activity (Thackray, 1972).

Acoustic stimuli must be adequately loud (at least 90 dB) to elicit a startle response. Although more intense stimuli produce larger amplitude responses and shorter response latencies (Blumenthal, 1996; Davis, 1984), a fine balance must be struck between using a sufficiently intense stimulus to elicit a measurable startle, and minimizing risk of damage to the sensory apparatus. Previous studies involving human participants have used brief acoustic stimuli of up to 150 dB (Valls-Solé, Solé, Valldeoriola, Muñoz, Gonzalez, & Tolosa, 1995), although many studies have utilized a stimulus of between 115 and 130 dB (Valls-Solé, Rothwell, Goulart, Cossu, & Muñoz, 1999; Abel, Waikar, Pedro, Hemsley, & Geyer, 1998; Brown et al., 1991a).

Landis and Hunt (1939, cited in Davis, 1984; Yeomans and Frankland, 1996) described the startle response as a patterned response consisting of several bilateral stereotyped muscle movements. This response started with blinking of the eyes and a characteristic facial expression, along with dorsiflexion of the head and neck. The

described response included a curling of the shoulders in a ventro-caudal direction, flexion of the elbows and fingers, bending of the trunk, and bending of the knees. This generalized flexion response has been hypothesized by Yeomans and Frankland (1996) to be an adaptive defence response in terrestrial mammals to a predatory attack from the rear, as the response results in reduced exposure of the dorsal surface of the neck, a vulnerable point of attack. Brown et al. (1991a) described a similar response pattern consisting of eye closure, grimacing, as well as neck, trunk and limb flexion. They reported a large range in the latencies of onset of electromyographic (EMG) activity in the muscles; however a majority of EMG onset times were found at short latencies.

Many studies have reported that the reticular formation is of central importance in the startle response circuit (e.g. Davis, 1984). Specifically, the giant neurons of the nucleus reticularis pontis caudalis (RPC) in the reticular formation have been implicated as important contributors to the startle response through the use of collision studies, lesion studies, and intracellular recordings (Yeomans and Frankland, 1996). A grading in the amplitude of the startle response along with the intensity of the stimulus has been suggested to be the result of the number of RPC giant neurons recruited. As the stimulus intensity increases, the number of RPC neurons activated increases, leading to a larger startle response. In this way, the RPC giant neurons may act as "command" neurons of the acoustic startle response (Yeomans and Frankland, 1996). The RPC neurons then conduct to the various levels of the spinal cord, along the reticulo-spinal tract, and activate motoneurons with both weak monosynaptic connections, and strong disynaptic connections involving interneurons (Yeomans and Frankland, 1996). This motor

activation then produces the measurable EMG response and movement associated with the startle.

The Trigger Effect

Motor programs were described by Keele (1968, p. 387) as "a set of muscle commands that are structured before a movement sequence begins and allows the entire sequence to be carried out uninfluenced by peripheral feedback." This concept has been tested using a movement blocking paradigm (e.g., Wadman et al., 1979). Although the arm did not move when rapid arm movements were unexpectedly blocked during a rapid aiming task, a triphasic electromyographic (EMG) pattern was still observed as if the arm had moved (Latash and Gottlieb, 1991; Wadman et al., 1979). However, because the blocking paradigm involved perturbing the intended movement, some movement modification due to proprioceptive feedback was always observed. Specifically, when the movement was blocked, the EMG pattern was modified 100 ms after the agonist onset (50 ms after movement onset), and was thought to be the result of reflexive activity (Nagelkerke, Oakey, Mussell and Franks, 2000). As such, when using the blocking paradigm, the investigation of prepared movements is limited to the first 100 ms after EMG onset.

In order to further investigate the nature of the response and its preparation, it was necessary to circumvent feedback-based contamination of the movement as observed in the blocking paradigm. This has been accomplished using a startle response to elicit a pre-programmed movement (Valls-Solé, Rothwell, Goulart, Cossu, and Muñoz, 1999). Using a reaction time paradigm, it was reported that premotor reaction time (time from stimulus presentation to EMG onset) was significantly reduced when participants were

startled by an unexpected loud acoustic stimulus (130 dB) presented in conjunction with a

visual imperative stimulus. Based on these findings, Valls-Solé et al. (1999) suggested

that "the whole motor programme [could] be triggered [by the startle] without the typical

command from the cerebral cortex" (1999 p.937). This conclusion was based on two

results from the startle condition: First, the premotor reaction times (PMTs) observed

were very short compared to a control (no startle) condition, and second, EMG activity

was unmodified from this control condition. In the fastest reactions observed by Valls-

Solé et al., PMT was 65 ms. In a typical RT paradigm, RTs of 180 ms are commonly

observed in response to visual stimuli, while RTs of 140 ms are commonly observed in

response to auditory stimuli (Brebner & Welford, 1980, p.11). It was argued by Valls-

Solé et al. (1999) that movements initiated in less than 70 ms (i.e. PMT < 70 ms) were

unlikely to have involved the cortex due to fixed amounts of time needed for both

transducing the auditory stimulus and for neural transmission. Thus they suggested that

sufficient details of a prepared movement may have been stored in the brainstem and

spinal centres so that it could be, in some cases, initiated subcortically and released early.

Since the EMG activity for wrist movements (flexion or extension) retained their

characteristic triphasic profile through both control (no startle) and experimental (startle)

trials, the prepared movement appeared to be "released" unaltered. Specifically, since the

observed EMG patterns were unchanged, Valls-Solé et al. (1999) believed the observed

response was not produced by an early startle reflex adding on to a later voluntary

response. However, since the simple wrist flexion / extension tasks employed by Valls-

Solé et al. did not require an accurate response, it is unclear whether when startled, the

released (speeded) response was produced as intended and unaltered.

Following on from the work of Valls-Solé et al. (1999), Carlsen, Chua, Inglis, Sanderson and Franks (in press) investigated the kinematics of the response that was produced in a startled RT task. Participants performed a simple RT task involving extension of the forearm at the elbow joint. The task, however, involved moving the arm a prescribed distance to a specific target located at 20, 40, or 60 deg from the starting point. Results showed that when startled, mean premotor RT (PMT) was significantly shorter than Control PMT although there were no differences in mean peak displacement or movement final position for any of the targets. The lack of an effect of the startle on aiming accuracy indicated that the response produced was indeed the prepared response. These findings support the hypothesis that a startle stimulus may act as an early trigger for a prepared movement.

The implication from the studies by Valls-Solé et al. (1999) and Carlsen et al. (in press) is that motor commands prepared in advance for voluntary action can be triggered by the same structures that are activated by the startle response. In order for this to take place, the motor commands must be accessible and ready to be released. The hypothesis is that adequate information about the movement may be stored in the brainstem and spinal centres so that in some cases, the whole motor programme can be triggered without the typical command from the cerebral cortex (Valls-Solé et al., 1999). The reticulo-spinal system, particularly the giant neurons of the nucleus reticularis pontis caudalis have been implicated in the production of the acoustic startle response and may act as control neurons, mediating the response (Yeomans and Frankland, 1996). Thus, it may be possible for activation of this system to trigger the motor commands required to correctly produce the desired motor response by bypassing the cortex and the normal process of

stimulus recognition. In this way, the reticulospinal system may be an important part of the response pathway in ballistic RT tasks (for more detail see Appendix A).

The aim of this thesis was to extend previous work investigating the use of startle in RT tasks. Of initial concern, however, was that the effect of the startle has been shown to decrease as the number of presentations of the stimulus increases (Davis, 1984). This is referred to as "habituation" to the stimulus. The first experiment investigated the process of startle habituation when participants were involved in a RT task. The results aided in informing the methods of the second experiment and will inform future studies. The second experiment investigated one of the major criticisms of the hypothesis that a startle "triggers" prepared movements. Instead, it has been suggested that the decrease in RT observed when participants are startled may be due to increased systemic activation from the startle, thereby decreasing neural thresholds. If this is the case, a decrease in RT should also be observed when a movement is not prepared in advance. Therefore, the second experiment investigated the effect of startle on PMT in simple RT tasks and in RT tasks in which a choice had to be made.

Experiment 1

Startle Response is Dishabituated During a Reaction Time Task

Habituation of the startle response is characterized by a gradual decrease in response magnitude as the number of exposures to the stimulus is increased, and has been observed in most studies involving the use of a startling stimulus (Abel et al., 1998; Davis, 1984; Davis and Heninger, 1972; Leaton, Cassella, and Borszcz, 1985; Schicatano and Blumenthal, 1998; Valls-Solé, Valldeoriola, Tolosa and Nobbe, 1997).While the habituation effect has been observed as a decrease in EMG response amplitude, observed response latency is unaffected (Schicatano and Blumenthal, 1998). EMG evidence has shown that in humans, many components of the startle response are no longer seen after two to six random presentations of the startling stimulus, indicating that the participants quickly habituate to the startling stimulus (Brown et al., 1991a). The observed pattern of habituation is not random, nor is it "all-or-none," as the response amplitude tends to decline gradually with repeated exposure (Abel et al., 1998) resulting in a disappearance of the response in peripheral muscles prior to more central muscles (Davis and Heninger, 1972). Results of experiments by Brown et al. (1991a) indicate that aside from the orbicularis occuli (OOc), which is also responsible for the eyeblink response, EMG activity in the sternocleidomastoid (SCM) muscle was the last to disappear when participants were repeatedly exposed to the startling stimulus, making it the most important independent indicator of a startle response.

Habituation has been described as one of the most basic forms of nonassociative learning, which involves a decrease in behavioural response to a repeated stimulus (Kupfermann, 1991). The decrease in response is thought to be caused by depressed

synaptic transmission in the involved neural circuit (Kandel, 1991). Although the neural mechanism of startle habituation is not well understood (Jordan, Strasser, & McHale, 2000), it is thought to be independent of processes underlying habituation of other systems. Two theories regarding the processes underlying habituation have been forefront in the literature (Rimpel, Geyer, & Hopf, 1982). The first theory involves a reduction in the effectiveness of synaptic transmission, in which repeated stimulation of the neuron itself results in diminished post-synaptic potentials, due to decreased neurotransmitter production and release (Rimpel et al., 1982). The other mechanism involves the build-up of activity in an inhibitory side chain. This theory holds that repeated stimulation acts not only on the neuron that habituates, but also on a side chain that may exert progressively increasing presynaptic or postsynaptic inhibition on the habituating neuron resulting in a depressed response (Wickelgren, 1967).

An unexpected, loud acoustic stimulus (124dB) has also been shown to elicit a startle response in participants preparing to react to a "go" signal (82 dB) during a simple reaction time (RT) task. Valls-Solé, Rothwell, Goulart, Cossu, & Muñoz (1999) demonstrated that premotor RT could be reduced by as much as 77 milliseconds when participants were startled. However, due to habituation of the startle response, employing it as a tool in scientific investigations can be problematic. Several difficulties arise when startling a participant multiple times in the course of an experiment. For instance, there are conflicting reports regarding the rate of habituation depending on the activity required of the participant. Brown et al. (1991a) found that when participants were sitting quietly, there was no measurable EMG response present following 2 to 6 random presentations of the startling stimulus. In contrast, a recent study by Siegmund, Inglis, and Sanderson

(2001), reported that <u>no habituation</u> occurred when participants were engaged in a RT task. Specifically, participants were instructed to make a swift rotational head movement in order to look at a target. Because reaction times remained speeded in the startle condition throughout the study, and response kinematics and EMG amplitudes were unchanged after 14 presentations of the startling stimulus, the authors argued that habituation did not occur. This was in contrast to observed habituation in startle only (no movement) trials. However, the most important independent indicator of startle, the SCM muscle (Brown et al., 1991a), was also the prime mover in this study. Therefore, the suggestion that a startle occurred was inferred from other factors. First, the RT during the startle (ST) trials was significantly shorter than control trials, and voluntary activation of the SCM and Paraspinal muscles (PARA) in the ST trials was aligned with startle activation of these muscles in the startle-only trials. Second, the amplitude of the EMG was significantly larger in the ST trials. Therefore, the inference that habituation did not occur was based on the fact that RTs in the startle condition were significantly shorter throughout the experiment, and that the amplitudes of the EMG responses did not change as the number of startle stimulus presentations increased. Thus, although the amplitudes and latencies revealed a startle-like pattern throughout the experiment, the results may have been contaminated, as voluntary activation was required by the same muscles. The activation of Orbicularis Oculi and Maseter muscles, which were also measured, have been shown to be unreliable and disputed indicators of a startle (Brown et al., 1991a).

In another experiment that investigated the effects of repeated startle stimulation, Valls-Solé et al. (1997) found that no habituation occurred under certain conditions. Specifically, in participants who were startled when preparing to react to a "go" signal in

a RT task, no habituation to the startling stimulus was observed. In their experiment, participants were exposed to five startling stimuli in each of four different conditions: Resting quietly, resting in a busy environment, preparing to react in a reaction time task, or focusing on an upcoming visual stimulus. The rate of habituation was significantly decreased when participants were startled in conjunction with a visual "go" signal in a RT task. Specifically, in this condition, peak EMG amplitude in the SCM and MAS did not decrease below 60% of initial amplitude, whereas in all other conditions, peak EMG amplitude in these muscles fell below 20% of initial values by the fifth presentation of the stimulus. Unfortunately, the study did not determine how many startling stimuli could be presented before habituation of the response occurred.

Taken together, it appears from these studies that habituation does not occur in a similar manner or with a similar time course when participants are engaged in voluntary activities compared to when they are sitting quietly. However, what remains unclear is the time course of the habituation process when a RT task is involved. It remains to be determined how many times a participant can be startled in a RT experiment before the stimulus becomes ineffective in producing a startle response and significantly speeding the prepared action in a reaction time task. The present experiment was designed to address this issue. The purpose of the present study was to determine the effects of repeated random startle stimulation on RT and on the EMG responses of both the startle indicators (orbicularis oculi and sternocleidomastiod), and the wrist extensors (extensor carpi radialis longus) and flexors (flexor carpi radialis). These results will be important in informing the design of subsequent experiments involving the startle response and RT tasks.

Method

Participants

Twelve right-handed volunteers (8M, 4F; ages 25 +/- 5 years) with no obvious upper body abnormalities or sensory or motor dysfunctions volunteered to participate in the study after giving informed consent. The participants were all naïve to the hypothesis under investigation. Testing of each participant took place in one afternoon session. This study was conducted in accordance with ethical guidelines established by the University of British Columbia.

Task

The experimental task was to perform a 20 deg wrist extension movement to a fixed target as quickly and as accurately as possible following an auditory stimulus. Participants were encouraged to react as soon as possible following the stimulus, and were offered a monetary bonus for doing so. This was done because RT studies in which the level of motivation of the participant was manipulated have indicated that RT can be affected by motivational instructions. Shankweiler (1959) has shown that positively motivating (success) instructions or negatively motivating (failure) instructions can result in decreases in RT of up to 32 ms as compared to non-motivating (standard) instructions. Thus, in the present study, a monetary bonus was provided for fast RTs. A target RT, based on RTs achieved during practice, served as a "time to be beaten" for the bonus during the testing phase. The performance bonus consisted of a payoff scheme that allowed the participants to earn money for each millisecond under the participants target RT achieved; one cent was paid on each trial to a maximum of 30 cents per trial.

Participant Position

The participants sat in a height-adjustable chair outfitted with an automobile racing harness (Racer Components Inc.) in order to constrain any movement to the wrist joint. The right arm was secured, in a semi-prone position with the palm facing inward, to a custom-made aluminium wrist manipulandum that moved in the transverse plane with an axis of rotation at the wrist joint. The hand was secured in the hand support portion of the manipulandum to restrict any unwanted movement with the wrist joint directly in line with the axis of rotation and the manipulandum arm. The manipulandum was oriented at an angle of 15 degrees to the right of the body midline, as this has been found to be a more comfortable position than orienting the manipulandum parallel to the body midline. The starting position (20 degrees of flexion from neutral) was indicated by a mechanical stop. Prior to testing, the arm / manipulandum unit was obscured from view so that direct visual feedback was not available.

Recording Equipment

Surface EMG data were collected from the muscle bellies of the following superficial muscles: right flexor carpi radialis (FCR), right extensor carpi radialis longus (ECR), left orbicularis oculi (OOc), and left sternocleidomastiod (SCM) muscles using bipolar preamplified Ag/AgCl surface electrodes (Therapeutics Unlimited). The recording sites were prepared and cleansed in order to decrease electrical impedance. The electrodes were oriented parallel to the muscle fibers, and then attached using double sided adhesive strips. A grounding electrode was placed on the participant's left radial styloid process. EMG data were amplified onsite and the electrodes were connected via shielded cabling to an external amplifier system (Therapeutics Unlimited Inc. Model

544). Wrist angular displacement data were collected using a potentiometer attached to the pivot point of the manipulandum. All data were digitally sampled at 2 kHz (National Instruments® AT-MIO-16) using a customized program written with LabVIEW® software (National Instruments Inc.).

Stimuli

The warning tone consisted of three short beeps (100 ms, 1000 Hz, 80 dB each, separated by 500ms) generated by the computer using a 16 bit sound card (Creative SoundBlaster 16®) and standard computer speakers (Juster® sp-691n). A fixed foreperiod of 2.5 sec. spanned the time between the end of the warning tone and the imperative stimulus. A computer program generated the trial imperative stimuli consisting of a narrow band noise pulse (1 kHz, 40ms duration). The signal was amplified and presented via a loudspeaker (<1 ms rise time) placed directly behind the head of the participant with an intensity of either 80 +/-2 dB (control imperative stimulus) or 124 +/- 2 dB (startle tone). The stimuli intensities were measured using a sound level meter (Cirrus Research model CR:252B) at a distance of 30 cm from the loudspeaker (approximately the distance to the ears of the participant). The control tone was similar in pitch, duration and amplitude to the warning tone sound.

Target and Feedback

The target was a fixed point in space located at 20 degrees of angular displacement into extension with respect to the right wrist's starting position. A computer screen placed directly in front of the participant provided real time feedback during trials by representing the position of the manipulandum with a vertical marker line (1 cm tall)

on the screen. The marker's movement corresponded directly to movement of the manipulandum and only moved in the horizontal plane. The starting position of the marker corresponded to it being stationary 5 cm from the left edge of the computer screen. The target was represented by a blue target line (1 cm tall), 10 cm from the right edge of the screen. After each trial, feedback information including trial outcome (good or bad), displacement error at the end of the initial impulse (deg), reaction time (ms) and movement time (ms) were displayed on the same computer monitor display.

Training

Participants were allowed to practice the task prior to testing to familiarize themselves with the task and equipment. The experimental RT task consisted of an active extension of the right wrist from the starting position to a fixed target located at 20 degrees of angular extension from the starting position. The participants were instructed that they would first hear a warning tone consisting of a series of 3 beeps, followed by a foreperiod (duration unknown to the participants), and finally a "go" tone (imperative stimulus). Instructions emphasised fast reaction times and fast movement times, as well as minimising target error. Participants were also instructed that the loudness of the stimulus would be variable. Participants received blocks of 10 practice trials, and were deemed to have reached an adequate level of task competence to start the testing trials when they could successfully hit the target (± 5 deg) 4 out of the last 5 practice trials in a block. No participants performed more than two practice blocks.

Experimental Trial Types

Control trials were trials in which the participant carried out the normal protocol of the experiment. Startle trials (ST) consisted of trials in which the startle stimulus was given in place of the imperative non-startle stimulus.

Participants performed 4 blocks of 25 good trials in which 5 ST trials were randomly dispersed for a total of 20 startle trials per participant out of 100 total good trials. Control Trials in which the participant did not react, in which displacement RT was more than 500 ms or less than 50 ms, or in which there was more than ±10 degrees error, were rejected. Startle trials were never rejected. ST trials did not occur within the first three trials of any block and there were never two consecutive ST trials. Four catch trials (also excluded from analysis) in which there was no imperative stimulus occurred randomly in each block. This was done to discourage incorrect anticipation and false starts.

Data Reduction

Displacement RT was defined as the first point of a change of more than 0.2 deg of angular displacement from the starting position following the stimulus. Peak displacement was determined by identifying the point at which velocity first returned to zero following movement onset. The final position of the movement was defined as the first point at which angular velocity remained below 8 deg/sec for at least 100 ms. Movement time was defined as the time (in ms) between displacement onset and final position. Surface EMG burst onsets were defined as the point at which the EMG first began a sustained rise above baseline levels. The location of this point was determined by first displaying the EMG pattern on a computer monitor with a superimposed line

indicating the point at which activity increased to more than 2 standard deviations above baseline (mean of 50 ms of EMG activity preceding movement). Onset was then verified by visually locating and manually adjusting the onset mark to the point at which the activity first increased. This method allowed for correction of errors due to the strictness of the algorithm. Premotor RT was defined as EMG onset in the ECR muscle. Peak EMG amplitudes were defined as the largest EMG amplitude, rectified and filtered with a 25 Hz lowpass elliptic filter, recorded within an interval of 100 ms following EMG burst onset. EMG offsets were marked in a similar fashion, with the activity between EMG onset and EMG offset being defined as a distinct burst. To normalise the EMG for comparison between participants, ST trial EMG burst amplitudes for the ECR and FCR were expressed as a percentage of the mean peak EMG amplitude for each respective muscle in the Control condition for each participant. Since there was not normally SCM or OOc activity in the Control condition, ST trial peak EMG amplitude for these muscles was expressed as a percentage of the first ST trial EMG amplitude for the SCM and OOc muscles respectively.

Statistical Analyses

Dependent measures (premotor RT, peak displacement, movement final position, peak EMG amplitude, and EMG burst timings) were analyzed using one-way repeated measures analysis of variance (ANOVA), to determine if differences existed between Control and Test trials. Differences with a probability of less than .05 were considered to be significant. Tukey's Honestly Significant Difference (HSD) post-hoc tests were administered to determine the locus of the differences.

Results

Startle Response Indicators

The amplitudes of rectified and filtered EMG from both startle response indicators, SCM and OOc, were compared between the successive ST trials and results are presented in Figure 1. Amplitudes were subjected to a one-way (20 ST trials) repeated measures ANOVA. No main effect was found for trial position for either the SCM, $F(19, 209) = 1.334$, $p = 0.165$, or the OOc, $F(19, 209) = 1.503$, $p = 0.124$, indicating EMG amplitude was not different for any of the ST trials for either SCM or OOc. No significant trend was found for the SCM. However, there was a significant linear trend in OOc, $F(1, 11) = 23.230$, $p = 0.001$, indicating that in the OOc, EMG amplitude tended to decrease linearly from the first ST trial to the 20th ST trial.

Although startle response EMG burst activity in the OOc was present in 89.4 % of the ST trials, SCM burst activity was only present in 66.1 % of the ST trials. However, the incidence of ST trials in which there was no SCM activity recorded was no higher in the last 10 ST trials (39.2 % of ST trials) compared to the first 10 ST trials (27.5 %), $\chi^2 = 3.15$, $p > 0.05$, across all participants (see Fig. 2).

Figure 1. Mean peak EMG amplitude (SE) of startle indicator muscles,

sternocleidomastoid (SCM) and orbicularis oculi (OOc), for each startle (ST) trial in

order of presentation as a percentage of the EMG amplitude in the first ST trial in which

activity was observed (activity was absent in the first ST trial for 2 participants therefore

% amplitude in ST1 was less than 100).

