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UNEXPECTED ACOUSTIC STIMULATION DURING ACTION PREPARATION REVEALS GRADUAL RE-SPECIFICATION OF MOVEMENT DIRECTION

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Abstract—A loud acoustic stimulus (LAS) is often used as a tool to investigate motor preparation in simple reaction time (RT) tasks, where all movement parameters are known in advance. In this report, we used a LAS to examine direction specification in simple and choice RT tasks. This allowed us to investigate how the specification of movement direction unfolds during the preparation period. In two experiments, participants responded to the appearance of an imperative stimulus (IS) with a ballistic wrist force directed toward one of two targets. In probe trials, a LAS (120 dBa) was delivered around the time of IS presentation. In Experiment 1, RTs in the simple RT task were faster when the LAS was presented, but the effect on the movement kinematics was negligible. In the Choice RT task, however, movement direction variability increased when the LAS was presented. In Experiment 2, when we primed movements toward one direction, our analyses revealed that the longer participants took to start a movement, the more accurate their responses became. Our results show not only that movement direction reprogramming occurs quickly and continuously, but also that LAS can be a valuable tool to obtain meaningful readouts of the motor system's preparatory state.
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Key words: acoustic stimulus, motor control, movement direction, preparation.

INTRODUCTION

Execution of voluntary acts is preceded by preparatory processes in the central nervous system (CNS). The task specifies the act required – a speech act, a manipulative act, a locomotor act – and preparatory processes specify when and how the act will be executed so that the task requirements are met in the prevailing conditions (Requin et al., 1991; Jeannerod, 1994). Thus, preparatory processes must incorporate information about task requirements and environmental conditions in order to specify task-appropriate movement parameters, which are passed to the neural machinery that generates motor commands to the muscles. The process of preparation is therefore often referred to as *motor planning* or *motor programming* (Keele et al., 1990; Kawato, 1999; Schmidt and Lee, 2011).

The process of incorporating task and environmental information into a motor plan has been studied using reaction time (RT) and other speeded tasks in which the response is a target-directed movement of some kind (Leonard, 1958; Schouten and Bekker, 1967; Rosenbaum and Kornblum, 1982; Ghez et al., 1990; Marinovic et al., 2010; Haith et al., 2015). The person executing the task is provided with some initial information, which may be either sufficient or insufficient to determine the necessary response. At a later time, but prior to executing the response, additional information is provided that either changes the task requirements initially specified (in the case that the initial information was sufficient; (Haith et al., 2015) or supplements initially insufficient information so the required response is fully specified (Rosenbaum and Kornblum, 1982; Ghez et al., 1990; Schutte and Spencer, 2007). Using these methods it has been found that motor plans are initially established using information available from task instructions, prior experience with the task, and perception of the task layout (Ghez et al., 1990, 1997; Hudson et al., 2007; Schutte and Spencer, 2007; Haith et al., 2015). Where the target is not initially specified, the initial planning state represents the information available concerning all potential targets (Findlay, 1982; He and Kowler, 1989; Favilla et al., 1990; Ghez et al., 1997; Cisek and Kalaska, 2002; Hudson et al., 2007; Stewart et al., 2014; Gallivan et al., 2015; Haith et al., 2015), and many forms for this representation have been proposed (Kopecz and Schoner, 1995; Erlhagen and Schoner, 2002; Cisek and Kalaska, 2005; Stewart et al., 2014; Gallivan et al.,

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Abbreviations: CDE, constant directional error; CDF, cumulative distribution function; ECRB, extensor carpi radialis brevis; EMG, electromyogram; IS, imperative stimulus; LAS, loud acoustic stimulus; RT, reaction time; VDE, variable directional error.

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2015; Haith et al., 2015). Incorporation of new information into the motor plan can occur at any time prior to initiation of descending motor commands (Favilla et al., 1990; Ghez et al., 1997), and indeed there may be little or no distinction between the processes that underlie this plan updating and those responsible for feedback corrections of ongoing movements (van Sonderen et al., 1989; Flash and Henis, 1991; Prablanc and Martin, 1992; Flanagan et al., 1993; Hudson et al., 2007; Nashed et al., 2014).