Figure 2. Individual participant data indicating startle (ST) trials in which a

sternocleidomastoid (SCM) burst was observed (grey) or not (white). * indicates

participants designated as low-responders (no startle response in first two ST trials).

Response EMG

Analysis of premotor RT revealed that RT was significantly shorter in the ST condition (98.6 ms) compared to the Control condition (127.9 ms), $F(1,11) = 35.057$, $p < 0.001$. Furthermore, there was no difference in premotor RT in the ST condition between the first startle and the 20th startle, $F(19, 209) = 0.632$, $p = 0.767$, indicating that throughout the experiment in the ST condition, RT remained consistently shorter than in the Control condition (see Fig. 3).

Given that in some ST trials startle EMG activity was absent, it was unclear if the participants were actually startled. Therefore, we separated ST trials in which there was no startle indicator activity from the other ST trials. Premotor RT was compared between Control trials, ST trials in which SCM activity was observed (ST+) (n = 160), and ST trials in which no SCM activity was observed (ST-) (n = 80). Results are summarized and illustrated in Figure 4 and Table 1. A main effect was found for trial type, $F(2,18) = 27.786$, $p < 0.001$, with post-hoc analysis indicating that premotor RT was significantly different ($p < 0.05$) between all three conditions. Premotor RT was significantly shorter in ST+ (91.3 ms) than ST- trials (110.8 ms). Furthermore, RT was significantly shorter in both ST situations than in Control trials (127.9 ms).

Similar analysis was also performed on ST trials with or without OOc activity. In contrast to differences in RT with and without the presence of SCM activity, there were no differences in RT between ST trials in which OOc activity was observed (99.9 ms) versus ST trials with no OOc activity (99.8 ms).

Figure 3. Mean premotor reaction time (SE) for each startle (ST) trial in order.

Figure 4. Premotor reaction time (SE) in each condition. Control trials (striped) can be compared to startle (ST) trials (black) or the components of the ST trials (white). Startle (ST) trials are comprised of ST trials in which sternocleidomastoid (SCM) activity was observed (ST+) and ST trials in which no SCM activity was observed (ST-).

Table 1

Wrist EMG and Kinematic Measures in Each Condition

	Control		ST-		ST+	
EMG Measure						
ECR Premotor RT (ms)	127.92	(23.17)	*†110.79	(22.06)	*91.35	(17.08)
Ag1 Duration (ms)	62.69	(09.33)	67.17	(15.60)	68.66	(09.13)
Ant Duration (ms)	45.78	(08.59)	47.62	(11.43)	43.24	(08.66)
Ag2 Duration (ms)	55.86	(09.63)	54.12	(10.13)	51.14	(09.57)
Ag1 to Ant interval (ms)	74.92	(19.78)	74.37	(13.31)	76.08	(14.52)
Ag1 to Ag2 interval (ms)	125.43	(27.42)	130.85	(26.45)	131.87	(21.03)
Ag1 Peak Amplitude (%)	100.00	(0)	106.12	(09.92)	*120.33	(21.04)
Ant Peak Amplitude (%)	100.00	(0)	†112.34	(34.43)	*169.51	(84.94)
Ag2 Peak Amplitude (%)	100.00	(0)	†101.68	(23.22)	*125.03	(33.35)
Kinematic Measure						
Peak Displacement (deg)	24.92	(03.08)	*29.02	(02.47)	*31.18	(05.94)
Time to Peak Dx (ms)	119.24	(23.22)	113.97	(20.16)	*105.80	(19.23)
Final Position (deg)	19.87	(00.92)	20.77	(02.74)	21.01	(02.58)
Movement time (ms)	269.41	(55.88)	285.23	(68.20)	287.52	(58.39)

Note. ST+ refers to ST trials in which SCM activity was observed. ST- refers to ST trials in which no SCM activity was observed. Ag1 refers to the first agonist (ECR) burst, Ag2 is the second agonist burst, and Ant is the antagonist (FCR) burst. Intervals are times from onset to onset. Standard deviations are shown in parentheses. * denotes significant difference from control condition. † denotes significant difference from ST+.

Analysis of the timing characteristics of the triphasic EMG pattern revealed no differences between the Startle and Control conditions in the initial agonist (ECR1) burst duration, $F(2, 18) = 0.768$, $p = 0.479$, antagonist (FCR) burst duration, $F(2, 18) = 0.298$, $p = 0.746$, second agonist (ECR2) burst duration, $F(2, 18) = 1.356$, $p = 0.283$, ECR to FCR inter-onset time, $F(2, 18) = 0.329$, $p = 0.724$, or in ECR1 to ECR2 inter-onset time, $F(2, 18) = 0.348$, $p = 0.711$, (Table 1), suggesting that the timing of the triphasic EMG pattern was unchanged across conditions. However, EMG amplitude differences were found, between the conditions in all three bursts including ECR1, $F(2, 18) = 4.573$, $p = 0.025$, FCR, $F(2, 18) = 6.359$, $p = 0.008$, and ECR2, $F(2, 18) = 3.885$, $p = 0.040$ (Table 1). Post-hoc analysis revealed that EMG burst amplitude was larger ($p < 0.05$) in the ST+ condition than the ST- and Control conditions for all bursts except ECR1, in which ST+ amplitude was found to be larger than Control amplitude, however, not different than ST-amplitude (see Table 1).

Response Kinematics

Response kinematics were analyzed to determine if differences existed in movement production variables between the conditions. No significant differences were found between the conditions in final position, $F(2, 18) = 2.385$, $p = 0.115$, or movement time, $F(2, 18) = 0.957$, $p = 0.403$, (see Table 1). However, significant differences in peak displacement, $F(2, 18) = 13.703$, $p < 0.001$, and time to peak displacement, $F(2, 18) = 15.843$, $p < 0.001$, were found. Post-hoc comparison revealed that in both ST situations (ST+ and ST-), peak displacement was significantly larger than in the Control condition, although peak displacement was not different between the ST+ and ST- trials. In

addition, time to peak displacement was significantly shorter for the ST+ condition compared to the ST- and Control conditions (Table 1).

Discussion

Startle Response Habituation

Previous reports have indicated that in humans sitting quietly, and not engaged in a motor activity, startle habituation was complete (disappearance of startle response EMG activity) after 2 to 6 random presentations of the startling stimulus (Brown et al., 1991a; Valls-Solé et al., 1997). However, other evidence suggested that when participants were prepared to perform a RT task, habituation rate was diminished or absent (Siegmund et al., 2001; Valls-Solé et al., 1997). In the present study, peak EMG amplitude in both the sternocleidomastoid (SCM) and orbicularis oculi (OOc) muscles was used to measure the startle response amplitude, with emphasis on the SCM. Our findings indicate that when engaged in a RT task, startle response habituation was absent, even after 20 startle trials. This finding is in agreement with previous reports (Valls-Solé et al., 1997), and extends the previous findings to include up to 20 startle trials. Specifically, we found no significant decrease in SCM peak amplitude from the first startle trial (ST1) to ST20 across subjects. Furthermore, there was no significant trend towards a decrease in amplitude and there was no significant decrease in OOc amplitude from ST1 to ST20. However, there was a significant linear trend towards a decrease in OOc EMG amplitude. This same trend (a linear decrease in OOc activity) has been previously reported by Ornitz, Russell, Yuan, & Liu, (1996) and Fox, (1978), but not within the context of a startled RT task.

The previously observed reduction in startle habituation when participants were engaged in a RT task (Siegmund et al., 2001; Valls-Solé et al., 1997) has been attributed to two main factors. First, since the startle response has been shown to be modulated by cortical structures, cortical processes such as attention and gating might play a role in the excitability of the startle circuit. Although it has been argued that startle habituation is a process that occurs in the brainstem (Leaton et al., 1985), several studies have implicated higher brain centres in modulating the habituation. For example, in a review of lesioning studies involving the startle circuit, Davis (1984) reported that a decrease in habituation was observed in rats with lesions of either the hippocampus, the midbrain reticular formation, or with complete cerebral cortex transection. In addition, studies involving humans with cortical lesions have revealed decreased habituation and an increase in startle response (Liégeois-Chauvel et al., 1989). Similarly, Timmann, Musso, Kolb, Rijntjes, Jüptner, Müller, Diener, and Weiller (1998), using positron emission tomography (PET), reported that during habituation, there is a decrease in cerebellar activity reflecting a decrease in tonic activity on reticular neurons involved in the startle circuit. These studies indicate that the excitability of the startle response may be at least partially under cortical or cerebellar control, and that the cortex as a whole may be inhibitory to the startle response.

Since cortical structures can influence the excitability of the startle response, cortical processes may also play a role in the modulation of the startle response. Behavioural evidence substantiates this possibility. For example, the use of a weak antecedent stimulus or "prepulse" results in reduced startle response amplitude (Graham, 1975). This type of reflex modification has become known as prepulse inhibition (PPI) of

startle (Davis, 1984; Hoffman, 1984; Lehmann, Pryce, & Feldon, 1999) and is thought to reflect the ability of higher brain centres to filter or "gate" incoming stimuli (Abel et al., 1998; Blumenthal, 1996; Fendt, Li, & Yeomans, 2001; Zhang, Engel, Ericson & Svensson, 1998). The extent of the startle modulation by a prepulse has been thought to be affected by the extent to which the prepulse can attract attention (Lipp, Siddle & Dall, 2000). Similarly, attention directed towards a stimulus of the same modality as the startling stimulus has been shown to increase startle amplitude, whereas directing attention towards a different stimulus modality has been shown to decrease startle amplitude (Acocella and Blumenthal, 1990; Richards, 2000; Schicatano and Blumenthal, 1998). Directed attention may modulate the startle response by enhancing the complimentary sensory systems and attenuating competing sensory systems (Richards, 1998; Richards, 2000). Thus, by directing attention to a given sensory modality, the excitability of the involved neural networks may be increased.

A second argument explaining the reduction in startle habituation when participants are engaged in a RT task involves the influence of motor preparation (Siegmund et al., 2001; Valls-Solé et al., 1997). It has been demonstrated repeatedly using electroencephelography (EEG) that motor readiness is reflected by a slowly increasing bilaterally recorded negative potential (e.g., Brunia, 1993). This negativity represents an increase in excitatory post-synaptic potentials (EPSPs), moreover, motor preparation results in increased excitability of all the structures involved in the execution of a motor command. For example, using transcranial magnetic stimulation (TMS) resulted in increased amplitude of evoked muscle potentials (MEPs) in the short time (up to 23 ms) preceding agonist onset, indicating an increased excitability of the motor

response pathway (MacKinnon and Rothwell, 2000; Rothwell, MacKinnon & Valls-Solé). Thus readiness to perform a motor act may increase the excitability of both the cortical and subcortical components of the response pathway.

<u>Dishabituation during a RT Task</u>

In the present study there were few ST trials in which OOc activity was absent (10.6 %). Since the activity in the OOc was almost always present in ST trials, it is unlikely that its presence was a good indicator of a startle response. This same position was taken by Brown et al., (1991a) who suggested that the blink reflex, also elicited by non-startling acoustic stimuli, may be physiologically separate from the startle response since the blink reflex continued to be produced despite no other manifestation of a startle response (Brown et al., 1991a). In contrast to ST trials with no OOc activity, we observed several ST trials in which SCM activity was absent (33.9 %). Only one participant exhibited SCM activity (indicating the presence of a startle response) in all 20 trials, and two participants out of 12 (16.7 %) did not exhibit SCM activity in either of the first two trials. This number of low responders agrees with previous reports (Abel et al., 1998; Geyer and Braff, 1982). However, data from these two participants were still taken into account in the present analysis. The incidence of observing a ST trial in which there was no SCM activity was no higher in the last 10 ST trials as compared to the first 10 ST trials ($\chi^2 = 3.15$). Thus if habituation was reduced by a RT task requirement, it is unclear why there was an observed incidence of non-startled ST trials (ST-) at random in nearly 34% of ST trials. Our contention is that habituation of the startle circuit itself may have still occurred normally as described previously (see Brown et al., 1991; Valls-Solé et al., 1997); but it may have been transiently overridden by other processes. Under normal

circumstances (participants sitting quietly), startle habituation is complete after 2 to 6 presentations of the stimulus (Brown et al., 1991). Similarly, Siegmund et al. (2001) showed that no measurable startle response was elicited in control ST trials (participants sitting quietly) following either 7 or 14 startled RT trials. This was observed although no habituation was evident when participants were actively performing the RT task. This evidence seems to indicate that while the normal process of habituation was still occurring, other factors were overriding the habituation, allowing the startle response to continue to be elicited. Thus the reduced habituation reported by both Valls-Solé et al. (1997) and Siegmund et al. (2001) as a result of a RT task requirement might have instead been an "overriding of habituation" or dishabituation as opposed to a reduction of the neural processes leading to habituation. Dishabituation has been previously described as a sensitizing stimulus overriding the effects of habituation (Kupfermann, 1991). In a similar way, in the present experiment, directed attention to the same stimulus modality as the startling stimulus, as well as motor readiness, may have both led to increased excitability of both the efferent and afferent pathways, transiently enabling the startle response. In this way, if participants were not sufficiently attending to the task, or if the participants were not sufficiently "ready" on a particular startle trial, the startle would not be enabled, leading to a non-startled ST trial (ST-), with no evidence of SCM activity.

<u>Reaction Time Data</u>

It has been shown that a startling acoustic stimulus can elicit a prepared ballistic response at very short onset latencies (Carlsen, Hunt, Inglis, Sanderson, & Chua, 2003; Siegmund et al., 2001; Valls-Solé et al., 1995; Valls-Solé et al., 1999). However, the phenomenon of non-startled ST trials was also evidenced in the RT data. Reaction time

was consistently and significantly lower across all ST trials (98.59 ms) compared to

Control trials (127.92 ms). This result agrees well with previous findings (Carlsen et al.,

in press; Siegmund et al., 2001; Valls-Solé et al., 1995; Valls-Solé et al., 1999) indicating

that the prepared response was speeded by the startle. Additionally, there was no

significant difference in RT in ST trials from ST1 to ST20, indicating that RT remained

significantly shortened throughout all ST trials. However, in comparing ST trials in

which SCM activity was observed (ST+) to ST trials in which no SCM activity was

observed (ST-), it was found that RT was significantly lower when SCM activity was

present (91.4 ms) than when SCM activity was not present (110.8 ms). It appears

therefore, that the prepared movement may have been initiated by separate processes in

these two situations. We suggest that in certain ST trials, the participant was not startled.

If the participant had habituated to the startle, but was not sufficiently ready, or was

insufficiently attending to the task, the habituation may not have been overridden and the

participant may not have been startled by the loud stimulus. Therefore if the reticular

formation was not sufficiently activated to produce a startle response (as evidenced by

activity in the SCM), it is unlikely that there would have been sufficient activity to trigger

or release the prepared response (as evidenced by significantly slower RTs). However,

RTs in ST- trials (110.8 ms) were still significantly shorter than in Control trials (127.9

ms). Since it has been shown that louder stimulus intensities result in shortened reaction

time (first recognized by Piéron, 1919, cited in Woodworth, 1938 p. 318; see also

Kohfeld, 1969) and the ST- trial responses occurred with a sufficient latency to have

involved cortical areas, we propose that in the ST- trials the shorter RT observed

compared to the Control RT was a result of sensory facilitation due to increased stimulus intensity.

Although the incidence of ST trials in which there was no OOc activity was much lower (10.6 %) than ST trials with no SCM, these were also analysed for differences in RT. In contrast to RT differences due to the presence of SCM activity, there was no difference in RT between ST trials with OOc activity (99.9 ms), or ST trials without OOc activity (99.8 ms). Because activity in the OOc did not allow for the discrimination between ST trials in which RT was significantly shortened or not, we presume that OOc was not a good indicator of the presence of a startle response.

<u>Kinematic Analysis</u>

Kinematic analysis revealed that there were no differences in movement time (MT) or final position between Control and ST trials, indicating that the required response was produced with similar timing and accuracy across conditions (see Table 1). This finding is in agreement with previous reports (Carlsen et al., 2000; Carlsen et al., in press). Furthermore, no differences were found in either EMG durations or EMG interburst intervals between Control and ST trials, further indicating that the response that was produced was unchanged (in terms of EMG timing characteristics) between the conditions (Table 1). However, results showed that peak displacement and the time to peak displacement were different between the ST+ and Control conditions. Specifically, compared to the Control condition, participants produced a movement in the ST+ trials with a larger peak displacement (31.2 deg vs. 24.9 deg), while reaching peak displacement in a shorter time (105.8 ms vs. 119.2 ms). Interestingly, however, final position was unchanged, as was MT. The observed larger peak displacement might be

explained by the differences observed in the EMG amplitudes which were found to be significantly larger in the ST+ trials compared to the Control condition. Increased amplitude of the initial agonist burst has been attributed to the startle volley summing with the voluntary response (Siegmund et al., 2001). In this way, an increased EMG burst amplitude due to startle and voluntary response summation may have resulted in a larger impulse and a larger peak displacement. Interestingly, in all conditions the movement was completed accurately and with similar MT. However, it is unclear how accurate completion of the task could have been accomplished if a motor program was released by the startle. It is unlikely that detection of an error and subsequent voluntary corrections to the movement could have been completed in the short amount of time (~150 ms) between peak displacement and final position, since this amount of time is similar to voluntary reaction time estimates. Furthermore, in the ST+ trials, EMG amplitude was elevated for all three phases of the triphasic pattern (Table 1). Summation with the startle volley cannot explain elevated amplitudes for the antagonist and second agonist bursts since they occur much later than the startle volley. One explanation for the observed pattern of results, is that what is triggered by the startle is not a prepared set of muscle actions (i.e. motor program, see Keele, 1968), but a single control variable that defines the movement endpoint or equilibrium point. This control variable has been proposed to be the threshold (λ) of a length sensitive reflex (Feldman, 1986; Latash and Gottlieb, 1991). Based on this model, the EMG would arise as a consequence of the movement. Thus, if the control variable was released, but EMG "leakage" from the startle volley (Siegmund et al., 2001) summed with the agonist EMG burst this would result in a larger peak displacement. Furthermore, since the control variable (λ) was unchanged, compensatory EMG would

result automatically in the antagonist to bring the wrist back to the correct endpoint. In this way, if the startle actually releases a control variable that defines the goal of the movement, the startled movement might be thought of as evidence for endpoint control. However, more research is required in order to support this hypothesis.

Conclusions

In summary, we suggest that although physiological habituation of the startle response occurs even when the participant is engaged in a RT task, that the increased excitability of the response pathway due to motor readiness and attentional processes may be sufficient to allow the startle response to be elicited indefinitely. Furthermore, it appears that activity in the SCM is the minimum adequate EMG indicator of whether a physiological startle response has been elicited. Results indicate that when there is activity in the SCM, there is sufficient activity to trigger a prepared response, whereas if there is no SCM activity, the response is triggered normally via cortical control. We suggest that the startle is a useful tool for probing RTs and investigating neural processes involved in response preparation; however, startle trials in which there is no SCM activity present should be treated separately from ones in which there is SCM activity observed. This would allow for the treatment of truly startled trials as a fully separate group of trials from stimulus intensity facilitated trials.

Experiment 2

Startle and Choice RT

Simple and Choice Reaction Time

There are three stages of processing involved in human information processing models, namely stimulus identification, response selection and response programming. The Reaction Time (RT) method has been used extensively since the mid-nineteenth century in the investigation of these motor control processes (Brebner & Welford, 1980). This method assumes that the time between the presentation of a stimulus and the beginning of response production is a valid temporal measure of the processes underlying the control of movement. Therefore, differences in the amount of time taken to complete the underlying processes should manifest as differences in RT. Certain factors generally add a constant amount of time to the RT. These include the translation of a stimulus into the neural language of the central nervous system by sensory transduction apparatus (such as the inner ear during an auditory reaction time task), as well as efferent and afferent neural conduction (Martin and Jessel, 1991). Due to their nature, these factors do not usually change as a function of experimental manipulations (for more detail see Appendix A – Startle Literature Review and Appendix B – Reaction Time and Precuing Literature Review).

Simple RT

In a Simple RT situation, there is a single stimulus requiring a single response, and as such, few processes occur between the stimulus onset and the production of the response (i.e. during the RT interval). Evidence of preprogramming (completing the

response programming stage in advance of the imperative stimulus) has been shown in several studies in which the complexity of the response was manipulated. Because RT has been found to increase along with response complexity in certain situations, it has been argued that more complex responses take more time to program during the RT interval (Henry and Rogers, 1960). Klapp (1996) however, demonstrated that in certain cases, the complexity of the response had no effect on the RT. His results demonstrated that in a task involving pronouncing words, the number of syllables to be pronounced did not affect Simple RT. Similarly, in a RT task involving short or long duration responses (Morse code elements dit-dah), RT was unaffected. Klapp (1996) suggested that when the response was known in advance, programming of the response could occur before stimulus onset so that only the triggering of the response was necessary following this imperative stimulus.

Choice RT

In a Choice reaction time (Choice RT) paradigm the processes that occur are more involved than in a Simple RT paradigm. More processes underlie the control of movement and take more time to complete before the response is produced. Donders (1868/1969) was among the first to investigate the time course of these processes. He believed that the information processing stages were independent and serial. Using subtractive logic, he attempted to determine the time course of each process. In order to accomplish this he devised three different reaction time tasks. The A-reaction was a Simple RT task, requiring a single action (pressing a key) in response to a single stimulus (a light illuminating). The B-reaction was a Choice RT task, requiring different responses (key press with right hand or left hand) in response to different stimuli (red light or blue

light). The C-reaction was a go/no-go task, in which a single response was required (key press) but still involved two stimuli (red light = press key, blue light = do not press key). Donders (1868/1969) argued that differences in RT between these tasks reflected differences in processing during various stages of the information processor. In this way, Donders demonstrated that it was possible to fractionate RT. In other words, it was possible to manipulate tasks in such a way that the time taken by each of the information processing stages could be measured.

In a serial-ordered model, as described by Donders (1868/1969), processing stages must follow sequentially. Therefore, if the appropriate response is to be selected from several alternatives (such as in a Choice RT paradigm), the response cannot be programmed in advance. It follows that in a Choice RT paradigm, response selection and programming must occur during the RT interval. Experimental evidence has supported this notion. Because of the need to discriminate between response alternatives, response selection is thought to require more processing time, thus increasing the RT interval. Hence Choice RT is usually longer than Simple RT. This difference was the focus of a classical study by Hick (1952). In Hick's study, participants reacted to the illumination of one of ten pea lamps by pressing a corresponding telegraph key. The number of possible stimulus-response (S-R) alternatives was manipulated in various ways, from increasing the number of choices in a regular manner, to random ordered numbers of choice alternatives. Results showed that as the number of S-R alternatives increased, so did RT. The increase seen in RT with the number of response alternatives, however, was not regular (linear). Hick suggested that when making decisions, uncertainty is resolved or "information is gained" at a constant rate. For example, each time the number of response

alternatives doubled, reaction time increased by a relatively constant amount (~150 ms). If the Log_2 of the number of alternatives represent the number of "bits" of information that needed to be gained to solve the uncertainty about the response (one bit being a binary choice whose probability was 0.5), each bit took a certain amount of time to process. In other words, each time a stimulus array had to be split in two to arrive at the correct stimulus-response pair, a constant amount of processing time was required, which increased RT in a logarithmic fashion. This evidence supported the notion that in a Choice RT paradigm, central processing was required to select the appropriate response during the RT interval. Similar evidence was provided by Klapp (1996), who found that more complex responses (longer duration) resulted in no difference in RT. In a Choice RT situation however, the increased duration (complexity) of the responses (number of syllables, or duration of keypresses) led to longer RTs. Because the more complex responses resulted in longer RTs, this was taken as evidence that in these cases, programming of the response had to have taken place following the imperative stimulus rather than prior to it (Klapp, 1996).

In contrast to the notion of response programming during the RT interval, it has been hypothesized that in some cases participants might prepare multiple complete and distinct programs in advance, and then simply select the correct one following the test stimulus. To investigate this, Rosenbaum (1980) instructed the participants to construct multiple responses based on the information available. If four responses were possible, the participant was instructed to construct the four possible responses in advance. From the results, Rosenbaum argued that since participants committed many more response errors when instructed to prepare multiple responses, that it was likely that the

participants were able prepare multiple responses when instructed to do so. However, he noted that when not specifically instructed to do so participants did not prepare multiple responses, as it was an inefficient strategy (Rosenbaum, 1980).

Recent studies have shown the importance of cortical involvement in the execution of movements requiring a choice of action. Schluter, Rushworth, Passingham, and Mills (1998) found that transcranial magnetic stimulation (TMS) was effective in interfering with the selection process in a visual Choice RT task. In this series of studies, TMS was applied over the motor cortex, dorsal premotor cortex and sensorimotor cortex at different latencies with respect to the visual cue. In the first experiment, they found that stimulation over the dorsal premotor cortex contralateral to the response hand 140 ms following the imperative stimulus was effective in delaying the response. The authors suggested that the RT delay resulting from this stimulation was due to a disruption in the response selection process. Stimulation over the motor cortex at longer latencies was also effective in delaying the response (Schluter et al., 1998). In the second experiment, stimulation was again given over the same areas and with the same latencies; however, it was given over the hemisphere ipsilateral to the response hand. Results showed that only stimulation over the left premotor cortex at 140 ms following the visual cue delayed response onset. Stimulation on the right side of this area had no effect. A third experiment was designed to investigate whether delays seen when stimulating over the premotor cortex actually reflected interference with the selection process as suggested previously. Participants performed either a Simple RT task or a Choice RT task. Stimulation was given over the ipsilateral premotor cortex at varying latencies. Again findings showed that stimulation over the left side at 100 ms following the visual cue resulted in response

delays in the Choice RT task. There was, however, no effect of this stimulation on the Simple RT task. Thus, the authors concluded that the left premotor cortex played a dominant role in response selection in a Choice RT task (Schluter et al., 1998)

Following these experiments, Schluter, Krams, Rushworth, and Passingham (2001) used positron emission tomography (PET) to study the cerebral dominance in the selection of actions. Participants performed either a Simple or Choice RT task that involved responding to a visual stimulus using left or right hands while being scanned by a PET scanner. There was significantly more activation in the left prefrontal, premotor and intraparietal areas during the Choice RT task as compared to the Simple RT task irrespective of which hand was used to respond (Schluter et al., 2001). These results supported the earlier findings that TMS disrupted processing during a Choice RT task when applied over the left premotor cortex (Schluter et al., 1998).

It has been suggested that a Choice RT task differs from a Simple RT task in that a visual discrimination must be made between the various stimuli and the appropriate response must be selected in the Choice RT task (Schluter et al., 2001). Furthermore, Schluter et al. (2001) suggested that activation in the left premotor and parietal areas were unlikely to be associated with a demand for visual discrimination, leaving only response selection as the source of this activation. It appears therefore that the process of response selection is a cortical event occurring in higher centres during the RT interval.

In contrast to the involvement of cortical areas during a Choice RT task, Valls-Solé et al. (1999) suggested that a prepared movement could be triggered by a startle from subcortical areas without the involvement of the cortex. This is important since it has been argued that pre-programming can occur in Simple RT paradigms, but not in

Choice RT Paradigms. Therefore, if the movement elicited by the startle is indeed the appropriate prepared movement released from subcortical structures, none should be triggered in a Choice RT paradigm. This is due to two pieces of data: First, making a choice involves cortical structures (Schluter et al., 1998; 2001), thus activation of subcortical structures should have no effect on Choice RT. Second, due to the serial nature of the human information-processing model, movement programming cannot occur until response selection has been completed, thus no response should be preloaded in subcortical areas in a Choice situation.

Generally, previous findings have shown that a startle actually produces decrements in performance on cognitive tasks. For example, Woodhead (1959) found that in a decision making task in which participants had to match moving symbols to stationary ones, that performance was impaired following a 110 dB stimulus for up to 31 sec. Similarly, findings from a later study (Woodhead, 1963) showed that when engaged in an arithmetic task, a 100 dB noise burst impaired calculation performance. The explanation forwarded by Woodhead (1963) for the performance decrement was that the presence of the loud stimulus caused a division of the participants' attention that would have otherwise been focussed on the cognitive task. In a similar study by Vlasak (1969), participants were instructed to subtract 7 in consecutive increments from 1000 in writing. In the first 30 seconds following a startling stimulus, Vlasak (1969) noted a significant performance decrement, from 10.3 correct subtractions to 7.4 correct. Vlassak (1969) suggested that the strong stimulus penetrated into the CNS, interrupting and superseding cognitive processes for a short time. These studies, taken together, indicate that a loud

stimulus may have detrimental effects on cognitive performance for a short time following the stimulus.

The aim of Experiment 2 was to determine whether a startling stimulus would have an effect on Choice RT. Specifically, when performing a task involving a choice between several equally likely response alternatives, would RT be speeded, remain the same, or be slowed in the presence of a startle. If the startle acts to elicit a prepared response in a Simple RT task (e.g., Valls-Solé et al., 1999), then no voluntary response should be elicited during a startle trial if choice is required. Alternatively, if the speeded response observed in startle serves to increase activation throughout the central nervous system, (Valls-Solé et al.,1995) a speeded voluntary response may be observed in a Choice RT task. However, if a startle results in slowed responses then the startle might provide cortical interference (Vlassak, 1969; Woodhead, 1963) leading to long RTs.

<div align="center">Method</div>

Participants

Twenty right-handed volunteers (7M, 13F; ages 23 +/- 4 years) with no obvious upper body abnormalities or sensory or motor dysfunctions volunteered to participate in the study after giving informed consent. The participants were all naïve to the hypothesis under investigation. Testing of each participant took place in one afternoon session. This study was conducted in accordance with ethical guidelines established by the University of British Columbia.

Only data from participants who showed speeded RTs due to the presence of a startle response were included in the analysis, since it was of interest if the startle acted differentially between the conditions. Therefore, data from six participants were excluded

from analysis. Two participants did not show evidence of a startle response, and four did not show evidence that the presence of a startle resulted in decreased reaction time. Data from fourteen right handed volunteers (4M, 10F; ages 23 +/- 3 years) were used in the final analysis.

Task and Instructions

The experimental task was a Simple / Choice RT task involving an active wrist flexion or extension of either the right or left hand to a fixed target region located at +/- 20 degrees of angular displacement from the starting position. The participants were instructed that they would first hear a warning tone consisting of a series of 3 beeps, followed by a pause, and then a target box indicating the correct target would appear. The instructions were to move from the starting position to the target denoted by the imperative stimulus "as fast and accurately as possible," stopping on the target, and staying there for a brief period of time (at least 1 sec). Instructions emphasized fast reaction times and fast movement times, as well as minimizing target and response selection error. Participants were instructed that an auditory tone would accompany the visual stimulus.

Participants were offered a monetary bonus for fast reaction times. This was done because RT studies in which the level of motivation of the participant was manipulated have indicated that RT can be affected by motivational instructions (Shankweiler, 1959). Thus, in the present study, a monetary bonus was provided for fast RTs. A target RT, based on RTs achieved during practice prior to each block of trials, served as a "time to be beaten" for the bonus during the following testing phase. The performance bonus

consisted of a payoff scheme that allowed the participants to earn money for each millisecond under the participants target RT achieved.

Positioning

The participants sat in a height-adjustable chair outfitted with an automobile racing harness (Racer Components Inc.) in order to constrain any movement to the wrists. The arms were secured, in a semi-prone position with the palms facing inward, to two custom-made aluminium wrist manipulanda that moved in the transverse plane with an axis of rotation at the wrist joint. The hands were secured in the hand support portion of the manipulanda. The manipulanda were oriented at an angle of 15 degrees outward from body midline, as this has been found to be a more comfortable position than orienting the manipulanda parallel to the body midline. The starting position was neutral (neither flexion nor extension) and was indicated by both online visual feedback on a computer monitor and magnetic detent. Rare earth magnets (1/2 inch) were secured to each manipulandum arm, and another was mounted 1 cm away from each arm in the attracting position so that greatest attraction was when the manipulandum arm was oriented neutrally (0 deg). This provided a tactile indication of the "home" position.

Recording Equipment

Surface EMG data were collected from the muscle belly of the following superficial muscles: right and left flexor carpi radialis (FCR), right and left extensor carpi radialis longus (ECR), left orbicularis oculi (OOc), and left sternocleidomastiod (SCM) muscles using bipolar preamplified Ag/AgCl surface electrodes (Therapeutics Unlimited). The recording sites were prepared and cleansed in order to decrease electrical

impedance. The electrodes were oriented parallel to the muscle fibers, and then attached

using double sided adhesive strips. A grounding electrode was placed on the participant's

left lateral malleolus. EMG data were amplified onsite and the electrodes were connected

via shielded cabling to an external amplifier system (Therapeutics Unlimited Inc. Model

544). Wrist angular displacement data were collected using potentiometers attached to the

pivot points of the manipulanda. All data were digitally sampled at 1 kHz (National

Instruments® PCI-6024E) for 3 sec using a customized program written with

LabVIEW® software (National Instruments Inc.). Data collection was initiated by the

computer 500 ms prior to the imperative stimulus.

Stimuli

The warning tone consisted of three short beeps (100 ms, 1000 Hz, 80 dB each,

separated by 500ms) generated by the computer using a 16 bit sound card (Creative

SoundBlaster® 16) and standard computer speakers (Juster® sp-691n). A fixed

foreperiod of 2.5 sec. spanned the time between the end of the warning tone and the

imperative stimulus. A computer program generated the trial auditory stimuli consisting

of a narrow band noise pulse (1 kHz, 40ms duration). The signal was amplified and

presented via a loudspeaker (<1 ms rise time) placed directly behind the head of the

participant with an intensity of either 80 +/-2 dB (control stimulus) or 124 +/-2 dB (ST

tone). The stimulus intensities were measured using a sound level meter (Cirrus Research

model CR:252B) at a distance of 30 cm from the loudspeaker (approximately the distance

to the ears of the participant). The control tone was similar in pitch, duration and

amplitude to the warning tone sound. Visual imperative stimuli consisted of 4 possible

boxes (3 x 3 cm) that could appear around the targets aligned across the computer screen

facing the participant. One of these boxes (denoting a specific response) would appear (yellow) following the fixed foreperiod. Either the control auditory stimulus or the ST stimulus was presented in conjunction with the visual imperative stimulus on every trial.

<u>Response Targets and Feedback</u>

Four response targets were used in this experiment; each consisting of a fixed point at 20 degrees of angular displacement into either flexion or extension with respect to wrist's starting position. One target was located 20 degrees of flexion from the starting position for the right wrist, and another located at 20 degrees of extension of the right wrist. These were duplicated for the left wrist. A computer screen was placed directly in front of the participant at a distance of 1 m at about eye level. Real time feedback was given during trials by representing the positions of the manipulanda with two vertical graphical lines within horizontal (1cm x 15cm) black rectangular areas on the computer screen using a custom LabVIEW program. The starting position of the graphical bars was the middle of the black rectangles. Two blue lines, 2 cm from the right and left edges of the rectangles represented the targets for flexion and extension. In this way, four targets were aligned horizontally across the screen. The movement of each yellow vertical line corresponded directly to movement of the respective manipulandum. For example if the right wrist was flexing, both the right hand and the line in the right rectangle moved to the left. After each trial, the computer monitor displayed feedback information about the trial just completed including target accuracy (degrees), and reaction time (in ms).

Trial Types

There were three levels of choice, indicated by the number of targets presented in the black rectangles described earlier. In the 1 S-R alternative condition, only one response alternative was present (Simple RT). Additionally, in the 1 alternative condition, the target always indicated an extension with the right wrist. In the 2 S-R alternative condition, two of the four targets were visible. These two targets indicated either a flexion or extension movement for the right wrist. Finally in the 4 alternative condition all four targets were visible (both flexion and extension movements for both wrists).

Participants performed 10 to 20 practice trials prior to each block of trials using the online feedback described above in order to become familiar with the task and equipment.

Control trials were simply trials in which the control auditory tone accompanied the visual imperative stimulus, and the participant carried out the normal protocol of the experiment. Startle trials were trials in which the ST stimulus was given in conjunction with the visual imperative stimulus; however, startle trials only occurred on the right-hand extension movement. Catch trials (no stimulus presented), occurred randomly with a probability of 1 in 20. These were included to discourage false starts.

Choice levels were presented in a blocked order. Thus all trials for each choice level were presented together. The order of the choice-level blocks was randomized and balanced across participants. In the Simple RT condition 21 trials were completed, in the 2 Choice condition, 42 trials were completed and in the 4 Choice condition, 84 trials were completed. In each choice level, the probability of any target appearing was equal. Thus in the 1 S-R alternative condition, the target probability was 1, while in the 4 alternative

condition, each target probability was 0.25. Therefore in all choice level conditions, there were 20 incidences of the right hand extension target, consisting of 17 control and 3 ST trials. In the 2 and 4-choice conditions, all other targets had 20 occurrences consisting of 20 control trials.

After each trial the trial was recorded as either "good" or "error." Erroneous trials were trials in which the participant did not react or in which the initial movement (> 0.5 deg) was made towards the wrong target.

Data Reduction

Data were only analysed from the right hand extension movement. Displacement RT was defined as the first point of a change of more than 0.2 deg of angular displacement from the starting position following the stimulus. Peak displacement was determined by identifying the point at which velocity first returned to zero following movement onset. The final position of the movement was defined as the first point at which angular velocity remained below 8 deg/sec for at least 100 ms. Movement time was defined as the time (in ms) between displacement onset and final position. Surface EMG burst onsets were defined as the point at which the EMG first began a sustained rise above baseline levels. The location of this point was determined by first displaying the EMG pattern on a computer monitor with a superimposed line indicating the point at which activity increased to more than 2 standard deviations above baseline (mean of 100 ms of EMG activity preceding movement). Onset was then verified by visually locating and manually adjusting the onset mark to the point at which the activity first increased. This method allowed for correction of errors due to the strictness of the algorithm. Premotor RT was defined as EMG onset in the ECR muscle. Peak EMG amplitudes were

defined as the largest EMG amplitude, rectified and filtered with a 25 Hz lowpass elliptic filter, recorded within an interval of 100 ms following EMG burst onset. EMG offsets were marked in a similar fashion, with the activity between EMG onset and EMG offset being defined as a distinct burst. To normalise the EMG for comparison between participants, ST trial EMG burst amplitudes for the ECR and FCR were expressed as a percentage of the mean peak EMG amplitude for each respective muscle in the Control condition for each participant. Since there was normally no SCM or OOc activity in the Control condition, ST trial peak EMG amplitude for these muscles was expressed as a percentage of the first ST trial EMG amplitude for the SCM and OOc muscles respectively.

Statistical Analyses

Dependent measures (premotor RT, peak displacement, peak velocity, movement final position, peak EMG amplitude, and EMG burst timings) were analyzed for differences between S-R alternative condition (1, 2, and 4 S-R alternatives) as well as Stimulus conditions (Control vs. Startle) using a 3 x 2 repeated measures analysis of variance (ANOVA). Differences with a probability of less than .05 were considered to be significant. Tukey's Honestly Significant Difference (HSD) post-hoc tests were administered to determine the locus of the differences.

Results

Raw data from a typical participant exemplifying the differences observed in Simple RT trials between the Control (A) and Startle (B) conditions are shown in Figure 5. Activity was present in the startle response indicators (sternocleidomastoid and orbicularis oculi) during ST trials that was not observed in Control trials. Furthermore,

the latencies of premotor RTs were shorter while the kinematics of the response were mostly unchanged. Premotor RT differences were absent between the Startle and Control conditions in both the 2 and 4 choice conditions.

Independent Startle Indicators

EMG activity in both the SCM and OOc muscles were measured to serve as an indication that a startle response occurred. Results are summarized in Table 2 and show that across participants, OOc burst activity was present in 95.5% of the ST trials. However, Brown et al. (1991) have suggested that the eyeblink (OOc EMG activity) by itself may not be an adequate indicator of startle. It has been shown that activity in the SCM may be a better indicator that a startle response actually occurred (Carlsen et al., 2003; Carlsen et al., in press, see also Experiment 1). SCM activity occurred following the startling stimulus in fewer ST trials than did OOc activity (86.1 percent of ST trials). The results of Experiment 1 indicated that if no SCM activity was present, then no startle response was present. Therefore, all subsequent analysis of the ST condition was limited to trials in which SCM activity was observed. As such, data from two of the original 20 participants in which no SCM activity was observed were excluded from analysis. SCM activity was absent from no more than 2 of 9 ST trials in any other participant.

Figure 5. Individual trial data from a typical participant in the 1 S-R alternative (Simple

RT) condition. Top panel (A) is a Control trial, and bottom panel (B) is a 60 deg Startle

(ST) trial. Time zero is stimulus onset. Displacement (deg) and raw rectified EMG from

ECR, FCR, SCM and OOc are shown. Note that while RT latency is shortened in ST

trial, triphasic EMG configuration and kinematics are unaffected.

Table 2

Experimental Results for Each Auditory Tone Condition and Number of S-R Alternatives

S-R Alternatives	Control				Startle			
	1	2	4	Mean	1	2	4	Mean
Startle indicators								
OOc burst (% of trials)	0.00	0.00	0.00	0.00	98.3	93.3	95	95.5
SCM burst (% of trials)	0.00	0.00	0.00	0.00	85.0	88.3	85.0	86.1
Kinematic measures								
Peak Velocity (deg/s)	389.9 (106.3)	374.6 (119.2)	351.0 (127.7)	371.8	*571.8 (157.8)	438.5 (102.4)	349.0 (130.9)	453.1
Peak displacement (deg)	26.2 (3.0)	25.9 (3.6)	26.4 (4.1)	26.2	*33.8 (7.3)	27.4 (4.6)	28.4 (5.6)	29.9
Final Position (deg)	19.3 (1.2)	19.5 (1.8)	20.0 (1.4)	19.6	21.3 (3.6)	18.5 (4.1)	20.8 (4.1)	20.2
Movement time (ms)	287.9 (45.5)	286.6 (46.9)	285.1 (37.1)	286.5	*320.4 (65.3)	307.1 (52.2)	319.6 (43.3)	315.7
EMG								
ECR1 Premotor RT (ms)	†141.6 (13.7)	†204.3 (33.1)	†235.8 (32.6)	-	*†85.9 (15.7)	†202.7 (44.0)	†234.0 (37.2)	-
Peak ECR1 amplitude (% control)	100	100	100	100	*120.9 (31.8)	116.4 (28.2)	104.9 (27.6)	114.1

Note. Standard deviations in parentheses, * signifies significant difference between Control and Startle conditions, † signifies significant difference between S-R alternative conditions, "-" signifies N/A or not meaningful. SCM is sternocleidomastoid, OOc is orbicularis oculi, ECR1 is initial right extensor carpi radialis longus EMG burst.

Premotor RT

Premotor RT was analyzed for differences between S-R alternative condition (1, 2, and 4 S-R alternatives) as well as Stimulus condition (Control vs. Startle). Main effects were found for number of S-R alternatives, $F(2,20) = 62.354$, $p < 0.001$, as well as for Stimulus condition, $F(1,10) = 16.884$, $p = 0.002$. Additionally, an Alternatives x Stimulus interaction was found, $F(2,20) = 13.601$, $p < 0.001$. PMT data are presented in Figure 6 and Table 2. Post-Hoc analysis showed that PMTs in all three levels of S-R alternatives were significantly ($p < 0.05$) different from each other, with one S-R alternative resulting in the fastest PMT, and 4 S-R alternatives resulting in the slowest PMT in both the Startle and Control conditions (see Fig. 6 and Table 2). However, it was also found that PMT was significantly shorter when a startling stimulus was presented during the 1 S-R alternative condition, than when no startling stimulus was presented (Control), $p < 0.05$. In contrast, simple main effects analysis, used to test whether a variable has an effect at each level of a second variable (see Howell, 1997, p. 412), further revealed that there was no difference in PMT between the ST and Control conditions for either the 2 alternative condition, $F(1,11) = 0.001$, $p = 0.970$, or the 4 alternative condition, $F(1,10) = 0.060$, $p = 0.812$, (see Fig. 6).

Response Kinematics

Response kinematics were analyzed to determine if differences existed in movement production variables between the conditions. No significant differences were found between any of the conditions in movement final position (Table 2). However, significant differences in peak displacement, peak velocity, and movement time were

found between some of the conditions. Significant main effects for S-R alternatives, $F_{(2, 22)} = 14.041$, $p < 0.001$, Stimulus condition, $F_{(1, 11)} = 7.975$, $p = 0.017$, and a significant Alternative x Stimulus Condition interaction effect for peak velocity were found, $F_{(2, 22)} = 12.249$, $p < 0.001$. Post-hoc comparisons revealed that peak velocity was larger in the 1 S-R alternative Startle condition than all other conditions, $p < 0.05$, (see Table 2). No other differences in peak velocity were significant. Similarly, for peak displacement, main effects for both Stimulus, $F_{(1, 11)} = 7.947$, $p = 0.017$, and Alternatives, $F_{(2, 22)} = 6.438$, $p = 0.006$, as well as interaction effects were found, $F_{(2, 22)} = 7.966$, $p = 0.002$. Further analysis revealed that peak displacement was larger in the Startled 1 S-R alternative condition than all other conditions ($p < 0.05$). No other differences in peak displacement were significant. Finally, a main effect of Stimulus condition was found for movement time, $F_{(1, 11)} = 15.529$, $p = 0.002$. Tukey's HSD post-hoc analysis revealed that movement time was longer, $p < 0.05$ in the 1 S-R alternative condition when a startle was presented than when no startle was given (Table 2).

Figure 6. Premotor reaction time (SD) in each condition. Control condition (open boxes) can be compared to Startle condition (filled boxes) or across number of S-R alternatives.

EMG Characteristics

Analysis of the triphasic EMG configuration revealed no differences between any of the conditions in initial agonist (ECR1) burst duration, ECR1 to antagonist (FCR) inter-onset time, or in ECR1 to second agonist (ECR2) inter-onset time (Fig. 7). This indicates that neither the number of S-R alternatives nor the Stimulus type had an effect on the EMG internal timing pattern. A main effect due to Stimulus type was found for ECR1 peak amplitude, $F(1, 11) = 5.055$, $p = 0.046$. Post-hoc comparisons showed that ECR1 peak amplitude was larger in the 1 S-R alternative condition when the participant was startled, than when no startle occurred, $p < 0.05$, (Table 2). No other EMG amplitude differences reached conventional levels of significance.