Incorporating new information into an existing motor plan appears to be rapid, but not instantaneous. If new information is provided during the RT interval, new task parameters are not reflected in the resulting movement for hundreds of milliseconds (e.g., van Sonderen et al., 1988, 1989; Ghez et al., 1997; Marinovic et al., 2010). However, it is uncertain to what degree estimates of the time–costs of motor plan updating are inflated by processing demands related to task instructions (e.g. pay attention to a sequence of tones to start moving, (Ghez et al., 1990, 1997; Haith et al., 2015), which could interfere with the ability to attend to and incorporate new information. For example, using traditional and forced RT tasks, Haith and colleagues (2016) showed that up to one-third of the RT is expended on processes unrelated to movement programming but were rather concerned with adhering to task instructions and meeting task demands. Here we investigate movement direction plan updating when the use of strategies to deal with short preparation intervals are minimized and participants only need to prepare for a binary choice (right or left) during a trial. More precisely, this study aimed to reveal the time course of direction specification when the state of preparation for action required rapid adjustments to update the plan. To achieve this, we used RT tasks in combination with the delivery of loud acoustic stimuli (LAS) to induce the early release of prepared actions at different levels of preparation.

A LAS presented unexpectedly during movement preparation can trigger the initiation of the prepared action, a phenomenon termed the StartReact effect (Valls-Solé et al., 1999). Although most research on the StartReact has employed simple RT tasks (for recent reviews, see Nonnekes et al., 2015; Marinovic and Tresilian, 2016), some studies have investigated the early release of motor actions by LAS using choice RT tasks. Kumru et al. (2006) showed that a LAS could trigger whatever motor response was prepared at the time of stimulation (e.g. a correct or an incorrect hand movement). Similarly, Forgaard et al. (2011) found participants released motor acts whose amplitude fell between targets when their movements were triggered by LAS. However, some authors failed to detect any facilitation of movement initiation in tasks where participants had multiple movement choices (Carlsen et al., 2004). Thus, this relatively simple technique may be able to provide a readout of the state of motor preparation slightly prior to the voluntary decision to move in some circumstances and/or tasks, but not in others. We sought to obtain a read-out of the state of preparatory direction specification, but no studies have yet investigated the impact of a LAS on the directional accuracy of movement trajectories. Thus, it is necessary to determine whether a LAS can speed the initiation of motor responses in our task and to examine how it affects initial movement direction in simple and choice RT conditions. The results of experiment 1 showed that a LAS speeds movement initiation, but has no effects on response accuracy in simple RT tasks (where all movement parameters can be specified well in advance of the movement imperative). In contrast, the results showed that a LAS affects both movement initiation and accuracy under choice RT conditions, which indicates that movement accuracy progressively improves as initiation time is delayed and more time is available to prepare the specified movement. The aim of Experiment 2 was to further examine how direction reprogramming develops over time, by manipulating (i) target probability to induce larger directional biases during planning, and (ii) the inter-stimulus-interval (ISI) between the imperative stimulus (IS, or visual target) and the LAS, to probe different preparatory states. Our results showed that as RT increased, movement accuracy improved: the process appears to be continuous, but evolves rapidly.

EXPERIMENTAL PROCEDURES

Participants

Nineteen volunteers (3 women) participated in Experiment 1 (mean age = 20.5, range = 18–39). Twenty-six volunteers (3 women) participated in Experiment 2 (mean age = 20.4, range = 18–39). Participants gave written informed consent prior to commencement of the study, which was in accordance with the Declaration of Helsinki and approved by the local Ethics Committee of the University of Queensland. All participants reported normal or corrected to normal vision, stated that they were right handed, and had no known neurological conditions that could have affected their performance in the tasks. Participants received course credit for their participation in the studies.

Procedures and design

Participants sat in a chair in front of a 22-in Samsung LCD monitor (120-Hz refresh rate, 1680 × 1050 resolution) located 0.9 m away from them. The experiments involved isometric wrist contractions using a custom-built device (see de Rugy et al., 2012) that held the hand and forearm in a neutral position throughout the experiment (see Fig. 1A). Participants had their hands snugly fit into the device to reduce any time lag between muscle contractions and recording of forces generate by their wrists. Participants moved a circular cursor from the center of the monitor to targets presented radially, by applying forces with the wrist in two-dimensions (abduction/flexion–extension). Forces were measured by a six-degree of freedom force/torque sensor (JR3 45E15A-I63-A 400N60S, Woodland, CA), and converted to cursor location such that 20 N was required to move the cursor to the targets. In control trials, the cursor was visible throughout the trial and provided participants with information about the distance and the directional error to

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