Response Errors

Response errors were classified according to the type of error. Frequencies and types of errors observed are presented in Table 3. No response errors were observed in the 1 S-R alternative (Simple RT) condition, irrespective of Stimulus type.. All erroneous trials were excluded from analysis as their inclusion would have biased the results. In general, three classes of errors were observed when participants were startled in either the 2 or 4 S-R alternative (Choice) conditions. Examples of each error in the presence of a startle response are presented in Figure 8. The top panel (A) is an example of a "Target" error. In target errors, movement was initiated towards the wrong target following the imperative stimulus. This was also the only type of error that was observed when no startling stimulus was present (observed in less than 1% of trials). However, target errors were observed in approximately 8% of the startled conditions. The other two error types were limited to the startled 2 and 4 alternative conditions. The middle panel (B) in Figure

8 is an example of a "no movement" error. In this error the participant was startled, yet no movement was initiated to the appropriate target. "No movement" errors were observed in approximately 12% of the startled conditions, however, data from only two participants accounted for all of these errors. The bottom panel (C) in Figure 8 is an example of a "late movement" error. Observed in approximately 8% of the startled conditions, it was identified by trials in which RT was greater than 2 standard deviations above the mean for that condition, or exceeded 600 ms.

Figure 7. Boxplots (SD) of mean EMG configuration with respect to stimulus onset in

between Control and Startle conditions for all three levels of S-R alternatives.

Figure 8. Examples of three types of observed errors within the startle condition, shown as individual trial

data. Top panel (A) is a "wrong target" error, the middle panel (B) is "no movement" error, and the bottom

panel (C) is a "late movement" error. Time zero is stimulus onset. Displacement (deg) and raw rectified

EMG from ECR, FCR, SCM and OOc are shown.

Table 3

Number of Errors by Condition and Number of S-R Alternatives

	Control				Startle			
S-R Alternatives	1	2	4	Total	1	2	4	Total
Error Type								
Wrong Target	0	2	2	4	0	4	3	7
No Movement	0	0	0	0	0	4	6	10
Late Movement	0	0	0	0	0	0	7	7
Total	0	2	2	4	0	8	16	24

Discussion

Experimental results from the present study supported previous findings regarding the effect of the number of S-R alternatives on RT. In line with previous reports (Hick, 1952), increasing the number of S-R alternatives in the Control condition resulted in an increase in PMT (Fig. 6). Choice takes time and the observed increase in RT has been attributed to increased processing demands associated with the requirement of stimulus discrimination and response selection. Klapp (1996) reasoned that in a Simple RT situation, when the response was known in advance, preprogramming of the response could occur and only a trigger was required to initiate the response after the imperative stimulus. However, when the correct response was not known in advance of the imperative stimulus (e.g. in a Choice RT situation), Klapp suggested that central processing was required to select the appropriate response during the RT interval before the response could be produced. This previously described increase in RT has been attributed to the process of resolving uncertainty or "gaining information" in order to select the correct target (Hick, 1952). Additionally, more recent experiments have shown that the process of response selection involves higher cortical centres during the RT interval (Schluter et al., 1998; 2001).

Observed Startle Effects

The main finding of the current study was that the startling stimulus had the effect of significantly reducing PMT for the Simple condition while leaving the PMT for the Choice condition unaffected (see Figs. 5 & 6). Furthermore, the internal timing characteristics of the response EMG were not changed by the startle in any of the S-R

alternative conditions (see Fig. 7). These results support previous research findings that a startle may act as an early trigger for a prepared response. Recent experiments (Valls-Solé et al., 1999; Carlsen et al., 2003; Carlsen et al., in press) have provided evidence that a startle could trigger a prepared movement. Because the observed PMTs were so short (several RTs < 70 ms), it was suggested that cortical areas could not have been involved, and that the movement must have been stored subcortically. One of the major criticisms of this interpretation, however, was that the startle may simply have acted to increase the activation level of the sensorimotor system, leading to decreased neural thresholds, thereby allowing a response to be generated and propagated more quickly, and resulting in a shorter RT. If this interpretation were correct, then the presentation of a startle should also result in the relative shortening of PMTs even when cortical involvement was required during the RT interval (e.g. Schluter et al., 1998; 2001) and the response could not be prepared in advance (e.g. Choice RT situation). However, if the startle acted as a trigger for a prepared movement, then PMTs should be speeded in a Simple RT situation, and not speeded when the response could not be prepared in advance.

Clearly the present results favour the interpretation that a startling stimulus triggers the prepared response from subcortical areas, and does not simply speed the response through increased systemic activation. As shown in Figure 6, PMT was significantly shorter in the Simple RT condition when a startling stimulus was presented in conjunction with the imperative stimulus, but not shorter in the Choice RT conditions. Additionally, mean PMT was very short (85.9 ms) in the startled Simple RT condition. The shortest PMT observed was 54 ms with several more trials being less than 70 ms. Since the minimum time required for stimulus transduction, and neural conduction to the

brain and back to the arm is on the order of 60 ms, Valls-Solé et al. (1999) suggested that

in the shortest reactions, there was not sufficient time for stimulus identification

processes and the triggering of the prepared movement by cortical areas. Thus it was

postulated that the motor program may have been prepared and stored subcortically, and

triggered by the same reticular structures that were activated by the startling stimulus.

Carlsen et al., (in press) suggested that reticular formation cell assemblies may provide a

mechanism for this hypothesis. However, when a choice was required between either 2 or

4 targets (the response could not be prepared in advance), the presentation of a startling

stimulus did not result in significantly different PMTs (probabilities of .97 and .81

respectively). In fact, statistical power calculations revealed that in the 2 and 4 S-R

alternative conditions, the power for detecting a decrease in PMT similar to that observed

in the Simple RT condition was greater than .99. Based on these values we could not

reject the null hypothesis and can assert with confidence that the startle had no effect in

reducing PMT in these conditions.

No changes were detected in the internal timing characteristics of the EMG

profiles between any of the conditions. Figure 7 exemplifies this result, as it can be seen

that the EMG patterns were not advanced or modified by the startle in the 2 and 4 S-R

alternative conditions. However, while the internal timing characteristics of the EMG

pattern was unaffected by the startle in the 1 S-R alternative condition, the pattern was

advanced in time by a mean of 55.7 ms from 141.6 ms to 85.9 ms. This result is

consistent with previous findings (Valls-Solé et al., 1999; Carlsen et al., in press; see also

Experiment 1), and is especially important for the 1 S-R alternative condition in which

the response was advanced. Since the EMG pattern was unchanged, this provides support

that the early response was not simply an early startle response with a later voluntary response attached or superimposed upon it. This would have been evidenced by a lengthening of the duration of the initial agonist EMG burst, but the results show that this was not the case.

Kinematic Analysis

Results of the kinematic analyses also agree well with previous reports (Carlsen et al., in press; see also Experiment 1). No differences were found in movement end point (final position) between any of the conditions. When a startling stimulus was presented in the Simple RT condition, an increase in peak velocity, peak displacement and movement time was observed (see Table 2). These results have also been reported previously (Carlsen et al., in press; see also Experiment 1). It has been suggested that the descending startle volley may sum with the prepared movement resulting in increased response EMG amplitude (Siegmund et al., 2001). Increased EMG amplitude was observed in the present experiment in the 1 alternative Startle condition (Table 2). This increased EMG leads to the observed increase in velocity, and peak displacement with a corresponding increase in movement time. It is interesting to point out that no increase in EMG amplitude (and no corresponding change in kinematic variables) was observed in the 2 and 4 alternative Startle conditions compared to their corresponding Control conditions (Table 2). This is not to say that the startle did not affect production of the movement, as a greater number of movement production errors were observed in these cases.

Movement Production Errors

Movement errors were observed in less than 1% of all Control trials in any single S-R alternative condition. No errors were observed in the 1 S-R alternative condition irrespective of whether a startling stimulus was presented or not. However, many more errors were observed in the 2 and 4 alternative conditions when a startling stimulus was presented in conjunction with the imperative stimulus (Table 3).

Previous experiments involving the use of a startling stimulus have found that a startle may affect cortical processing for a certain amount of time following the startling stimulus. For example, Woodhead (1963) showed that the presentation of a startle impaired mathematical calculation performance. Vlasak (1969) also found similar cognitive decrements in calculation. More importantly, in light of the present experiment, previous results have also shown that the presence of a startle resulted in impaired performance on a decision making task (Woodhead, 1959). It appears in the present experiment that the startle may also have acted to impair cognitive ability for the duration of the trial. This conclusion is based on the observation of an increase in both the number and types of errors produced when a startle was presented in the 2 and 4 S-R alternative conditions (see Table 3 & Fig. 8). Woodhead (1963) postulated that the presence of the loud stimulus caused a division of the participant's attention resulting in the performance decrement. Vlassak (1969) went further by suggesting that the startling stimulus was able to penetrate into cortical areas, resulting in the interruption and superseding of cognitive processes for a short time. In the present experiment, errors involving both failure to perform the task (Fig. 8B) and late movements (Fig. 8C) were observed, indicating an interruption of the decision making processes. Since it has been shown that the decision

making processes are cortical events (Schluter et al., 1998; 2001), it is reasonable to assume that in some cases, the startle interrupted these cortical processes. A similar result was found by Fitzpatrick (unpublished dissertation) who also reported a RT delay when participants were startled during a Choice RT task. Individual participant reports support the suggestion that cognitive ability was impaired by the startle, with general comments indicating that the participant did not know if they had moved right away, and that the startle was disruptive.

Summary and Conclusions

The results from the present experiment both support and extend previous research involving the use of a startling stimulus during RT tasks. As previously shown, during a Simple RT task (1 S-R alternative), PMT was speeded with many trials resulting in PMT of less than 70 ms. However, when response preparation was not possible (i.e. when the correct response had to be selected during the RT interval), the response was not speeded. In fact, the startle may have interfered with cognitive processes during trials in which a choice had to be made, as evidenced by the greater number and type of errors produced.

General Discussion

Experiment 1 was designed to investigate the process and timeline of startle response habituation during a reaction time (RT) task. The rationale was that later experiments would be able to take advantage of the findings in order to provide the optimal number of startle trials used in one experiment. In a simple RT situation, over the course of the experiment (100 trials), 20 trials in which a startling stimulus accompanied the imperative stimulus were presented. Results showed that when engaged in a RT task, habituation is indefinitely overridden. More specifically, it appeared as though no habituation occurred. However, it was apparent that no startle response was produced in several trials for each participant (as evidenced by an absence of sternocleidomastoid (SCM) activity). Therefore the process of habituation likely continued, but the demands of the task (increased focussed attention, and motor readiness) led to the dishabituation of the startle. In other words, the increased system-wide neural activation due to the task transiently liberated the startle response allowing it to continue to be produced indefinitely. Also, startle (ST) trials in which SCM activity was produced resulted in significantly shorter premotor RT (PMT) than ST trials in which no SCM was present. These results were taken into consideration while designing Experiment 2. A conservative number of ST trials (9 per participant) were used during Experiment 2 in order to minimise the number of ST trials in which a startle response was not evident (see Experiment 1). In doing so, data from two participants were excluded from analysis as no startle response was evident in any of the trials. Only 14% of the remaining ST trials were discarded, and no more than 2 of 9 ST trials were discarded from any one participant.

Experiment 2 was designed to investigate one of the major criticisms of the hypothesis that a startle "triggers" prepared movements. It was suggested that the observed decrease in RT when participants were startled may have been attributable simply to increased systemic activation from the startle. Thus decreased neural thresholds may have allowed the response to propagate much faster than in Control trials. However, if this were the case, a decrease in RT should also have been observed when a movement was not prepared in advance. In the 2 and 4 S-R alternative conditions, it was reasoned that cortical processing was required during the RT interval in order to select and prepare the correct response. Yet when participants were startled in these conditions, no speeding of the response was observed. This indicated that the speeded response observed during the 1 S-R alternative condition was not due to increased activation brought on by startle, but was a prepared response that was triggered from subcortical areas.

Appendix A

Startle Literature Review

<u>The Auditory Pathway</u>

Sound is produced when some mechanical action, such as the vibration of the vocal cords, causes differential changes in the surrounding air pressure. These pressure changes emanate from the source and can be transduced into neural pulses by the mechanisms inside the ears (Kelly, 1991). The human ear is sensitive to a range of pressure wave frequencies from 20 Hz to 20000 Hz (Kelly, 1991). Frequency, however, is not the only attribute that the sound carries; the wave amplitude is also an important component of sound. The amplitude, or maximum change in air pressure in either direction, is measured with the logarithmic decibel (dB) scale:

Sound pressure level (SPL) [in dB] = $20 \log_{10} P_t / P_r$

Where P_t is the test (or measured) pressure, and P_r is the reference pressure of 20 $\mu N / m^2$. (This reference pressure is the pressure required to make a sound between 1 and 3 kHz just audible to the average listener). (Kelly, 1991)

Thus, a sound with a measured pressure ten times greater than the reference (200 $\mu N / m^2$) would have a loudness of 20 dB, because:

$20 \times (\log_{10} 200/20) =$

$20 \times (\log_{10} 10) =$

$20 \times 1 =$

20.

Sound pressure level, (SPL) is directly related to subjectively experienced loudness, therefore, SPL is also logarithmically related to loudness. For reference,

normal human conversation is about 65 dB, or 1778 times the reference pressure, while a

jet engine is about 138 dB and a rock concert is about 115 dB.

The pressure, or sound waves cause the tympanic membrane, or eardrum, to

oscillate at the frequency of the sound waves. This vibration is transmitted to the inner

ear via three small bones, the malleus, the incus and the stapes, otherwise known as the

hammer, anvil and stirrup. This in turn causes the fluid of the inner ear, or cochlea, to

vibrate. Specifically, the stapes transmits the oscillations produced by the sound to the

fluid filled compartments of the cochlea through the oval window. Because fluid is not

compressible, these oscillations are transmitted as fluid waves throughout the cochlea and

cause movements of the basilar membrane and the sensory transduction apparatus, the

organ of Corti (Kelly, 1991).

Movement of the basilar membrane results in excitation or inhibition of the hair

cells, which are the sensory receptor cells of the inner ear. This is because movement of

the organ of Corti with respect to the overlying tectorial membrane results in bending of

the hair cell stereocilia with respect to the hair cell body. Bending of the stereocilia in one

direction leads to depolarization of the cell and a release of neurotransmitter at the basal

end, while bending of the stereocilia in the opposite direction results in hyperpolarization

of the cell. Spiral ganglion cells, which make up much of the auditory nerve, fire in

response to transmitter released by the hair cells. Thus, oscillations in the cochlear fluid

and basilar membrane cause oscillatory changes in potential of the hair cell, which cause

oscillatory release of neurotransmitter, and oscillatory firing of the auditory nerve. The

neural coding of the auditory signal is not of crucial relevance to this specific study,

however, it should be noted that wave amplitude (loudness) is coded via the firing rate of the neurons (Kelly, 1991).

The central auditory pathway consists of several structures, starting with the eighth cranial nerve. Auditory neurons in the eighth nerve, project from the cochlea and terminate in the ventral cochlear nucleus, at the level of the medulla, in the brainstem (Kelly, 1991; Yeomans and Frankland, 1996). There are three main pathways along which axons stream out of the cochlear nucleus on either side, but the most important pathway leads to the superior olivary nuclei, (one on each side of the brainstem), which are concerned with sound localization. From there, axons join others (crossed and uncrossed) from the cochlear nuclei in an ascending pathway, where some axons synapse in the nuclei of the lateral lemniscus, at the level of the pons. At this point, there is some further crossing between the two sides. All ascending fibres passing through the lateral lemniscus synapse at the inferior colliculus, at the level of the midbrain. Postsynaptic cells of the colliculus project to the medial genticulate nucleus of the thalamus on the same side as the respective colliculus. The neurons of the genticulate body terminate in the ipsilateral primary auditory cortex (Kelly, 1991) (Fig. 9).

Figure 9. The auditory neural pathways (adapted from Kelly, 1991, p.495).

Evoked potential experiments have suggested that the neural signal produced by an Acoustic stimulus takes 6-7 milliseconds (ms) to reach the nucleus of the lateral lemniscus, while middle latency auditory potentials suggest that the first volley of the acoustic signal reaches the auditory cortex with a latency of about 35 ms (Erwin and Bushwald, 1986).

The Acoustic Startle Response

In examining the use of the acoustic startle as a research tool, it is important to first understand what a startle is, what produces it, what are the effects on the human, and what factors may affect the startle response, either increasing or decreasing the startle latency and / or amplitude. The following is a discussion of these considerations.

The startle reflex is a generalized and diffuse protective response consisting of a characteristic set of muscle actions initiated by a sudden, intense stimulus (Davis, 1984; Yeomans and Frankland, 1996). More specifically, a sudden, unexpected, acoustic, tactile or vestibular stimulus (Scott et al., 1999; Yeomans and Frankland, 1996) leads to a generalized flexion response in mammals although extensor contraction has also been observed (Brown et al., 1991a). The startle response consists of characteristic pattern of muscle contraction, as well as an increase in central nervous system and autonomic activity (Thackray, 1972).

The Startling Stimulus

Acoustic stimuli must be adequately loud (at least 85 dB) to elicit a startle response, although more intense stimuli produce larger responses, and shorter response latencies (Blumenthal, 1996; Davis, 1984). A fine balance must be struck between using

a sufficiently intense stimulus to elicit a measurable startle, and minimizing risk of damage to the sensory apparatus. Previous studies involving human participants have used brief acoustic stimuli of up to 150 dB (Valls-Solé et al., 1995), and many studies have utilized a stimulus of between 115 and 130 dB (Abel et al., 1998; Brown et al., 1991a; Valls-Solé et al., 1999). Prolonged exposure to sound levels above 120 dB, however, is cautioned against by the authors.

Acoustic stimulus rise time (the time it takes for the stimulus to reach maximum intensity) must be less than 12ms in order to elicit a startle response. If longer rise times are used, even extremely intense sound levels (140 dB) fail to produce a startle response (Davis, 1984). Akin to this, summation of acoustic stimuli results in an increase in the startle response. Effects include increased startle amplitude and lower startle threshold. It has been suggested that these benefits do not last more than 8 - 12 ms, with startle amplitudes returning to baseline after 12 ms (Davis, 1984; Yeomans and Frankland, 1996). For stimulus durations of less than 8 ms, longer stimuli increase startle amplitudes, suggesting that some temporal summation occurs (Marsh, Hoffman, & Sitt, 1973). More recent evidence suggests that acoustic stimulus summation effects are most pronounced at inter-stimulus intervals (ISIs) of 4 - 6 ms. Li and Yeomans (1999) used pairs of 2 ms broadband noise pulses at varying ISIs to determine the temporal summation of acoustic stimuli on startle amplitudes, and found startle amplitudes increased by up to four times the baseline level when the ISI was between 4 and 6 ms. Additionally, they found that as ISI increased further (between 6 and 15 ms), response amplitudes returned to normal baseline levels.

Because a startle can be elicited at all frequencies in the audible range (Pilz, Schnitzler, & Menne, 1987), Li and Yeomans (1999) argued that a broadband noise pulse may be a more effective startling stimulus than a single tone. Thus, they argued that the frequency of the startle stimulus is not a critical consideration. Conversely, Graham (1975) argued that broadband noise was not as effective a stimulus in evoking a startle as a single tone, as his results showed that blink threshold (the intensity of stimulus needed to elicit the blink response) was lower for a 1000 Hz tone than for white noise of the same duration. Additionally, higher frequency tones have been shown to elicit startle at lower intensities than lower frequencies in rats; Fleshler (1965) showed that startle threshold decreased as stimulus frequency increased from 720 Hz to 13.3 kHz. Shnerson and Willott (1980) showed similar results, however they found that a 20 kHz tone was less effective in producing a startle. This latter evidence suggests that a narrow band noise pulse of between 13 kHz and 15kHz may be the most effective acoustic startling stimulus.

The preceding review of startle literature suggests that an acoustic stimulus with the following characteristics would be most effective in producing a startle response:

1. Frequency of about 13 - 15 kHz

2. Loudness of over 120 dB

3. Minimal rise time (preferably less than 1 ms)

4. Duration of at least 6 ms but less than 12 ms, or two, 2 ms pulses separated by no more than 4 - 6 ms.

The Overt Startle Response

Landis and Hunt (1939, cited in Davis, 1984; and in Yeomans and Frankland, 1996) described the startle response as a patterned response consisting of several bilateral stereotyped muscle movements. This response started with blinking of the eyes and a characteristic facial expression, along with dorsiflexion of the head and neck. The described response included a curling of the shoulders in a ventro-caudal direction, flexion of the elbows and fingers, bending of the trunk, and bending of the knees. This generalized flexion response has been hypothesized by Yeomans and Frankland (1996) to be an adaptive defence response in terrestrial mammals to a predatory attack from the rear, as the response results in reduced exposure of the dorsal surface of the neck, a vulnerable point of attack. Landis and Hunt used super speed photography, which has been described as tedious demanding and expensive (Jones and Kennedy, 1951), to capture and later describe the response. Because of this, other measures have been employed which are more economical and easily analysed. Since the work of Jones and Kennedy (1951), the startle response has been primarily measured as an electromyographic (EMG) response. This is due to the short latency of the EMG bursts observed in response to a startling stimulus, the reliability of the response (Brown et al., 1991a), and the practicality of the method (Jones and Kennedey, 1951). Additional observable and measured responses have included physiological indices such as changes in heart rate and changes in galvanic skin response (Graham and Clifton, 1966; O'Gorman and Jamieson, 1977; Shalev, Peri, Orr, Bonne, and Pitman, 1997; Thackray, 1972).

Brown et al. (1991a) described a response pattern of response consisting of eye closure, grimacing, neck flexion, trunk flexion, abduction of the arms, flexion of the elbows, and pronation of the forearms. They reported a large range in the latencies of onset of electromyographic (EMG) activity in the muscles, however a majority of EMG onset times were found at short latencies (Table 4).

Table 4: EMG onset latency to startle (ms) (Adapted from Brown et al., 1991a).

Muscle	Median	Lowest	Highest	n
Orbicularis oculi	36.7	25.0	69.0	70
Masseter	59.0	39.4	122.2	29
Sternocleidomastoid	58.3	40.4	136.0	53
C4 paraspinals	60.2	47.9	120.0	23
Biceps	68.9	59.8	91.7	21
Triceps	71.0	53.2	147.8	12
Forearm Extensors	73.2	61.9	172.8	24
Forearm Flexors	81.9	60.1	199.9	27
Abductor pollicis brevis	98.6	74.5	178.9	26
First dorsal interosseous	98.8	71.7	175.5	26
Abductor digiti minimi	95.9	76.3	104.0	6
Rectus abdominus	82.3	76.6	98.8	11

Brown et al. (1991a) found that median EMG onset latencies in response to a startling stimulus ranged from 36.7 ms in orbicularis oculi (OOc) to 98.8 ms in first dorsal interosseous (see Table 4). Additionally, activity in OOc was always seen in response to the stimulus, while other components of the generalized flexion response were less reliable. This can be seen in the number (n) of observations (Table 4). EMG latencies increased with increasing segmental distance from the brainstem, with facial muscles being the first to be activated, followed in order by neck and paraspinal muscles, upper arm, lower arm, trunk, and finally leg muscles (Brown et al., 1991a). Interestingly, activation in the intrinsic hand muscles was disproportionately long, activating well after both the forearm muscles and even the abdominals (Brown et al., 1991a) (see Table 4).

Brown et al. (1991a) also noted that activity in sternocleidomastoid (SCM) was the first recordable EMG response to a startle after the eyeblink. Activity in the SCM was found to be the most consistent EMG response after the eyeblink, and the last to disappear due to repeated startle stimulation (habituation). Additionally, the authors noted that due to the activation pattern of cranial nerve innervated muscles, the pattern of activation was in a caudal to rostral direction, startling from approximately the eleventh cranial nerve (Brown et al., 1991a).

The blink reflex has been seen as a response to loud auditory stimuli in very many experiments (Blumenthal, 1996; Brown et al., 1991a; Brown et al., 1991b; Miwa, Nohara, Hotta, Shimo, & Amemiya, 1998; Säring and von Cramon, 1981; Valls-Solé et al., 1995; Valls-Solé et al., 1999). The eyeblink response has thus been used as an early indicator that a startle has occurred due to its short latency and reliability as an indicator (Blumenthal, 1996; Brown et al., 1991a; Valls-Solé et al., 1999; Valls-Solé et al., 1995).

Evidence published by Brown et al. (1991a), however, suggests that the eyeblink may not be a valid indicator of startle in and of itself. Two lines of evidence were given to support this position. First, the auditory blink response does not habituate in the same manner as the rest of the startle response: Although other components of the startle response in the participants were no longer seen in response to the startle, the eyeblink was seen even after presenting the acoustic stimulus at regular intervals (every 1 min) for 20 minutes. This indicates, suggest Brown et al. (1991a), that although the participant had habituated to the stimulus and was no longer being startled, the OOc was still activated by a separate auditory blink reflex. The second line of evidence concerns the configuration of the EMG activity from the OOc following habituation. When a true startle response was elicited (prior to habituation), the EMG activity in the OOc was much longer in duration. It was suggested that the response seen during a true startle was simply an auditory blink response with a separate OOc startle response grafted onto the end, and that the two responses are actually physiologically separate (Brown et al., 1991a).

The auditory (non-startle) blink reflex was reported by Brown et al. (1991a) to occur at a short latency (36.7 ms) and be of a brief duration (a range of OOc EMG response durations from 63.3 to 149.2 ms was reported). Säring and von Cramon (1981) also reported short duration blink responses, with a mean blink EMG response duration of 114 ± 18 ms. This is in contrast to the much longer duration EMG responses found by Brown et al. (1991a) when other startle response indicators were present. In addition, Brown et al. (1991a) suggested that in 36% of startle trials, two distinct components were visible.

If these two blink responses are physiologically separate, the neural pathways must also be different. The auditory blink reflex pathway is similar in many respects to the general auditory pathway described above. The nerve impulses are transmitted along an afferent pathway from the ventral cochlear nucleus, through the superior olivary nucleus. From there, the axons join others in an ascending pathway, where some synapse in the nuclei of the lateral lemniscus, at the level of the pons. All ascending neurons passing through the lateral lemniscus synapse at the inferior colliculus, in the midbrain. Here, the auditory blink reflex pathway deviates from that of the normal auditory pathway. Lesioning studies have shown that axons project from the inferior colliculus to the midbrain reticular formation (Hori, Yasuhara, Naito, & Yasuahra, 1986). Axons from the midbrain reticular formation synapse at the facial nucleus (Hienrichson and Watson, 1983; Hori et al., 1986), and then continue on through the facial nerve (VII) where they innervate OOc (Brown et al., 1991a).

As mentioned, this is a somewhat different pathway than the normal auditory pathway. In addition, this pathway is different than the acoustic startle response pathway (see below), giving strength to the assertion by Brown et al. (1991a) that the two responses are physiologically separate.

As discussed below, the acoustic startle response onset latency is very short and cannot include many synapses (Yeomans and Frankland, 1996). Many studies shave reported that the pontine reticular formation is of central importance in the startle circuit based on several types of studies (Davis, 1984). This is in sharp contrast to the midbrain reticular formation pathway described in the acoustic blink reflex. An explanation of the chain of events initiated when the startle occurs could be as follows:

The acoustic startle stimulus is presented and transduced by the ears. The acoustic signal is passed along 3 or more pathways. One pathway leads to the midbrain reticular formation which leads to a short latency blink reflex. Another pathway leads to the pontine reticular formation, which (if the signal is strong enough) activates the giant neurons of the nucleus reticularis pontis caudalis (RPC). This leads to a generalized startle response consisting of activation of motor pathways at increasingly longer latencies as segmental distance from the lower brainstem increases (Brown et al., 1991a). Additionally, the cranial nerves are activated in a caudal to rostral direction of propagation (Brown et al., 1991a) leading to activation of the SCM (innervated by cranial nerve XI), followed by activation of OOc (innervated by cranial nerve V), followed by activation of MAS (innervated by cranial nerve VII) (Brown et al., 1991a). A third pathway follows the normal auditory pathway to the primary auditory cortex. In this way, it is possible that the blink response is activated twice in short succession, first by the midbrain reticular formation, and secondly be the pontine reticular formation.

This evidence presents the need for further enquiry directly into the differences between the startle response and the normal auditory blink response, in order to more clearly describe the characteristics and enable their discrimination. In addition, in light of this evidence, one must question the validity of the eyeblink as a startle response indication, since many experiments have only used the eyeblink response as an indication that a startle response had occurred. As such, these studies must be regarded with careful consideration as to the validity of their conclusions.

As mentioned previously, physiological indices have also been used to measure the response to a startling stimulus. Increases in heart rate have been associated with a

startle response. The heart rate response has been measured in several ways, although they are all similar in method in that a prestimulus level is determined from a short interval preceding the stimulus, and a poststimulus level is determined from the first few seconds or beats following the stimulus. Thackray and Touchstone (1970) computed mean HR in 5-second intervals throughout the trial. O'Gorman and Jamieson (1977) measured HR (as interbeat interval converted to beats per minute (BPM) from an EKG) for 5 beats prior to a startling stimulus, and then for 20 beats following the stimulus. Ornitz et al. (1996) measured interbeat intervals as well, but took 3 measures: a mean of BPM for 5 beats pre-stimulus (baseline), and then a mean of BPM for 5 seconds starting .5 seconds following the stimulus (poststimulus 1) and another starting immediately following for another 5 seconds (poststimulus 2). Shalev et al. (1997) determined the prestimulus level as the mean HR of 2 seconds preceding the stimulus, whereas poststimulus level was the maximum level reached within 4 seconds following the stimulus.

Graham and Clifton (1966) reviewed the effect of stimuli of differing intensities on the heart rate (HR) and concluded that the literature showed differential effects on HR based primarily on stimulus intensity. When a startle response was elicited, an accompanying increase in HR was observed. When a stimulus evoked a different, "orienting" response, a slowing of HR was observed. Unfortunately, no independent indicators of a startle response, other than a blink response being present, were reported (Graham and Clifton, 1966). Since then, Thackray (1965), Thackray and Touchstone (1970), and Ornitz et al., (1996) have all reported increases in HR following a startling stimulus. More recently, O'Gorman and Jamieson (1997) also reported a significant

increase in HR (in the mean of beats 3 and 4 poststimulus) over baseline (the mean HR of 3 beats prestimulus) in response to stimuli of 90 and 100 dB, but not in response to an 80 dB stimulus. They concluded that their findings (in agreement with those of Graham and Clifton (1966)), suggested that a short latency HR acceleration is a component of the startle response, occurring within the first 2 seconds after onset of a startling stimulus (O'Gorman and Jamieson, 1977).

In addition to heart rate, skin conductance has been used as a measure of startle response. Significant increases in conductance have been reported in response to an intense auditory stimulus (Shalev et al., 1997; Thackray, 1965; Thackray and Touchstone, 1970). Thackray (1972), however, cautioned that stimuli low enough in intensity (as low as 40 dB) to only evoke "orienting" responses and not startle responses, were also accompanied by increases in galvanic skin response, and that these differences in skin conductance between stimulus intensities were not abrupt enough to allow for discrimination of the responses.

The above evidence suggests that the best measure of whether a startle has been elicited may be derived from a short latency burst of EMG activity in the SCM, and secondarily from the C4 paraspinals (C4P), or masseter (Mas), as these show the shortest latency and the most reliability. In addition, it appears that the EMG response from the OOc may be a good indicator, as long as the distinction is made (through measurement of EMG burst duration) between a simple auditory blink response and a longer duration EMG response due to a startle. Additionally, differences in changes in heart rate following the stimulus may help to further distinguish startle responses from non-startle responses.

Factors Affecting the Startle Response

In a preceding section, the effects of differences in the acoustic startle-eliciting stimulus were discussed, yet there are many factors such as external environment and prior experience, which may affect the startle response. These may also lead to differences in startle response latency, startle response amplitude, or both. Some of these factors will be discussed below.

Habituation.

Habituation to a startle involves a gradual decrease in response amplitude as exposure to the stimulus is repeated. In terms of EMG response, habituation affects amplitude, but it does not, however affect response latency (Schicatano and Blumenthal, 1998). Evidence has been shown in humans (Brown et al., 1991a) that many components of the startle response are no longer seen after 2 to 6 random presentations of the startling stimulus, indicating that the participants eventually have no overt response to a startling stimulus. The pattern of habituation is not random, however, nor is it all-or-none, as the response tends to decline in amplitude with repeated exposure (Abel et al., 1998) and disappear in peripheral regions first (Davis and Heninger, 1972). Because startle habituation has been observed in decerebrate rats (Leaton, Cassella, and Borszcz, 1985), habituation is thought to be a process that occurs in the brainstem.

With respect to the short latency acceleration of heart rate (HR) accompanying a startle, evidence is contradictory regarding its habituation. Graham and Slaby (1973) report that the HR response habituated within 5 trials in which a startling stimulus was presented. Similarly, O'Gorman and Jamieson (1977) also reported that in response to a 90 or 100 dB stimulus, HR following the stimulus was not significantly higher than

prestimulus levels after only 5 presentations. In contrast, however, Ornitz et al. (1996) reported that cardiac response failed to habituate. In fact, they not only reported that the HR response continued to be present following 15 presentations of the stimulus, they reported that tonic HR increased as the session progressed. This, they argued was the result of a heightened state of arousal of the participants during the session and sustained arousal due to the engaging activity of watching silent TV movies and cartoons throughout the session (Ornitz et al., 1996).

Valls-Solé et al., (1997) recently reported a reducing effect on startle habituation in participants who were preparing to react to a "go" signal. Participants were exposed to 5 startling stimuli in each of 4 different conditions. Participants were resting quietly, resting in a busy environment, preparing to react in a reaction time task, or focusing on an upcoming visual stimulus. Findings showed that the rate of habituation was significantly decreased when participants were startled in conjunction with a visual "go" signal in a RT task. Specifically, in this condition, peak EMG amplitude in the SCM and MAS did not decrease below 60% of initial amplitude, whereas in all other conditions, peak EMG amplitude in these muscles fell below 20% of initial values by the fifth presentation of the stimulus. The authors suggested that reduced cortical inhibition of the startle response as well as increased excitability of the motor pathway due to readiness to perform a motor act might have been the reason for the decreased habituation (Valls-Solé et al., 1997). Similar findings and conclusions were reported in a study involving startle stimulus effects on RT in participants with various Parkinsonian syndromes (Valldeoriola, Valls-Solé, Tolosa, Ventura, Nobbe & Marti, 1998). Similarly, in a recent study by Siegmund, et al. (2001), no habituation of the startle response was observed over 14 trials in which a

startling stimulus (124 dB) replaced the imperative stimulus in a RT task. The task involved either a rapid head flexion or a rapid head rotation to the right. No significant changes in muscle activation time or EMG amplitude were observed with repeated exposure to the startling stimulus. As suggested previously, readiness to perform a motor act was argued to be the most likely candidate for the decrease in habituation (Siegmund et al., 2001).

Interestingly, it seems that although readiness to perform a motor act delays the rate of habituation that an ongoing motor act does not. In investigating the effects of a startling stimulus on rifle aiming, Foss (1989) found that the disrupting effects in aiming proficiency caused by the startling stimulus decreased with repeated exposure to the stimulus. The effect of the noise on aiming proficiency, however, was never completely eliminated (Foss, 1989). Recovery of the effects (a decrease in the amount of habituation) was seen after both a 24-hour and a 7-day rest period.

The effect of caffeine ingestion on habituation of the startle response has thus far shown contradictory results. Schicatano and Blumenthal (1998) gave subjects either 1 mg caffeine per kg body weight, or a placebo, and found that the caffeine group had larger amplitude responses after 30 trials than the placebo group. In contrast, however, Andrews, Blumenthal and Flaten (1998), did not replicate these effects, as no delay in startle habituation was found with a caffeine group.

Prepulse inhibition.

Discussed previously was evidence showing that temporal summation of the acoustic signal occurs in the first 8 ms, leading to increased startle amplitudes. Similarly, a prepulse, which is described as a small change in the sensory environment that precedes

a startle inducing stimulus, has modification effects on the startle response. A prepulse occurring in short time frame (5 - 10 ms) prior to the presentation of the startling stimulus has been shown to reduce startle latencies (Graham, 1975). This might be seen as a corollary to the temporal summation. However, prepulses at longer intervals prior to the startling stimulus (15 - 2000 ms) have been shown to decrease startle amplitude, with a decaying effect as the prepulse interval lengthens (Graham, 1975). This type of reflex modification has become known as prepulse inhibition (PPI) of startle (Davis, 1984; Hoffman, 1984; Lehmann et al., 1999). This PPI has been suggested to reflect the ability of higher brain centres to gate or filter sensory information (Abel et al., 1998; Blumenthal, 1996; Zhang et al., 1998)

Evidence forwarded by Lipp et al.,(2000), however, suggests that at prepulse latencies of greater than 2000ms, startle response latencies were reduced. Additionally, the effects can occur even when the prepulse and startling stimulus modalities are different (e.g. tactile or light prepulse in conjunction with an auditory startle) (Lipp et al., 2000; Zhang et al., 1998), although effects of a prepulse are most pronounced if the prepulse and startle stimulus are in the same modality (Balaban, Anthony & Graham, 1985).

Other studies have focussed on the effects of the intensity of the prepulse. Recent evidence (Blumenthal, 1996), has shown that the intensity of a prepulse or the startle eliciting stimulus effects the amount of PPI observed. Specifically, they showed that the EMG amplitude of an eyeblink was significantly affected by the intensity of a prepulse. As prepulse intensity increased, the inhibition of startle amplitude also increased. This finding, however, was only applicable to startle responses to low startling stimulus

intensities (85 dB). At higher intensities (up to 105 dB) they found no difference in the amount of inhibition caused by a prepulse (Blumenthal, 1996). In light of the evidence presented by Brown et al. (1991a), it seems that at lower "startle" intensities a startle may not actually be elicited, and may be a separate auditory blink response. Thus, although these findings may be applicable to a blink response, the argument that the intensity of a prepulse affects the magnitude of PPI in a startle may be misleading. This finding, however, may present consequences regarding the use of a warning tone in a reaction time paradigm and should be considered when designing a task involving these variables.

The implication of prepulse inhibition to the current thesis is that the sensory environment must be kept sufficiently constant so that prepulse inhibition does not take place, thereby increasing the chances of successfully detecting a startle response when it occurs. Furthermore, care should be taken in the design of the task so that any warning / ready stimulus is given at least 2000 ms prior to the startle.

Gender differences.

Several studies have investigated the possibility of gender differences in startle response, as well as gender differences in effects of PPI. Evidence from these studies suggests that startle responses do not differ in either amplitude or latency between sexes (Abel et al., 1998). There has been evidence to suggest that PPI is greater in females than in males (Able et al., 1998; Lehmann et al., 1999). These differences should not affect the methodology in the present investigation, as PPI will be avoided.

<u>Arousal, attention and other considerations.</u>

Although many of the major contributors to differences seen in the startle

response have been reviewed, there are several other contributing factors that may

interact in a complex way to modulate the startle response. As complex interactions begin

to form between factors such as caffeine ingestion, arousal levels, attention, and affect,

their individual contributions to the modulation of the startle response becomes less clear.

Some of these factors will be discussed with evidence from the startle literature.

The effects of caffeine on startle latency and amplitude.

Although one might assume that as arousal increases, the startle response would

increase accordingly, the literature has shown contradictory results (Davis, 1984). One

method leading to increased arousal is having participants ingest caffeine (Andrews et al.,

1998). As previously stated, the effects of caffeine on <u>habituation</u> to the startle are also

controversial. Other effects of caffeine, however, have been well documented. Startle

response latencies have been found to be similar between subjects who were given

caffeine and subjects given a placebo (Andrews et al., 1998; Schicatano and Blumenthal,

1998). Interestingly, Andrews et al. (1998) did find that startle latency was increased if

the subjects expected caffeine. In their study, subjects given caffeinated coffee,

caffeinated juice or non-caffeinated juice all had similar startle response latencies,

whereas subjects given decaffeinated coffee had significantly higher response times

(Andrews et al., 1998). The authors speculated that because coffee is a caffeine-

associated stimulus that the effect of decaffeinated coffee suggests an antagonistic effect

of expectancy of caffeine on the startle response, indicating a high degree of affective

modulation of startle.

Startle response amplitudes, however, have been shown to increase with the use of caffeine (Andrews et al., 1998). These effects have been attributed to the effect of caffeine on the attentional processes and the arousal levels of the participants (Andrews et al., 1998; Schicatano and Blumenthal, 1998).

In summary, although its effects on startle latency and habituation are argued, caffeine seems to have two effects on the startle response. First, startle amplitudes have been shown to increase with caffeine ingestion. Secondly, the expectancy of caffeine without its actual presence seems to have a dampening effect on startle latencies, making them longer. These point to the effects of caffeine interacting with arousal to modulate the startle response. These effects were reviewed here, as caffeine ingestion is a commonly observed occurrence among many of the potential participants of this study, namely university students.

Attention.

Because participants will be attending to a "go" signal in the present investigation, a brief review of the startle literature with respect to attention was undertaken. Attention seems to affect the startle response in an interesting way. If attention is directed at a stimulus in the same modality as the startling stimulus, the startle response is enhanced (larger amplitude and lower latency), whereas attention directed toward a different sensory modality than the startle stimulus, seems to have no effect on the startle response (Richards, 2000).

In one study investigating the effect of the attentional process on the startle response (Schicatano and Blumenthal, 1998), subjects were instructed to attend to the startle stimulus, a visual task, or not given instruction to attend to anything in particular.

Results showed that startle latency, detected by an eyeblink response, was significantly longer, and that startle amplitude was significantly smaller when attending to the visual task. This, the authors suggest, provides evidence that attentional modulation of the startle response is sensitive to the attended sensory modality. Additionally, these differences were found to be larger in the presence of caffeine suggesting that caffeine may interact with the attentional processes (Schicatano and Blumenthal, 1998). Similarly, Richards (2000) showed that in infants, when attention was directed at a multi-modal audiovisual stimulus, blink reflex was enhanced. The enhancement however was greater than when the infant's attention was directed at unimodal stimuli.

Attention to prepulses has been found to have no significant effects on the amplitude or latency of the startle response (Acocella and Blumenthal, 1990). The suggestion with respect to attention effects on the startle response is that the afferent sensory pathways are enhanced with increased attention to a particular sensory modality. Thus the startle response from a stimulus in the same modality is facilitated (Richards, 2000).

Environment.

In investigating the factors that influence the startle response, researchers looked at the level of background noise present at the time that the startle stimulus was given. Initially the relevant finding was that as background noise was increased from 65 to 75 dB, the startle response increased. Upon further increases to 90 dB, however, researchers found that startle response magnitude returned to baseline (Ison and Hammond, 1971). Two hypotheses ware forwarded to account for this finding. First, the effect was thought to be produced by two competing functions. Background noise resulted in increase in

arousal, resulting in an increased startle response. As the level of background noise increased, however, the signal (startle) to noise (background noise) ratio decreased, eventually counteracting the effects of the increased arousal. The second hypothesis concerned the inverted U hypothesis concerning an optimal level of arousal (Davis, 1984). To investigate these two competing hypotheses, a new experiment was devised in which background noise and startle stimulus amplitude were varied. What was found was that if startle stimulus level was increased along with background noise, startle amplitude did not diminish. Only when the background noise became loud enough to cause masking of the startle stimulus did the startle response begin to decrease (Davis, 1984).

Along the same lines, length of time of exposure to background noise has been investigated to determine the effects on the startle response. Data have shown (Davis, 1974b) that as the length of exposure to background noise increased, from 5 to 75 minutes, mean startle response amplitude increased significantly, with the largest gains in the first 30 minutes.

Summary of other considerations.

Many other considerations regarding factors that might affect the startle response latency, amplitude or probability have been discussed, and should be considered when using the startle as a tool in research. In attempting to elicit a reliable and valid startle response, care must be taken to control the environment, including background noise and prepulses, as these may have a dramatic effect on startle amplitudes. In addition, consideration to attentional direction, gender, and caffeine consumption are considerations although their contribution to differences in the startle response may be relatively minor.

<u>Acoustic Startle Response Pathway:</u>

The pathways involved in the mediation of the startle response have been studied by various authors, resulting in as many as five models of the acoustic startle response pathway (Yeomans and Frankland, 1996). The most recent model is proposed by Yeomans and Frankland (1996) and involves many of the structures proposed by previous studies, but emphasizes the role of the nucleus reticularis pontis caudalis (RPC).

The methods used to investigate the startle response pathways, or circuits, range from direct electrical stimulation of nervous structures, to lesioning, to intracellular recording and collision tests. By directly stimulating a neural structure with an electrical current the response output can be compared to the startle response. In this way, the neural structures identified and tested and either included or ruled out in their contribution to the startle response. Similarly, experiments in which selected parts of the brain are lesioned help identify implicated neural structures. In this method, brain structures are destroyed either permanently by severing connections between structures in surgery, or temporarily by injecting an excitotoxic chemical into a structure. The startle stimulus is then given to determine if the response is still elicited. When the startle response is diminished or is no longer seen, the structure in question can be implicated in contributing to the startle and is included in the proposed startle circuit. The brains of the animals in which the lesion was performed are subsequently dissected and examined to determine if the targeted structure was in fact the structure that was lesioned. Intracellular recordings can identify whether specific neurons fire in response to a stimulus. In this way, neurons and their connections can be directly mapped in determining the sequence of firing neurons in the circuit. Finally, collision tests involve the extra cellular

stimulation of pairs of sites. This allows pathway components to be segregated into continuous-axon and synapse-separated sections. It also allows for direction of travel along a particular pathway to be determined (Yeomans and Frankland, 1996).

Because the startle response onset latency is very short, especially in rats, it has been suggested that the primary startle response circuit cannot include many synapses (Yeomans and Frankland, 1996). The transduction of the acoustic stimulus occurs as described above, yet the startle response circuit also activates several other structures, including the reticularis pontis caudalis (RPC), and the ventrolateral tegmental nucleus (VLTg) (Yeomans and Frankland, 1996). Several of the many studies investigating the startle response pathways have been comprehensively reviewed by Yeomans and Frankland (1996) and their conclusions will be discussed here.

Many studies shave reported that the RPC is of central importance in the startle circuit based on several types of studies (Davis, 1984). Specifically, the giant neurons of the RPC have been implicated as important contributors to the startle response through the use of collision studies, lesion studies, and intracellular recordings (Yeomans and Frankland, 1996). The grading seen in the amplitude of the startle response with the intensity of the stimulus (described earlier), has been suggested to be the result of the number of RPC giant neurons recruited. As the stimulus intensity increases, the number of RPC neurons activated increases, leading to a larger startle response. In this way, the RPC giant neurons may act as "command" neurons of the acoustic startle response (Yeomans and Frankland, 1996). The RPC neurons then conduct to the various levels of the spinal cord, along the reticulo-spinal tract, and activate motoneurons with both weak monosynaptic connections, and strong disynaptic connections involving interneurons

(Yeomans and Frankland, 1996). This motor activation then produces the measurable EMG response and movement associated with the startle.

Activation pathways of the RPC during startle are somewhat less well known (Yeomans and Frankland, 1996). Neurons projecting from the ventral cochlear nucleus (VCN) to the RPC have been identified as contributors to the startle response based on studies in which startle was diminished following lesion of the VCN. Several other structures, however, are thought to be important as well including dorsal cochlear nucleus, and cochlear root neurons (Yeomans and Frankland, 1996). Collision tests, however, have indicated that the connections from the VCN to the RPC may not be continuous. Yeomans and Frankland (1996) suggest that because the strongest input to the RPC comes from the ventral lateral lemniscus (VLL) and VLTg, and because lesions of these areas blocks acoustic startle, that input to the RPC from this area might be a stronger contributor to the startle response. The complete pathway proposed by Yeomans and Frankland (1996) is seen in Fig. 10.

Figure 10. The acoustic startle response pathway as proposed by Yeomans and Frankland (1996, p.303).

In summary, the suggestion by Yeomans and Frankland (1996) is that strong disynaptic connections from the VCN, through the VLTg, to the RPC sum with weaker monosynaptic connections possibly from VCN to RPC to activate the RPC giant neurons, which may mediate startle.

The Motor Program

In order for the reader to understand the connection between the use of a startle and the release of a movement, some understanding of the background regarding the notion of motor programs is needed. The control of human movement has been an area of interest to several researchers for many years. Since as early as 1820, scientists and researchers have examined the nature of movement from different perspectives such as neurophysiology and behavioural psychology. This has led to a tradition of theory and experimentation and the formation of the field known as motor control (Schmidt and Lee, 1999).

James put forward one of the first theories regarding how the human controls movement in 1890. His assertion was that movements were controlled or triggered by the movement preceding it, and that after initiation of the action, no further attention was needed to complete the movement. This was known as response chaining (Schmidt and Lee, 1999).

Response chaining, by definition, relies on peripheral feedback in order to complete the intended actions. In several much later experiments, however, it was shown that movements could be made in the absence of afferent feedback. Lashley (1917, cited in Schmidt and Lee, 1999) observed that in a deafferented gun shot victim, successful movement was possible without the presence of feedback. Similarly, Taub and Berman

(1968) showed that deafferented rhesus monkeys could coordinate motion and move without peripheral feedback. Adding to this, it has been suggested that response chaining becomes improbable for rapid movements that occur in less than 100 ms, and it is now generally accepted that the minimum time to process and use information from the periphery is about 100 ms (Keele, 1968; Nagelkerke et al., 2000; Schmidt and Lee, 1999; Wadman, 1979). Movements with short movement times (MT) are often referred to as "ballistic" movements (Ghez, 1991).

With evidence showing that movements can be carried out in the absence of peripheral feedback, it was suggested that some central mechanism might preside over the control of movements in order to explain the ability to accurately perform these movements. Thus, the idea of a motor program, defined as "a set of muscle commands that are structured before a movement sequence begins … that allows the sequence to be carried out uninfluenced by peripheral feedback" (Keele, 1968), was proposed as a possible central mechanism.

It has been suggested by Keele (1968) that the motor program may be formed by visual or kinesthetic information being transformed into muscle commands. Schmidt (1988) proposed that a period of automation followed the initiation of the program, where the program ran by itself for some minimum time while completion of feedback processing occurred. Once the feedback was processed the central nervous system was able to generate and initiate changes to the remaining movements in the sequence.

The evidence supporting a motor program comes from several lines of evidence. First, processing of feedback is slow, as it has been shown that feedback cannot be used in less than 100 ms. Thus, motor programs are thought to run automatically during the

time that feedback is being processed. Secondly, studies involving the deafferentation of subjects also show that movements can be performed in the absence of feedback. Evidence for the existence of motor programs comes from other studies as well.

One of the main characteristic features of the motor program is the existence of invariant timing within the motor program. Although overall duration of a movement may change, the relative proportion of time that each sub-task takes remains constant. This was illustrated by a classic relative timing study in which, Terzuolo and Viviani (1979, cited in Schmidt and Lee, 1999) studied expert typists to determine how their keystroke timing within words changed as a function of typing speed. Participants typed the word "trouble" repeatedly in the context of a sentence throughout a testing session (Fig. 11a). When the researchers analysed of all of the instances of the typed "trouble," invariance in timing proportions was seen in each individual. When the data were displayed by reordering the trials from fastest to slowest and normalizing the onset time for the first letter (Fig.11b), the onset times for the remaining letters "lined up" on sloped lines. After analysis, it was found that the proportion of time taken for each letter remained invariant (Fig. 11c).

Figure 11. Temporal structure in typing of the word "trouble" at different speeds. A. Unordered data. B. Ordered from fastest to slowest. C. Proportion of time for each letter in sequence (adapted from Schmidt and Lee, 1999, p. 164).

This representation was taken to be evidence in support of invariant timing within the as it appeared that the proportions were constant over the twenty-seven trials of typing the word "trouble" (Schmidt and Lee, 1999). This experiment showed that although overall timing or absolute timing was different, one feature of the similar movement pattern was always the same: the timing of the units of the sequence. This general concept has also been applied to the temporal structure of muscle contractions, and is generally known as phasing (Schmidt and Lee, 1999) (Fig 12).

Movement 1

Movement 2

Figure 12. Illustration of two hypothetical movements with different movement times.

EMG ratios remain constant with different absolute durations (adapted from Schmidt and

Lee, 1999, p. 160)

As previously mentioned, it is generally accepted that the minimum time to process and use information from the periphery is about 100 ms. This has been estimated based on several experiments. Wadman, Denier van der Gon, Geuze, & Mol (1979) performed one of the most well known experiments revealing this result. In a unique experiment, subjects were instructed to make a rapid elbow extension movement to a target. EMG was recorded, and a triphasic burst pattern was seen (Fig. 13). The first agonist burst accelerated the arm, which was followed by a "quiet period" in the agonist. During this quiet period, there was a burst of EMG activity from the antagonist in order to slow the limb. Finally, a second agonist burst was seen, which locked (or clamped) the limb on the movement endpoint. It was suggested that this burst served to dampen oscillations produced from rapidly accelerating and slowing the arm (Wadman et al., 1979).

Figure 13. Triphasic burst pattern (adapted from Wadman et al., 1979, p. 8).

On selected trials, the movement was blocked, and the subject was not able to move their arm. Again, EMG activity was recorded, and it was found that the burst pattern remained unchanged for the first 100 ms, even though the arm did not move. This, it was suggested, was evidence supporting the idea that pre-programmed movements were initiated and then run off automatically until feedback could be processed. Similar results have been shown recently in our own lab (Nagelkerke et al., 2000), however, these results suggest that feedback is actually used 50 ms following the first point at which the feedback indicating a block had occurred could have been sent. Although the EMG remained unchanged for 100ms, it took 50 ms for the EMG activity to grow to the point at which the inertial properties of the arm could be overcome and the limb started to move. It was only 50 ms after the limb started to move that the EMG was modified. This suggests that although the feedback can still not be used for a short period of time following initiation of the movement, it may be considerably less than previously thought.

<p align="center">Startle and the Control of Movement</p>

A Performance Decrement in Response to a Startle

Since the 1960's, experimenters have researched the effect of a startle on motor performance. Firstly it was to determine the nature of a "freezing" phenomenon when a person is frightened, and later it was used to determine how pilots might respond to loud stimuli such as sonic booms. In one of the earliest studies to combine a startle with a reaction time task, Sternbach (1960) attempted to determine why some people seemed to freeze with fright while others were able to act rapidly to a dangerous or frightening situation. More specifically, he wanted to determine if it were possible to discriminate

between fast and slow reactors based on resting physiological measures. Participants sat in a room and waited (12 min) for a loud stimulus (106 dB), which acted as the imperative stimulus in a RT task. The participants were told to respond by pressing a button as fast as possible. The 10 fastest and 10 slowest reactors were separated into two groups for analysis. The fast group had a mean RT of 200 ms, while the slow group had a mean RT of 1695 ms. Findings showed that the fast reactors had smaller physiological responses to the startle, although no differences were found in prestimulus levels between the groups. Thus it was concluded that greater physiological response to the startle was associated with slower recovery leading to slower response times (Sternbach, 1960). This infers that one must first recover from a startling stimulus before one can react motorically.

Following on the previous findings, researchers thought it necessary to determine if a brief period of performance decrement following a loud stimulus would affect a pilot's ability to respond rapidly. In a study designed to mimic some of the responses required by pilots, Thackray (1965) had participants respond to a stimulus as quickly as possible by flipping a switch with the thumb and moving a control stick to the left. Participants rested for 5 minutes awaiting the presentation of the first stimulus, a 120 dB tone. Fifty 75 dB tones, to which the participant was to respond as well, were spaced every 15 seconds, and finally another 120 dB tone was the last stimulus. Findings showed that mean RT to the first startling stimulus was 893 ms, while mean RT to the second startling stimulus was 416 ms. RT to the second startle was not significantly different than the mean RT to the 75 dB stimulus of 368 ms. The variability of the response times was shown to be of interest, however, and Thackray (1965) suggested that the effect of

the startling tone was to exaggerate pre-existing differences in RT. Specifically, participants with slow RT's were even slower when startled, whereas fast responders became even faster. Suggestions regarding explanations for this effect were that increased activation by the startle facilitated performance in the fast responders. This increased activation led to over-arousal in the slow responders, leading to slower responses. Unfortunately, physiological data did not back this hypothesis, and an alternate explanation was suggested involving the level of readiness of the participant. Specifically, Thackray (1965) suggested that slow responders were unable to maintain a readiness to respond to the stimulus.

Several other studies have noted increased RT in response to a startling stimulus. Vlasak (1969) found that simple visual RT increased from a mean of 550 ms to 680 ms following a 100 dB startling stimulus occurring in the irregular 3-5 second intertrial interval. Similarly, Klimovitch (1977) found that when a 110 dB startling stimulus was presented 1-2 seconds preceding the imperative stimulus, RT in a hand-grip task increased significantly by 16.1 ms. More importantly, the findings revealed that the RT increase was restricted to premotor RT, with motor time being unaffected (Klimovitch, 1977).

Cognitive Decrements

In a similar vein to performance (RT) decrements, cognitive decrements have been observed following a startling stimulus. Woodhead (1959) found that in a decision making task in which participants had to match moving symbols to stationary ones, that performance was impaired following a 110 dB stimulus for up to 31 sec. Similarly, findings from a later study (Woodhead, 1963) showed that when engaged in an arithmetic

task, a 100 dB noise burst impaired calculation performance. The explanation forwarded by Woodhead (1963) for the performance decrement was that the presence of the loud stimulus caused a division of the participants' attention that would have otherwise been focussed on the cognitive task.

In a similar study by Vlasak (1969), participants were instructed to subtract 7 in consecutive increments from 1000 in writing. In performance in the first 30 seconds following a startling stimulus, Vlasak (1969) noted a significant performance decrement, from 10.3 correct subtractions to 7.4 correct. Vlassak (1969) suggested that the strong stimulus penetrates into the CNS and interrupts and supersedes cognitive processes for a short time. In a different type of study involving cognitive effects, researchers focussed on the effects of a startling stimulus on response selection and response programming processes. Findings reported included delayed RT's in choice RT paradigms (Fitzpatrick, 1997). These studies, taken together, indicate that a loud stimulus has detrimental effects on cognitive performance for a short time following the stimulus.

Continuous Control Task Effects

Based on the findings regarding cognitive decrements, researchers sought to determine if a brief period of cognitive decrement following a loud stimulus would affect a pilot's proficiency possibly posing a threat to the flight. Vlassak (1969) had participants perform a line trace task, in which an irregularly prescribed line with outside boundaries 4mm either side of the line was traced with a pencil. A klaxon-hoot of 100 dB occurred at the mid point of the trace task resulting in significantly more errors (deviations from the prescribed line) in the first 1 to 2 seconds following the startle. The errors were

interpreted as resulting from a motor disturbance caused by the generalized motor response (as described by Landis and Hunt, 1939) accompanying a startle.

In order to further investigate the extent and duration of performance disruptions following a startle, Thackray and Touchstone (1970) performed an experiment involving a compensatory pursuit-tracking task. Participants attempted to keep a spot generated by an oscilloscope in the middle of the oscilloscope screen, as the horizontal and vertical position changed continuously. A small control stick (joystick) compensated for the spot's movement. The participant was also told to respond to any auditory tones by pressing a button on top of the joystick as quickly as possible. One continuous 30-minute trial was performed, and at the 2-minute mark, a 115 dB startle tone was presented. Fifteen minutes later a second startle tone was presented. In between these two, fifteen 75 dB tones were randomly presented. Findings showed that mean tracking error increased 65% during the first 5 seconds following the startle. This decreased to only a 16% increase above baseline (prestimulus) level in the second 5 second interval, indicating a rapid recovery of the decrement in tracking performance reported by Vlasak (1969).

Another series of studies examining the adaptation to intense stimuli investigated the effect of startle inducing stimuli on aiming a rifle (Foss, 1989). In the first experiment, participants performed two blocks of 30 fifteen-second aiming trials during which the participant was instructed to aim the rifle at a target as accurately as possible. On 10 of the 30 trials, a startling (110 dB to 135 dB) stimulus was presented when the trial had been running for between 5 and 10 seconds. In a second experiment the same protocol was carried out, however, three sessions were completed, the second 24 hours later and the third one-week later. Findings revealed that the startling stimuli disrupted

the ability of the participants to maintain their aim on the target, measured as mean absolute deviation from the target, for approximately 1 to 2 seconds. Further, the findings showed that this effect was larger with more intense stimuli, and decreased with repeated exposure to the stimuli, however, the effect of the noise on aiming proficiency was never completely eliminated (Foss, 1989).

RT Facilitation by Startle

Interestingly, contrary to previous findings (Sternbach, 1960; Thackray, 1965; Vlasak, 1969), Thackray and Touchstone (1970) observed a facilitative effect of the startle on RT during a continuous tracking task. The participant was also told to respond to any auditory tones by pressing a button on top of the joystick used in the experiment as quickly as possible. One continuous 30-minute trial was performed, and at the 2-minute mark, a 115 dB startle tone was presented. Fifteen minutes later a second startle tone was presented. In between these two, fifteen 75 dB tones were randomly presented. The observed mean RT's to 2 startle stimuli were 401 and 402 ms respectively. These were significantly shorter than the mean RT of 462 ms in response to fifteen, 75 dB control tones. The authors suggested that the RT's were possibly facilitated by the startle response since the flexion movement was more compatible with the previously reported generalized flexion response than the movements used in previous studies (Thackray and Touchstone, 1970).

The same pattern was reported in another, much later study by Valls-Solé et al. (1995), where an unexpected, loud acoustic stimulus of up to 150dB was given in conjunction with a RT task. The subjects were asked to respond to a visual stimulus by raising their arm and pushing a button, while EMG onset, movement onset and task

completion times were measured. EMG activity was recorded in the wrist extensors, and various startle response indicators including orbicularis oculi (OOc), orbicularis oris (OOr), masseter (MAS), sternocleidomastoid (SCM), pectoralis (PEC) and biceps brachii (BIC). Mean premotor RT was found to be 151.8 ms. In random trials (p = .3 to .4), the startling stimulus was given at various intervals (0, 25, 50, 75, 100, and 150 ms) following the "go" signal. Results showed that in the trials in which the startling stimulus was given between 0 and 75 ms before the go signal, premotor RT was shortened significantly by a mean of 72.1 ms.

Two hypotheses were forwarded to account for these results. Firstly, the startle may act to enhance the excitability of certain neural structures that are used in the execution of voluntary commands. In this way, the time needed to activate the same structures a short time later would be significantly reduced. The alternative explanation forwarded by the authors hypothesized that the startle reaction was initiated by the loud stimulus, onto which a voluntary response was grafted. In this way, an initial startle reaction was possibly driven to correct completion once it was perceived that the movement was already underway (Valls-Solé et al., 1995).

In order to investigate this effect further, Valls -Solé et al. (1999) performed further experimentation. Subjects were instructed to respond to a visual stimulus by performing a fast wrist extension or wrist flexion movement. EMG activity was recorded from the wrist extensors (WE) and the wrist flexors (WF), as well as from several startle response indicators (OOc, and SCM). On random trials, a sudden loud (130 dB) acoustic startling stimulus was given in conjunction with the "go" signal.

As seen previously, many ballistic limb movements have a characteristic triphasic EMG profile (Wadman et al., 1979). The authors hypothesized that if the EMG response observed was simply an early startle reflex followed by an overlapping voluntary response, that a disruption of the triphasic EMG pattern (with respect to control EMG patterns) would be evident. Alternatively, if the EMG was not altered, this could be considered evidence that the startling stimulus leads to a response that is somehow speeded, possibly bypassing some of the normal neural circuitry (Valls-Solé et al., 1999).

Findings supported the latter hypothesis, as mean premotor RT was decreased in the startle condition by a mean of 94 ms, while EMG profile remained largely unchanged. Specifically, the form, amplitude and duration of the triphasic EMG bursts were very similar in the control (no startle) and test (startle) trials (Valls-Solé et al., 1999) (Fig. 14).

Valls-Solé et al. (1999) asserted that because the EMG configuration was unaltered, this was evidence that the prepared response was triggered by the startle, and not simply added on to it. If the voluntary commands and startle responses acted through completely separate channels, they argued that one would expect to see the outputs in terms of the EMG response to be superimposed. Because this was not the case, Valls-Solé et al. (1999) argued that there must be some interaction of the voluntary and startle systems at the supraspinal, subcortical level.

Mean EMG onset latencies of 77 ms were found in the agonist, which Valls-Solé et al. (1999) argued was too short to be accounted for by voluntary commands generated by the motor cortex. As mentioned previously, the first volley of neural pulses to reach the auditory cortex takes about 35ms, while efferent conduction time to the forearm is roughly 20 ms, leaving only 10-20 ms for cortico-cortical activation of the motor cortex and subsequent generation of the first agonist burst (Valls-Solé et al., 1999).

The implication is that an action plan (consisting of motor commands) possibly prepared for voluntary action can be triggered by the same structures that are activated by the startle response. In order for this to take place, the motor commands must be accessible and ready to be released. The suggestion is that "sufficient detail of the movement characteristics may be stored in the brainstem and spinal centres so that, on occasion, the whole motor programme can be triggered without the expected command from the cerebral cortex" (Valls-Solé et al., 1999). Thus, the reticulospinal system may be important part of the response pathway in ballistic RT tasks. It may be possible for activation of this system to trigger motor commands required to correctly produce the

desired motor response, thereby bypassing the cortex and the normal process of stimulus recognition (Valls-Solé et al., 1999).

Following on from the work of Valls-Solé and colleagues, Carlsen, Nagelkerke, Garry, Hodges and Franks (2000) investigated the kinematics of the response that was produced in a startled reaction time task. Participants performed a simple RT task involving extension of the forearm at the elbow joint. The task, however, was not simply the movement itself, rather it involved moving the arm a prescribed distance to a specific target. In other words, the participants were directed to perform an elbow extension movement to a target located 15 degrees from the starting point. Findings showed that when startled, premotor RT was decreased by 40 ms although there were no differences in mean peak displacement or movement final position. However, variability of peak displacement was increased. The lack of an effect of the startle on final position and aiming accuracy suggested that the response produced was indeed the prepared response (Carlsen et al., 2000). These findings lend support to the hypothesis that, in response to a startle stimulus, a prepared movement may be released earlier in comparison to voluntary initiation.

Working on the hypothesis forwarded by Valls-Solé et al. (1999) that a prepared movement might, in fact, be triggered by a startling stimulus, Carlsen, Hunt, Sanderson, Inglis and Chua (2003) sought to determine whether the startle paradigm could be used to study the time-course of movement preparation. They employed a movement task in which a secondary movement was prepared and executed based on the execution of a primary movement. Since previous findings (Cordo et al., 1990) indicated that proprioceptive information (joint angle, angular velocity) could be used in triggering a

secondary movement, an experiment was devised that investigated whether a movement, that was prepared and then initiated on the basis of proprioceptive information about joint angle, could be triggered by a startle stimulus. Participants completed 60 trials in which they performed an active elbow extension at 22 degrees /sec and opened their hand when their arm passed through a fixed target 55 degrees from the starting point. A startling (124 dB) auditory stimulus was presented at 5, 25, or 45 degrees into the movement on 9 trials. Findings indicated that when the startle stimulus occurred late in the movement (10 degrees prior to hand opening) the secondary movement was elicited earlier with respect to the target (mean opening angle of 51.8 degrees) compared to control trials (mean opening angle of 54.9 degrees). The authors suggested that the secondary movement was "loaded" into lower brain structures at some point during the movement in preparation to be triggered, and was subsequently triggered by the startling stimulus. Furthermore, Carlsen et al. (2003) argued that since the secondary movement was only elicited late in the movement sequence and not early, that the secondary program was not loaded until late in the movement sequence.

<center>Regarding Voluntary Responses and Actions</center>

An interesting finding of Brown et al., (1991a) was that the efferent pathway used by the startle response is slower than the pathway used when the muscles are activated by transcranial magnetic stimulation (TMS). "The difference in latency of onset of EMG activity between sternocleidomastoid and rectus abdominus (24.0 ms) is about 16 ms longer than the difference in latency between these muscles when they are activated by magnetic stimulation" (Brown et al., 1991a). This finding suggests that the efferent pathways used by the startle have relatively slow conduction velocities compared to

normal efferent motor pathways. This provides additional evidence that it is unlikely that

the motor cortex could be involved in voluntary actions released by a startle, as the

conduction takes even longer than previously suggested.

Appendix B

Reaction Time and Precuing Literature Review

<u>Simple and Choice Reaction Time</u>

The Reaction Time (RT) method has been used extensively since the mid-nineteenth century in the investigation of motor control processes. This method measures the amount of time between the presentation of a stimulus and the production of a response by the participant. The method relies on the premise that the processes underlying the control of movement take certain amounts of time to complete before the response is produced. Therefore, differences in the amount of time taken to complete the underlying processes should manifest as differences in RT. Sensory transduction apparatuses as well as efferent and afferent nervous conduction generally add a constant amount of time to the RT. For example, there is a minimum amount of time, due to physical limitations, that it must take for the afferent and efferent signals to travel along neural pathways. This has been empirically determined to be 80 –120 metres /sec for large myelinated nerve fibres (Martin and Jessel, 1991). However, due to their nature, these variables do not usually change as a function of experimental RT manipulations.

<u>Simple RT</u>

In a simple RT situation, there is a single stimulus requiring a single response. Because of this simplicity, it has been suggested that few processes occur between the stimulus onset and the production of the response. Specifically, because the required response is known in advance, the response can be preprogrammed (Klapp, 1996). Thus, the only processes occurring in a simple RT paradigm are: 1) those that identify that the stimulus has been presented, and 2) the triggering of the response. Therefore, in this

situation, the RT consists of only these processes and nervous conduction time. Evidence of preprogramming in a simple RT situation comes from several studies in which the complexity of the response was manipulated to determine RT effects. Because RT has been found to increase along with response complexity in certain situations, it has been argued that more complex responses take more time to program during the RT interval (Henry and Rogers, 1960). Klapp (1996) however, demonstrated that in certain cases, the complexity of the response had no effect on the RT. Findings showed that in a task involving pronouncing words, the number of syllables to be pronounced did not affect simple RT. Similarly, in a simple RT task involving short or long duration responses, RT was unaffected by the duration (short or long) of the response. These results were taken as evidence that in some cases, programming of the response can occur in advance of the stimulus so that only the triggering of the response was necessary following the imperative stimulus (Klapp, 1996).

Choice RT

In a Choice reaction time (Choice RT) paradigm the processes occurring are more complex than in a Simple RT paradigm. There are more processes underlying the control of movement that take more time to complete before the response is produced. These processes, in human information processing models, usually involve three stages of processing: Stimulus identification, response selection and response programming (Schmidt and Lee, 1999 pp. 42-55). Donders (1969) was among the first to investigate the time course of these processes. He believed that the information processing stages were independent and serial. Using subtractive logic, he attempted to determine the time course of each process. In order to accomplish this he devised three different reaction

time tasks. The A-reaction was a Simple RT task, requiring a single action (pressing a key) in response to a single stimulus (a light illuminating). The B-reaction was a Choice RT task, requiring different responses (key press with right hand or left hand) in response to different stimuli (red light or blue light). The C-reaction was a go/no-go task, in which a single response was required (key press) but still involved two stimuli (red light = press key, blue light = do not press key). Donders argued that differences in RT between these tasks reflected differences in processing during various stages of the information processor (Schmidt and Lee, 1998, p. 43). The results from Donders' original studies indicated that making a Choice takes cognitive processing time. Presumably, in a simple reaction time task (such as the one used in Experiment 1), there is little or no response selection required, as there is only one possible response. Pre-programming could be completed before the warning tone and therefore executed in advance of the imperative stimulus. Thus, stimulus identification is the only processing required. However, when the reaction time task involves more than one response alternative the individual must select the appropriate response. Since this is not known in advance, extra processing is required following the imperative stimulus. So unlike a Simple RT paradigm, in a Choice RT paradigm the required response is not known; therefore, the appropriate response must be selected and programmed following the imperative stimulus. In other words, in a Choice situation, response selection processes and response programming processes must both occur during the RT interval.

Response Selection

Evidence that the selection of an appropriate response adds time during the RT interval comes from several sources. In a Choice RT paradigm, more response

alternatives exist. Because of the need to discriminate between response alternatives, response selection is thought to require more processing time increasing the RT interval. Hence Choice RT is usually longer than Simple RT. This was the focus of a classical study by Hick (1952)

In Hick's (1952) study, participants reacted to the illumination of one of ten pea lamps by pressing a corresponding telegraph key. The number of possible choice alternatives was manipulated in various ways, from increasing the number of choices in a regular manner, to random ordered numbers of choice alternatives. Findings showed that as the number of stimulus-response alternatives increased, so did reaction time. The increase seen in reaction time with the number of response alternatives, however, was not regular (linear). Hick noticed that each time the number of response alternatives doubled, reaction time increased by a relatively constant amount (~150 ms). This is a logarithmic relation, and Hick suggested that the Log_2 of the number of alternatives represented the number of "bits" of information that needed to be gained to solve the motor problem (one bit being a binary choice whose probability was 0.5), and each bit took a certain amount of time to process (Hick, 1952). In other words, each time a stimulus array had to be split in two to arrive at the correct stimulus-response pair, a constant amount of processing time was required, which increased RT in a logarithmic fashion. This evidence supports the notion that in a Choice RT paradigm, central processing is required to select the appropriate response during the RT interval.

More recently, studies have shown the importance of cortical involvement in the execution of movements requiring a choice of action. Specifically, Schluter et al., (1998) found that transcranial magnetic stimulation (TMS) was effective in interfering with the

selection process in a visual choice RT task. In a series of studies, TMS was applied over the motor cortex, dorsal premotor cortex and sensorimotor cortex at different latencies with respect to the visual cue. In the first experiment, they found that stimulation over the dorsal premotor cortex contralateral to the response hand 140 ms following the cue was effective in delaying the response. The authors suggested that the RT delay resulting from stimulation over this area at this latency was due to a disruption in the response selection process. Stimulation over the motor cortex at longer latencies was also effective in delaying the response (Schluter et al., 1998). In the second experiment, stimulation was again given over the same areas and with the same latencies; however, it was given over the hemisphere ipsilateral to the response hand. This time findings showed that only stimulation over the left premotor cortex at 140 ms following the visual cue delayed response onset. Stimulation on the right side of this area had no effect. A third experiment was designed to investigate whether delays seen when stimulating over the premotor cortex actually reflected interference with the selection process as suggested previously. This time participants performed either a Simple RT task or a Choice RT task. Stimulation was given over the ipsilateral premotor cortex at varying latencies. Again findings showed that stimulation over the left side at 100 ms following the visual cue resulted in response delays in the Choice RT task. There was no effect of this stimulation in the Simple RT task. Thus, the authors concluded that the left premotor cortex plays a dominant role in response selection in a Choice RT task (Schluter et al., 1998)

Following these experiments, Schluter et al., (2001) used positron emission tomography (PET) to study the cerebral dominance in the selection of actions. Participants performed either a Simple or Choice RT task that involved responding to a

visual stimulus using left or right hands while being scanned by the PET scanner. There was significantly more activation in the left prefrontal, premotor and intraparietal areas during the Choice RT task as compared to the Simple RT task irrespective of which hand was used to respond (Schluter et al., 2001). These findings supported the earlier findings the TMS disrupts processing in a Choice RT task when applied over the left premotor cortex (Schluter et al., 1998).

Schluter et al. (2001) suggested that a Choice RT task differs from a Simple RT task in that a visual discrimination must be made between the various stimuli and the appropriate response must be selected in the Choice RT task. Further, they suggested that activations in the left premotor and parietal areas were unlikely to be associated with a demand for visual discrimination, leaving only response selection as the reason for this activation (Schluter et al., 2001). It appears therefore that the process of response selection is a cortical event occurring in higher centres during the RT interval. Evidence was presented implicating the dominance of the left premotor cortex in this process.

Response Programming

The notion that the information processing stages occur serially was first suggested by Donders (1969), and has since been a prevalent part of an information processing model of motor control. In such a serial-ordered model, if the appropriate response is not known in advance (such as in a Choice RT paradigm), the response cannot be programmed in advance. Thus in a Choice RT paradigm, programming must occur during the RT interval. Evidence has shown that in a Choice RT paradigm, more complex responses have led to longer RTs than less complex responses (Klapp, 1996). Specifically, findings showed that in a task involving pronouncing words, RT was

significantly longer for words containing 2 syllables than words containing only one syllable. Similarly, in a Choice RT task involving short or long duration responses, RT was longer for long duration keypresses than for short duration keypresses. These results were taken as evidence that in these cases, programming of the response took place during the RT interval. Because more complex responses (2 syllables, long duration) take longer to program (Henry and Rogers, 1960), these responses led to longer RTs (Klapp, 1996). This occurred because the appropriate response was not known beforehand, thus programming was not possible until after the stimulus was presented. This result was in contrast to the findings for Simple RT in which response complexity had no effect on RT (Klapp, 1996). Because response complexity had no effect on Simple RT, Klapp argued that the response could was prepared in advance. If a response could be prepared in advance, the nature of the response would have no effect on RT since no time would be required for the motor programming stage of the 3-stage model of information processing.

<center>Precuing</center>

Are there situations in which preprogramming might occur in a Choice RT paradigm? One particularly relevant variation on the Choice RT paradigm was used by Rosenbaum (1980). This method, which Rosenbaum (1980) called the "precuing" method, was designed to determine the extent of motor preparation that might occur prior to the response signal. He suggested two advance preparation possibilities for Choice RT tasks. First, rather than waiting until a response was selected before programming, all possible responses might be pre-programmed and the appropriate response simply selected and implemented following the imperative stimulus. Conversely, the other

suggestion implied that an individual might construct and pre-program a "protoprogram" which contains information common to all of the possible responses, with only the information which distinguishes it from the other responses being added following the RT stimulus.

In examining these possibilities, Rosenbaum had participants perform a task in which a movement to press a button was made with either the right or left hand, towards or away from the body, and either to a near or far target, leading to an eight-choice RT task. Rosenbaum then gave advance information about one or more aspects (parameters) of the upcoming movement by presenting a series letters on a screen for 3 seconds. One letter represented information about each movement parameter. Hand was cued by presenting either (L)eft or (R)ight; direction was cued by presenting either (F)orward or ' (B)ackward; and extent was cued by presenting either (N)ear or (D)istant. For example, he could give information that the left arm was going to be used (1 parameter), that a forward movement with the left arm was going to be required (2 parameter) or that a forward movement with the left arm to the near target was going to be required (all 3 parameters). If an aspect of the movement was not cued, an (X) would appear in place of the informative cue. The control condition was one in which no aspects of the upcoming movement were be specified. It was assumed that the participant was able to plan and prepare the parameters specified by the precue in advance of the imperative stimulus, leaving only the remaining parameters to be specified during the RT interval.

Following the precue and a random foreperiod, participants were shown a coloured dot which corresponded to one of the eight response choices, and participants were expected to react as fast as possible by pressing the correct button. As expected,

Rosenbaum found that as more information was given in the precue, RTs decreased. However, each piece of information was not weighted equally in processing the movement. When only information regarding which arm was to be used was cued, RT decreased more compared to a no-cued-parameters condition than when either direction or extent was cued. Similarly, when direction was cued, RT was shorter than when only extent was precued. Based on these findings, Rosenbaum argued that the three parameters tended to be specified individually, and each aspect required a different amount of time to program. Additionally, Rosenbaum suggested that since precuing more parameters leads to shorter RTs, the response aspects must be specified in a serial order. This is due to the assumption that if aspects can be programmed in parallel, there would be no difference in programming 1, 2, or 3 parameters (Rosenbaum, 1980). Thus, Rosenbaum argued that the precuing method allowed the participants to pre-program the precued aspects of a Choice RT task. Furthermore, he argued that the data revealed differences in programming time for each aspect after non-motoric decisions had been made.

A second experiment was designed to determine if the precues affected mainly the stimulus identification processes rather than the programming processes. Rosenbaum wished to investigate if it might have been easier to identify the correct stimulus if the arm information was given in advance, as opposed to either direction or extent of movement. In this experiment, a precue was shown as before, and following a foreperiod, a test (imperative) stimulus was given. However, in this experiment, sometimes the precue was incorrect (false or invalid) with respect to the test stimulus. In other words, the precue gave false information about the upcoming stimulus. No movement was required, only the identification if the precue was valid or not by verbal response.

Findings indicated that there was no difference in the RT to detect the validity of the precue in relation to the type of information given. This, Rosenbaum argued, indicated that the precuing effects were not attributable to stimulus identification, but to response preparation.

In order to investigate the hypothetical distinction between a parameterization model and a response competition model, a third experiment was performed. To investigate if the participants constructed several complete and distinct programs, and simply selected the correct one following the test stimulus, Rosenbaum instructed the participants to construct multiple responses based on the precues available. Thus if only the arm was precued, the participant was instructed to construct the four possible responses in advance. From the results, Rosenbaum argued that since there were many more response errors in Experiment 3 as compared to Experiment 1, that it was likely that the participants were able to follow the instructions and prepare multiple responses. Additionally, RTs were larger between the 2 and 1 precued aspects in Experiment 3 as compared to Experiment 1. This, Rosenbaum suggested, indicated that it took longer to select the correct response from 4 responses than it took to specify 2 response aspects. Findings thus indicated that there were no differences in RT between the different precued aspects. For instance, if arm and direction were known, there was no advantage over any other two precues. In other words, when the participants were instructed to construct separate programs, the differential effects of the precues disappeared. It was argued that this result provided evidence that the participants in Experiment 1 used a parameterization scheme, whereas a multiple response scheme was used in Experiment 3 (Rosenbaum 1980).

Processes Affected by Precues

Rosenbaum's assertion that the precue effect was due to the precues affecting the response programming or motoric processes was met with some skepticism. Alternate explanations of the effect of the precue emerged. From an information processing perspective, the precue could act on either the non-motoric processes or on the motoric processes. The non-motoric processes include stimulus identification and response selection processes, whereas motoric processes are responsible for response programming. Evidence from various authors implicated some of these processes over others, and will be discussed below with emphasis on the processes thought to be affected by the precue.

In the following review, since movement parameters or dimensions are discussed in some detail, it will be helpful to keep terms in order. These movement dimensions will be identified by who supplies the information. If the parameter is known or given in advance by the experimenter, the parameter will be described as <u>cued</u> or <u>precued</u>. Similarly, if the participant must specify the movement dimension following the reaction (imperative) signal, the parameter will be described as being <u>specified</u>.

Historical Developments

Following up on these experimental results, Goodman and Kelso (1980) were able to experimentally replicate the results from Rosenbaum's (1980) first experiment. They argued, however, that the conditions were not natural, in that a complex stimulus-response transformation was required. Specifically, in Rosenbaum's methods, participants received three letters that had to be decoded in order to gain any information

regarding the upcoming movement. Secondly, a colour to position transformation also had to be completed before the movement could be made (see above).

In order to control for these factors, Goodman and Kelso (1980) mapped the precues in a much more visuo-spatially direct fashion. In a second experiment, a board with eight LEDs (in two vertical columns of four) was placed in front of the participant corresponding to eight buttons on a board similar to the one used by Rosenbaum (1980). To cue an upcoming movement, a number of the LEDs were illuminated for 3 seconds prior to the foreperiod. In order to precue hand, all four LEDs in one column were illuminated. Similarly, to precue extent or direction, the appropriate LEDs were illuminated. This, they argued, was a much more natural stimulus-response situation. Since the precues were linked spatially to the responses, they required much less cognitive transformation (Goodman and Kelso, 1980). Findings showed that although more cued parameters resulted in decreased RTs, there were no differential effects of the cued parameters. In other words, cuing one parameter resulted in no greater RT gains than cuing any other. These results cast into doubt Rosenbaum's (1980) notion that the remaining movement parameters were differentially specified following response selection. Moreover, the results indicated that the reduction in RT was simply a function of a decrease in stimulus response alternatives (Goodman and Kelso, 1980). Thus, rather than the precues facilitating the response programming process, the precue method simply facilitated the response selection process by decreasing the number of response alternatives.

Rather than abandoning the parameter specification model, Goodman and Kelso (1980) suggested that it was possible that individual parameters were still specified, but

that specification time was no different between the response aspects. This specific case was termed "nondifferential parameter specification." In order to determine if response parameters were specified serially, but were masked by the differences in response selection, Goodman and Kelso employed an "ambiguous" precue. The ambiguous precue decreased the number of stimulus-response pairs, while providing no specific parameter cues. For example, an ambiguous precue would specify the right, forward, near target as well as the left, backward, far target. Thus the number of stimulus-response alternatives was only two, but all three parameters remained to be specified. The other precue conditions precued two parameters, leaving the participant to specify the third during the RT interval. This also kept the number of stimulus-response alternatives at two. Goodman and Kelso (1980) argued that if the parameters were specified serially, then having to specify more parameters (3 in the ambiguous condition vs. 1 in all other conditions) would result in an increased RT. Findings indicated that no differences existed in RT between the precue conditions. More importantly, no differences were observed between the conditions in which one parameter remained to be specified, and the ambiguous condition in which all three parameters remained to be specified. These findings failed to support the model of serial-ordered parameterization of a motor program. Rather they supported a view that precues simply affected the response selection stage by reducing the number of stimulus-response pairs. Based on these findings, Goodman and Kelso (1980) argued that the precuing method had little to do with the parameterization of motor programs.

More evidence indicating that the precues affected mainly the response selection processes was presented by Zelaznik and Hahn (1985). In attempting to avoid the

problem of confounding the number of stimulus-response alternatives with the programming processes, Zelaznik and Hahn used a somewhat different precuing method. When the number of parameters that are cued increases, there is a corresponding decrease in the number of stimulus-response alternatives. Because of this, in the precuing method used by Rosenbaum, the manipulation of the number of cued dimensions confounds the motoric processes of response programming with the processes of response selection. The method used by Zelaznik and Hahn held constant the stimulus-response (S-R) pairs at two, while manipulating the number of cued parameters (S-R constant method). In addition, rather than precuing hand, direction, and extent, Zelaznik and Hahn used the parameters of hand, digit, and duration. The responses could be long (300 ms) or short (150 ms) keypresses, completed by either the thumb or index finger of either hand (8 choices). Stimuli consisted of 4 areas of a computer screen (forming four corners of a virtual square) that could illuminate with either a short bar or a long bar (indicating a long or short response). In order keep the number of S-R pairs constant, only 2 of 8 possible response choices were presented in advance in any one trial. The advance stimulus could have indicated (cued) zero response parameters by cuing the upper-left-short-bar and the lower-right-long-bar. Thus, neither arm, digit, nor duration was cued, although there were only 2 response choices. Similarly, two response parameters could be cued by presenting the left-upper-short bar and the left-lower-short bar. In this case, both arm and duration would be cued, while digit remained to be specified by the participant. One parameter could be cued in a similar manner. Findings were similar to those of Goodman and Kelso (1980) in that neither the amount nor the type of information regarding the upcoming movement affected RT differentially. Specifically, when the number of S-R alternatives

was held constant, precuing more parameters did not lead to shorter RTs. Due to the null

findings, the authors suggested that the variables they employed in the precuing (hand,

digit, duration) might not have been closely related to the "language" of the motor system

(Zelaznik and Hahn, 1985). These findings further indicated that the precue only affected

the response selection stage of the RT.

In an experiment conducted by Larish and Frekany (1985), the S-R constant

method (in which the number of S-R alternatives was invariant across precue conditions)

was contrasted against the S-R variable method (in which the number of S-R alternatives

varies with the number of precued parameters). However, they employed an experimental

setup similar to that of Goodman and Kelso (1980) in that a visual array of lights

indicated precues for an eight-choice button press task involving arm, direction, and

extent. They described results similar to those of Zelaznik and Hahn (1985). When the

number of S-R alternatives was held constant, in all conditions in which direction was

uncertain (uncued, or specified by the participant following the reaction signal), there was

no resultant decrease in RT as the number of precued parameters increased. This

provided evidence that if the "direction" parameter was unknown, no other information

could be prepared in advance. In other words, there was no decrease in RT as the number

of precued parameters increased so long as direction was unknown. In contrast, however,

in the S-R variable method, RT decreased as the number of precued parameters increased.

This evidence implicated the non-motoric decision processes as the main beneficiary (in

terms of RT decrease) of precues (in agreement with Goodman and Kelso (1980)).

Furthermore, since the RT did not increase as the number of parameters to be specified

increased, Larish and Frekany (1985) argued that if more than one parameter had to be

specified by the participant, it was done in a parallel fashion. This suggestion was in contrast to Rosenbaum (1980) who indicated that parameters were specified in a serial fashion.

The findings of the study by Larish and Frekany (1985) were not, however, entirely explained by the precues affecting non-motoric processes. In one specific case, motoric processes were implicated as the main beneficiary of the precue. In the case where direction was precued, Larish and Frekany (1985) found that movement preparation could occur in advance of the reaction stimulus. The authors argued that knowledge of direction was a parameter that was necessary in order to utilize precues about arm and extent, since direction provided knowledge about the pattern of muscle innervation. Once the agonist-antagonist relationship was established, decisions about the arm and force (extent) could be made (Larish and Frekany, 1985).

In the conditions where the S-R alternatives were held constant (two S-R alternatives), knowledge about direction of movement (direction precued condition) resulted in a shorter RT than the zero parameters precued condition. Additionally, if another parameter was precued along with direction (either arm or extent), RT was shorter than only one parameter precued. This finding was in sharp contrast to previous findings using the S-R constant method (Goodman and Kelso, 1980; Zelaznik and Hahn, 1985), and indicated that certain types of precues might indeed affect motoric (response programming) processes. These findings also supported a serial parameterization model as proposed by Rosenbaum (1980), since RT was found to be additive as a function of the number of movement parameters to be specified.

The notion of serial-ordered parameterization was once again challenged in a study involving an 8-choice task. Lepine, Glencross, and Requin (1989) employed a task involving the movement dimensions of arm, direction, and extent. In contrast to pointing movements or button presses as used in previous experiments (Goodman and Kelso, 1980; Larish and Frekany, 1985; Rosenbaum, 1980; Zelaznik and Hahn, 1985), the movement required was a monoarticular flexion/extension of the left or right wrist in the sagittal plane. This moved one of two handles, which in turn controlled one of two cursors that moved in the vertical plane to one of eight targets on a screen placed in front of the participant. A design was used in which the number of S-R alternatives was held constant as the number of precued dimensions was manipulated (similar to the S-R constant condition used by Larish and Frekany (1985)).

Overall, findings echoed those of Rosenbaum (1980) in that RT decreased as the number of precued dimensions increased. This was found even though the S-R compatibility was high and the number of S-R alternatives was held constant. Thus, although both major criticisms (Goodman and Kelso, 1980; Zelaznik and Hahn, 1985) of the initial precuing method as described by Rosenbaum (1980) were controlled for, a precuing effect was observed (Lepine et al., 1989). Results showed that when the participant was only required to specify one parameter, extent was found to take the least amount of time to program (the RT decrease when extent was precued was smaller than the other dimensions). This finding agreed well with previous studies (Rosenbaum, 1980; Larish and Frekany, 1985).

In a serial parameterization model, as proposed by Rosenbaum (1980), the parameter programming times are separate and additive. As such, if the amount of

programming time required to specify arm is longer than the amount of time to specify extent, then these differences should remain if another parameter is added to be specified by the participant. For example, the difference in time for the participant to specify arm plus direction compared to extent plus direction should be the same as the difference in time to specify arm versus extent alone (Zelaznik and Hahn, 1985). Furthermore, the programming times should be additive. Thus each extra parameter to be specified by the participant should add a certain amount of time to the RT. This additivity can be attributed to processing time required in the motoric stage since the time required for the non-motoric processes are held constant (i.e. when the number of S-R alternatives is held constant and S-R compatibility is high).

In contrast to a serial parameterization model that predicts parameter additivity (Rosenbaum, 1980), the findings of Lepine et al. (1989), revealed an underadditive situation. This occurred when the number of dimensions to be specified was two or more and the number of S-R alternatives was held constant a two. Thus, when the number of choices was two, there was no difference in RT between no advance information (participant to specify three parameters) and one parameter cued (participant to specify two parameters). According to Rosenbaum (1980), a certain amount of time should have been added in order to specify the extra (3rd) movement dimension. Lepine et al. (1989) suggested that in these situations, the participant might use a form of "dimensional reduction." Consider the case of an 8-choice task involving arm direction and extent where one dimension, extent, is precued. In this case, Lepine et al. (1989) argued that the remaining dimensions are highly correlated in the 2-choice (constant S-R) situation. For example, if the left hand were linked to a forward movement, the right hand would

necessarily be correlated with a backward movement. Thus these two dimensions could be effectively reduced to one. The same holds true for a two-choice task in which the participant must specify all three dimensions. This "dimensional reduction" would predict no differences in RT between the zero- and one-precued dimension conditions, a finding reported by Lepine et al. (1989).

Since a precuing effect was observed (time to program extent was shortest), the authors attributed the difference in time to program the different parameters to differential features of the movement dimensions (Lepine et al., 1989). The authors reasoned that the three dimension values could not be evaluated on the same scale since they were very different in nature. Arm and direction are binary in nature (with respect to the specific task). Thus the only choices for arm are "left" or "right," and the only choices for direction are "forward" and "backward." In contrast, however, it was argued that "near" and "distant" are two values on a single continuous dimension, and this difference lead to the difference in programming time (Lepine et al., 1989). However, Lepine et al. (1989) suggested that in some cases, specification times were "more additive" than in other cases due to dimensional reduction being achieved less efficiently. In the cases that included two movement dimensions where the one dimension to be specified was not binary discrete such as extent, the RT was "more additive." It was argued that the continuous dimensions were less easily correlated with binary dimensions (Lepine et al., 1989).

Another continuous dimension, duration, was investigated by Vidal, Bonnet, and Macar (1991). They sought to determine if the duration of a motor activity could be specified in advance in a precuing paradigm. Zelaznik and Hahn (1985) had also used

duration as a movement dimension, but found no precuing effect. In contrast, Klapp (1996) has shown that in a Choice RT paradigm, more complex responses have led to longer RTs than less complex responses (Klapp, 1996). This has been termed the short-long effect (Vidal et al., 1991). Thus a long duration movement in which duration is unknown should require more programming time (and thus exhibit a longer RT) than a short duration movement. Conversely, if duration is a parameter known in advance (precued) then RT should be no different between long and short duration movements (if all other variables are controlled). Results indicated that there was no difference in RT between the conditions in which duration was cued (duration-only cued and full precue conditions). Similarly, when duration was to be specified by the participant, short duration responses resulted in shorter RTs than longer duration responses. This finding indicated that duration could be prepared in advance whether or not the response hand was known in advance. When the number S-R alternatives were held constant, the same result was found: shorter RTs preceded short responses when the duration parameter was precued. However, it was found that there was no difference in RT between the conditions in which no parameters were precued, and when a short duration was precued. The authors suggested that the participants programmed a short duration movement by default in the zero-parameters precued condition and that an additional programming operation was required to specify the longer duration movement. Therefore when duration was uncued, an additional programming component lead to the longer RTs in the long duration movement (Vidal et al., 1991). This finding was corroborated by similar results shown by Vidal and Macar (1998).

It is apparent from the previous discussion that a range of findings has been reported in using the precuing method. There has been much disagreement in the RT effects of precuing different response parameters. Rosenbaum (1980) found that RT was reduced the most when arm was precued, whereas Larish and Frekany (1985) found that knowledge of direction lead to the greatest RT reductions. Lepine et al. (1989), in agreement with Rosenbaum (1980), reported that the extent-cued condition decreased the RT the least. They found, however, that there was no difference between the specification times of arm and direction (Lepine et al., 1989). In contrast to all of these, Goodman and Kelso (1980) and Zelaznik and Hahn (1985) found no evidence of precues acting on response programming processes. It seems therefore that the precuing method is not robust and the effects may be highly dependent on the methodology. As such, some of the evidence that the precues affect different information processing stages will be examined.

Precuing Affects Non-motoric Processes

As described previously, due to their null findings, both Goodman and Kelso (1980) and Zelaznik and Hahn (1985) attributed the decrease in RT observed by Rosenbaum (1980) to non-motoric processes. Findings from later studies also implicated the non-motoric processes as the main component of RT affected by the precues (Bock and Eversheim, 2000; Dornier and Reeve, 1990). Zelaznik and Hahn (1985) argued that the precuing method as described by Rosenbaum (1980) confounded the number of precued parameters with the number of response choices, and thus argued that the precuing effects could simply be attributable to time taken for response-selection processes. As described previously, response selection takes time (Hick, 1952). Thus, as the number of precued parameters increases, there is a corresponding decrease in the

number of stimulus-response alternatives. As such, in Rosenbaum's precuing method, the manipulation of the number of precued dimensions confounds the motoric processes of response programming with the processes of response selection.

The method used by Zelaznik and Hahn held constant the stimulus-response (S-R) pairs at two, while manipulating the number of precued parameters. This was done by precuing only two alternatives out of eight possible response alternatives in any one trial. To illustrate, if the two response alternatives precued indicated the two short-duration targets in the forward direction, direction and duration (2 parameters) were precued. Similarly, if the precues indicated the forward-left-short target and the backward-right-short target, only duration (1 parameter) was precued. This same method could be used to precue zero targets. In this way, Zelaznik and Hahn (1985) were able to control for the number of S-R alternatives, thus rendering response selection time as constant as possible. Although when using this method Zelaznik and Hahn found no significant differences in RT between the precue conditions, numerous studies that have since employed this method have found a significant precuing effect (Dornier and Reeve, 1990; Larish and Frekany, 1985; Lepine et al., 1989; Vidal et al., 1991).

Goodman and Kelso (1980) criticized Rosenbaum's (1980) precuing method based on the nature of the stimulus-response (S-R) sets used. It was argued that due to the complexity of the cognitive transformations involved, additional non-motoric processes were required. Specifically, it was argued that non-motoric processing was required to translate stimuli from symbolic information (coloured dots) to spatial information (target buttons). This in turn added to the response time (Goodman and Kelso, 1980).

Several studies that followed (Goodman and Kelso, 1980; Larish and Frekany, 1985; Lepine et al., 1989; Zelaznik and Hahn, 1985) used direct spatial relationships between stimuli and responses to overcome this problem. For example, Goodman and Kelso (1980) presented an array of lights in front of the participant that corresponded directly to the spatial layout of the buttons that were used to respond. Using this method, differences in RT between the precuing conditions disappeared. Several studies, however, have since found precuing effects in highly compatible conditions. For example, Larish and Frekany (1985) had precues, imperative stimuli and response buttons superimposed on one another, so that the S-R sets were truly spatially compatible. Larish and Frekany (1985) did find that in highly compatible conditions, a precuing effect could be observed, but only if direction was known in advance.

Although the preceding strategy that maximized S-R spatial compatibility seemed to resolve the S-R translation issue, Dornier and Reeve (1990) suggested that some translation processes might still be influencing the results of the precuing experiments. Thus, not all of the observed RT differences in response to precues could be attributable to motoric processes (response programming), but some non-motoric processes could still be affecting RT. Most of the precuing studies (Goodman and Kelso, 1980; Larish and Frekany, 1989; Lepine et al., 1990; Rosenbaum, 1980) involved an 8-choice button-press or pointing task, involving three distinct movement dimensions: Arm, direction and extent. Furthermore, the response targets were generally laid out in two columns of four targets (one column for each hand/arm). However, previous studies showed that spatial arrangement affected S-R translation, even when the stimuli and responses were spatially compatible (Dornier and Reeve, 1990). For example, Zelaznik

and Hahn (1985) suggested that participants tended to view the world from left to right, leading to RT advantages when arm had to be specified (left-right stimulus search) as compared to arm cued conditions where direction had to be specified (top-to-bottom stimulus search).

Dornier and Reeve (1990) examined the notion that the observed RT differences between arm cued and direction cued conditions were a function of S-R arrangement, rather than a result of hierarchically ordered response programming, by modifying the experimental design used in several previous studies (see Larish and Frekany, 1985; see also Rosenbaum, 1980). Specifically, Dornier and Reeve (1990) implemented a left-right stimulus set in both the arm cued and the direction cued conditions. In a RT task, participants moved their index finger from a central starting point to target buttons that illuminated. No differences in RT were found between the arm cued and the direction cued conditions using this modified method. To further strengthen their conclusions, the authors performed another experiment in which only direction was unknown in a 2-choice design. The stimuli were placed in either a left-right arrangement or an above-below arrangement with respect to the starting point. Results indicated that RTs were longer in the above-below condition as compared to the left-right condition, although the spatial S-R compatibility was unchanged (Dornier and Reeve, 1990). These results led the authors to conclude that the differential RT effects of precuing arm vs. direction observed in previous studies were likely due to spatial compatibility effects. As such, it was argued that the compatibility effects acted on non-motoric decision processes; an assertion that was at odds with interpretations of precues acting on motoric (programming) processes (Dornier and Reeve, 1990).

Based on previous research that found that RT was shortest when response choices were spaced closer together, a recent study investigated the possibility that other perceptual non-motoric processes were facilitated by the presence of a precue (Bock and Eversheim, 2000). The authors suggested that when precued targets are spaced closer together, the participant might focus spatial attention onto a small area if workspace, thus when the target appears in the precued area, attention would already be focussed there (Bock and Eversheim, 2000). In order to test this hypothesis, Bock and Eversheim (2000) designed a precuing experiment that manipulated both the number of precued targets and their spatial extent. A pointing task was employed in which the participant pointed to a dot that appeared on a computer screen, and participants performed 60 trials. Four possible precue conditions revealed advance information about the location of the upcoming dot. In one condition, no precue was given. In another condition, five dots spaced 15 degrees apart along a 60-degree arc were presented for 0.7 to 1.3 seconds. In a third condition, two dots separated by 15 degrees were presented, and in a fourth condition, two dots separated by 60 degrees were presented. Results revealed an interesting pattern. First, RT was shorter in all conditions in which a precue was given as compared to the control (no precue) condition. Results indicated that there was no difference in RT between the five-choice (60-degree) condition and the two-choice (60-degree) condition. Reaction time was, however, significantly shorter than all the other conditions in the two-choice (15-degree) precue condition. The authors argued that based on these findings, RT depended on the spatial extent of the precues rather than the number of S-R alternatives

Since the RT was not related to the number of precued choices, Bock and Eversheim (2000) hypothesised that the precue information could be used to partially prepare the upcoming response. In order to examine this possibility, the methods were changed so that only a tapping response was required, irrespective of the target that appeared. This resulted in a movement whose preparation could not be facilitated by any type of precue. Results mirrored the previous findings, indicating that the precues must have affected non-motoric processes. Thus, since the findings indicated that the precues did not act on the response selection or response programming stages, it was argued that in this task, the precues influenced a sensorimotor stage of processing that is concerned with the representation of space (Bock and Eversheim, 2000).

This finding calls into question some of the results from previous precuing studies. In precuing methods that directly indicate the possible targets (Goodman and Kelso, 1980; Larish and Frekany, 1985, Lepine et al., 1989), the spatial distance between certain sets of targets may be quite different. For example, consider an eight-choice button press task such as the one used by Goodman and Kelso (1980). When there are only two possible targets, they could be left-forward-distant and right-forward-distant, which would result in a small inter-stimulus spatial distance. Alternatively, the two targets could be left-forward-distant, and right-backward-distant, resulting in a much larger inter-stimulus spatial distance. Thus the difference observed in RT between these two conditions may not be due to the number or nature of the movement dimensions, but may simply be due to the spatial extent of the stimuli. However, it must be noted that the preceding study was qualitatively different than other precuing studies, since the use of movement dimensions was ignored. Thus the study had little to do with the precuing of

movement dimensions as such. The implications, however, are that when possible, the spatial extent of the precues should be controlled between precue conditions.

In sum, four lines of evidence suggested that the precuing effect was due to non-motoric processes. It was argued that the precuing effect was simply due to the difference in the number of S-R alternatives (Zelaznik and Hahn, 1985), thus implicating the (non-motoric) response selection processes. Other evidence implicated the (non-motoric) stimulus identification and stimulus translation processes (Bock and Eversheim, 2000; Dornier and Reeve, 1990; Goodman and Kelso, 1980). Goodman and Kelso (1980) argued that a complex S-R translation was required in Rosenbaum's (1980) precuing method, and that S-R compatibility effects were the locus of the precuing effect. Dornier and Reeve (1990) argued that even in spatially compatible methods, there is a bias towards viewing the world in a left to right fashion, leading to RT differences between stimuli that are arranged horizontally and stimuli arranged vertically. Finally, Bock and Eversheim (2000) suggested that the precuing effect might be due to the spatial distance separating the possible target stimuli.

Precuing Affects Motoric Processes

In contrast with the view that precues mainly act on non-motoric processes during the RT interval, findings from several studies suggest that the locus of the precue effect may be the motoric processes. This is based on the hypothesis that if precues can be used in advance to partially prepare an upcoming response, the time required for motor programming during the RT interval will be shorter. In his original study, Rosenbaum (1980) argued that the precues affected the response-programming portion of the RT interval. This was based on two pieces of evidence. First, when the number of S-R

alternatives was the same, RT was differentially related to the movement parameter that was precued. For example, when only "arm" was precued, RT was found to be shorter than when either only "direction" or "extent" were precued. Similarly, when both direction and extent were precued (i.e. arm remained to be specified by the participant), RT was longer than when the other combinations of two parameters were precued. This difference in RT, Rosenbaum (1980) argued, reflected the difference in "parameter specification time" required for each movement dimension. Rosenbaum realized that the observed RT difference may have been solely due to differences in stimulus identification time between the conditions, but a second experiment ruled out this explanation. Thus, Rosenbaum concluded that the participants were able to differentially utilize the precued movement dimension information to partially prepare the upcoming movement in advance, thus reducing RT.

More evidence that the precue affects motoric processes was provided by Larish and Frekany (1985). Differences in RT were found between conditions in which different movement parameters were precued. However, they argued that knowledge of direction was required in order to be able to use any other precues, since direction provided knowledge about the pattern of muscle innervation (Larish and Frekany, 1985). Thus a hierarchical model was proposed in which decisions about the arm and extent could not be made until the agonist-antagonist relationship was established (see Historical Developments section). This provides some rationale as to why the precuing effect was not found in some studies and was thus not thought to be robust (Goodman and Kelso, 1980; Zelaznik and Hahn, 1985), as response hierarchies may have diminished the precuing effect.

In a similar vein, Lepine et al. (1989) found that parameter specification times were underadditive, leading to smaller-than-expected differences in RT between precue conditions. This meant that the difference in RT for the participant to specify one dimension such as "arm" compared to another dimension such as "direction" was not equal to the difference between the same dimensions plus one other (e.g. arm + extent and direction + extent). Due to this finding, it was suggested that in a two-choice situation, the participant may perform a type of dimensional reduction that effectively reduces the number of unknown dimensions by correlating one dimensional value with another (see Historical developments section). Findings did, however, show that in precue conditions that included a movement dimension that was not binary discrete (such as extent), RTs were "more additive" providing evidence that serial parameterization was in fact occurring.

Since the short-long effect has been cited as evidence of advance motor preparation (Klapp, 1996), the existence of a short-long effect in a precuing paradigm would provide evidence that the precue affects motoric processes. Two experiments investigated the result of precuing duration and found no difference in RT between the conditions in which duration was cued. In addition, when duration was uncued, short duration responses resulted in shorter RTs than longer duration responses. This finding indicated that duration could be prepared in advance whether or not the response hand was known in advance (Vidal et al., 1991; Vidal and Macar, 1998).

The lateralised readiness potential (LRP).

Recent evidence that strengthens the notion that precues affect motoric processes comes from studies involving the measurement of the lateralised readiness potential

(LRP). The use of the LRP will be first be discussed in order to familiarize the reader with the measure, followed by its application with respect to the precuing method.

The LRP is a measure derived from the electroencephalogram (EEG) and is associated with activation of the motor system. Activity in the primary motor cortex that precedes voluntary movement causes a negative shift in the EEG known as the readiness potential (Leuthold, Sommer and Ulrich, 1996; Osman, Moore and Ulrich, 1995). The readiness potential is recorded from electrode sites C3' and C4', which are located over the left motor cortex and right motor cortex respectively. The LRP is derived by from this potential by computing a difference value (averaged over response side) between the two sites. This is possible since a greater negative shift occurs in the site over the motor cortex contralateral to the responding hand (Leuthold, et al., 1996; Sangals, Sommer and Leuthold, 2002). Because the LRP measures lateralised premovement activity from the motor cortex of the responding hand, it can be used as an index of preparation of specific motor acts (Leuthold, et al., 1996). More directly, the onset of the LRP can be taken as an indicator as to when the <u>response hand</u> has been selected at the level of the primary motor cortex (Sangals et al., 2002).

Since the LRP can indicate when a response has been selected, it can be used to break up the RT interval. As described previously, Donders (1969) used chronometric methods to fractionate RT. This was done in order to examine the processes that occurred during the RT interval. Since that time, many more attempts have been made to quantify the amount of time taken by various processes. For example, EMG has been widely used to break RT into premotor RT and motor time (Brebner and Welford, 1980). Similarly, the LRP has been recently used to fractionate the RT interval. This is accomplished by

time-locking the LRP measurement to one of two occurrences: The stimulus (stimulus-locked LRP) or the response (response-locked LRP) (Leuthold et al., 1996; Osman et al., 1995). A stimulus-locked LRP can be used to determine the duration of the processes that occur from the stimulus onset until the LRP onset. Conversely, the response-locked LRP can be used to determine the duration of processes that occur between the LRP onset and the response onset. Osman et al. (1995) attempted to produce an effect on the response-locked LRP (the LRP-response interval) in order to determine what types of processes occur at the end of the RT interval, and what types of manipulations would affect those processes. It was assumed that motor programming processes were most likely to be occurring during the interval in question, so a method was chosen that was thought to selectively influence the motor programming portion of RT: the precue method.

It was reasoned that the findings from an LRP- and precue-driven investigation might provide support for the parameter specification model as proposed by Rosenbaum (1980). This was because the temporal locus of the precue effects could be determined. The precue could affect duration of processes prior to LRP onset, processes following LRP onset, or both sets of processes (Osman et al., 1995). A four-choice button-press task, in which the buttons were arranged vertically, was employed. Precue information consisted of four types: hand, finger, ambiguous, or none. In all of the precue conditions except the one that provided no information, the choices were reduced from four to two.

Results indicated that when the hand was precued, an LRP was elicited during the foreperiod (foreperiod LRP). This was expected since the LRP is assumed to index the point in time at which the response hand is selected at the level of the primary motor cortex. Furthermore, this shows that hand precues activated the motor cortex specific to

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the precued hand (Osman et al., 1995). There was, however, no difference found in RT between the three informative precues (hand, finger, or ambiguous), a finding similar to that of Goodman and Kelso (1980) and Zelaznik and Hahn (1985). This alone might have led the Osman et al. (1995) to agree with Zelaznik and Hahn (1985) in suggesting that the precue must have acted on non-motoric processes. In opposition, however, was the finding that when finger was precued, the LRP-response interval was shorter than when no information about the upcoming movement was available (Osman et al., 1995). Therefore, precues affected the LRP-response interval, providing a method for measuring the duration of processes that occur at the end of the RT interval following LRP onset. This suggested that if the processes occurring during the LRP-response interval were mainly motoric processes, the precues affected the duration of the motoric processes.

In sum, this study provided two pieces of evidence that precues affected the motoric processes. First, since a foreperiod LRP was elicited when hand was precued, it can be inferred that the precue information was used in advance of the stimulus to activate the corresponding motor cortex (indicating advance response preparation). Second, the LRP-response interval was shorter in condition in which finger was precued, indicating that the processes occurring during this time (likely motor programming operations) were shortened. It can thus be inferred that less motor programming time was required in the finger precued condition, and that the precue enabled partial advance preparation of the response. The finding was, however, consistent with two hypotheses of motor preparation. First, LRP activation might reflect the selection of the response at a highly abstract level and therefore would not include muscle-specific information (abstract motor selection). Alternatively, the LRP onset might indicate when muscle

groups specific to the response are selected (muscle-specific response selection) (Osman et al., 1995).

Several studies were undertaken to follow up on the previous results including one by Leuthold et al. (1996) that sought to examine the differential effect of precues on early and late processes during the RT interval. This objective was similar to that of Osman et al. (1995), but included the use of the P300 measure, which is thought to index perceptual processes related to stimulus evaluation (Leuthold et al., 1996). In addition, rather than using an ambiguous precue, a full precue condition was used. Thus, a four-choice finger flexion/extension task was employed in which hand or direction could be precued, as well as a full precue that cued the exact movement to be performed or a no-precue condition in which no advance information was given.

Results indicated that although there was a difference in RT between the conditions in which existed a different number of S-R alternatives, there was no difference in RT between the two precue conditions (hand precued or direction precued) in which the number of S-R alternatives was the same. As mentioned previously, this pattern of results does not necessarily rule out a parameter specification model as proposed by Rosenbaum (1980), but could indicate non-differential parameter specification.

The authors argued that because the P300 latency was not different between the precue conditions, that the stimulus perception and evaluation processes were unaffected by the precue (Leuthold, 1996). In addition, it was found that the precues led to a shortening of the response-locked LRP interval, but not the stimulus-locked LRP interval,

which conforms to the notion of a motoric locus of the precue effect (Leuthold et al., 1996; Osman et al., 1995; Rosenbaum, 1980).

A second result indicated that in the conditions in which a foreperiod LRP was elicited (i.e. response hand known in advance), more LRP activation occurred in the full precue condition than the hand-only precued condition. This finding is consistent with the muscle-specific selection hypothesis as described previously (Leuthold et al., 1996; Osman et al., 1995). An abstract preparation hypothesis would not predict the LRP activation levels to differ between these conditions, whereas a muscle-specific hypothesis would predict more activation based on the number of cued parameters. This is because more cued parameters would allow for more muscles to be selected in advance. Additionally, if participants prepared both responses in advance, a muscle specific hypothesis would predict more LRP activation in the hand precued as compared to the full precue condition, however, this was clearly not the case (Leuthold et al., 1996).

In an effort to extend these findings, Ulrich, Leuthold, and Sommer (1998) performed a similar experiment but included force as another movement dimension, resulting in an eight-choice RT task. Results indicated that RT decreased as a function of the number of precued parameters, although there was no difference in RT in the two conditions in which two parameters were precued (hand + direction, hand + force). This is similar to the RT results described by Goodman and Kelso (1980) and Zelaznik and Hahn (1985), in that no differential effects on RT were found between the precue conditions when the number of S-R alternatives was kept constant. Findings similar to those of Leuthold et al. (1996) were reported in that LRP amplitude was larger in the full precue condition than the hand only precue condition.

An alternative hypothesis for an increased foreperiod LRP amplitude as reported previously (Leuthold et al., 1996; Ulrich et al., 1998) was forwarded by Sangals et al. (2002). They suggested that the difference in LRP amplitude may have reflected differential precue use by the participant based on the amount of precue information available. For example, they suggested that if precue information was incomplete (hand only precue conditon) it may be used less often, or to a lesser degree than if full precue information was available, leading to a lower forperiod LRP amplitude. However, in employing two strategies to encourage the full use of precues, the LRP amplitude difference remained, indicating that LRP amplitude does not merely reflect differential precue utilization (Sangals et al., 2002).

In summary, these studies provided evidence that precue information affects the duration of the motoric processes of the RT interval, since LRP was successfully used to fractionate RT. Additionally, due to a foreperiod LRP amplitude that differed based on the number and type of precues, it was asserted that the precues allowed muscle-specific preparation. Furthermore, the precues are not differentially utilized based on the amount of information they contain. Thus the LRP evidence has strengthened the idea that the presence of precues allowed advance motor programming which lead to decreased motor programming time during the RT interval.

Summary

Following these findings, it is reasonable to assert that in order to investigate the motoric processes involved in the preparation of movement, the non-motoric processes must be controlled and their influence on RT kept constant. The S-R relationships should be spatially compatible since it has been argued that incompatibilities lead to complex S-

R translation processes that interfere and confound the investigation of the motoric

processes (Goodman and Kelso, 1980). Furthermore, S-R alternatives should be kept

constant so that the decision processes do not interfere with and confound the

investigation of the motoric processes (Larish and Frekany, 1985; Zelaznik and Hahn,

1985).

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