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Research report

Functional dissociation of temporal processing mechanisms during speech production and hand movement: An ERP study

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A B S T R A C T

Skilled motor actions are mediated by neural mechanisms that incorporate sensory feedback for driving or suppressing movement with remarkable temporal precision. The predictive coding model proposes that the brain performs this function by establishing an internal representation of timing to accelerate movement response time. However, it is unclear whether different neural mechanisms are involved in temporal processing of movement initiation and cessation. The present study examined how temporal information is encoded for initiation and cessation of speech and hand movement. Event-related potentials (ERPs) were recorded while young healthy subjects performed speech and hand movement initiation and cessation in response to temporally predictable and unpredictable visual stimuli. We found that predictable stimuli elicited faster movement in both speech and hand modalities, with shorter reaction times associated with movement cessation compared with initiation. Analysis of ERPs revealed that premotor neural activities were significantly attenuated before speech initiation and hand movement initiation and cessation for temporally predictable vs. unpredictable conditions, but an opposite pattern was observed for speech cessation. In addition, we observed that the premotor ERPs were significantly modulated during speech initiation vs. cessation, but no such effect was found during hand movement. Finally, we found that the premotor ERPs were strongly correlated with motor reaction time during movement initiation and cessation for speech and hand modalities only in response to temporally predictable stimuli. These findings indicate that premotor ERPs reflect a temporal predictive code for planning of movement initiation and cessation and highlight functional dissociation of temporal processing mechanisms in speech and hand motor systems.

1. Introduction

The production and control of voluntary movement is an important function of the nervous system that enables humans and animals to interact with their environment. This critical function is mediated by complex neural mechanisms that incorporate sensory information to drive or suppress future motor actions. A fundamental aspect of sensorimotor processes underlying movement is to respond to sensory cues with an extremely high temporal precision. This capability is even more crucial for planning and execution of movement when the timing of sequential muscle activation (or deactivation) needs to be finely controlled for performing a goal-directed movement (e.g., driving, playing tennis, speaking, etc.). To accomplish such remarkable temporal precision, the brain has to optimally control movement reaction times for generating or suppressing motor responses to behaviorally relevant sensory stimuli. Although this inherent property of the sensorimotor system is crucial for survival, the underlying neural mechanisms of temporal processing during movement are not clearly understood. Therefore, the present study was motivated by the question as to what the neural correlates of temporal processing mechanisms for movement initiation and cessation are and how these neural processes are influenced by timing information embedded in external sensory stimuli.

The sensory processing of timing information has been previously studied using the odd-ball paradigm by showing that the auditory system extracts the patterns of temporal regularity in stimuli with predictable duration and time intervals, and it elicits a mismatch negativity (MMN) response when a deviant stimulus violates the established temporal predictive pattern [1–8]. Other studies have investigated the sensorimotor processing of temporal information by using the foreperiod (FP) paradigm in which the time interval between a prepare (prepare) and an imperative signal is manipulated while subjects perform a motor response reaction time task [9–17]. Findings of these studies have indicated that for temporally predictable (fixed duration) FPs, motor response reaction time for movement initiation was significantly shorter (faster movement), and movements were performed with greater temporal precision compared with those in

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response to unpredictable FPs with variable duration. These results support the notion that temporal predictability of sensory stimuli can facilitate motor function for driving faster movements, however, the underlying neural mechanisms of this effect remains to be elucidated.

In addition to studying movement initiation mechanisms (e.g., starting a hand motor response), more recent studies have investigated the underlying mechanisms of movement inhibition during tasks that involved withholding prepared motor actions in response to inhibitory cue signals [18–23]. Results of these studies have shown that motor response reaction time was decreased, and movement was executed faster as temporal predictability of inhibitory cue signals was increased, suggesting that temporal predictability of sensory stimuli can modulate movement inhibition mechanisms. Although these findings suggest temporal-specific effects of sensory stimuli on movement reaction time, there are still aspects of movement mechanisms that have remained relatively unexplored in this line of work. As an example, there is lack of knowledge about the effects of temporal information on movement mechanisms implicated in stopping (terminating) an ongoing motor action (e.g., hand movement or speech production). Hereafter, this latter motor response (i.e., stopping an ongoing movement) will be referred to as movement cessation in this paper, which is different from movement inhibition mechanisms investigated in previous studies [18–23].

In this study, we aimed to examine the effects of temporal predictability of sensory stimuli on neural mechanisms of movement initiation and cessation in the speech and hand motor systems. This work was motivated by a recent study in our lab [24] in which we designed an experimental paradigm to simultaneously measure motor response reaction times during initiation and cessation of speech and hand movements while subjects were cued to press a button or vocalize a steady vowel sound in response to a go signal, and stop their ongoing motor action in response to a stop signal. Results of that study [24] revealed that motor reaction time during both speech and hand movement initiation and cessation was significantly shorter in response to temporally predictable compared with unpredictable sensory stimuli (i.e. go-stop cues). According to recent models of movement control [25–28], our earlier findings [24] were consistent with the notion that the brain can internally simulate the behavior of the motor system during planning, execution and control of movement. According these models, the brain can learn the association between motor commands and expected sensory consequences of the movement and establish a predictive code for the next state of the movement. In the context of this model, extracting timing information from external cues may lead to establishing a predictive coding that fine tune motor commands and drive faster movement in responses to temporally predictable sensory stimuli. Although such a temporal predictive mechanism is implicated in a wide range of motor behaviors that are crucial for our survival, our knowledge about the neural mechanisms of such remarkable functionality in the sensorimotor system is relatively poor.

Novel insights into the underlying neural correlates of temporal processing mechanisms during movement initiation have been provided by neuroimaging studies that indicated functional disassociation between brain regions involved in processing sensory stimuli with predictable vs. unpredictable temporal patterns [15,29,30]. These studies have shown that neural activities in the caudal portion of supplementary motor area (SMA) [29], as well as the right dorsolateral prefrontal cortex (DLFPC) [15,30], and the left inferior parietal cortex (IPC) [31] were significantly stronger when movements were initiated in response to temporally unpredictable compared with predictable stimuli. In addition, single unit recordings from medial premotor cortex (MPC) in monkeys have shown that neurons in this area not only encode temporally predictable intervals in sensory stimuli, but are also activated to generate timed intervals during rhythmic movements [32–34]. This evidence suggests that premotor neurons are core components of a timing network that uses interval tuning to process temporal regularity in sensory stimuli during a variety of behaviorally relevant motor tasks. These findings further support the existence of specialized neural networks that process timing information during movement production. Similarly, studies have found distinct patterns of brain activations in response to predictable vs. unpredictable sensory stimuli that cued hand movement inhibition during a button press task [35,36]. Findings of these studies have revealed that the striatum was more strongly activated as the temporal predictability of the inhibitory cue signals was increased [35]. In addition, it has also been shown that when subjects performed hand movement inhibition during a stop signal task, two distinct areas in the basal ganglia were differentially activated in response to frequent vs. infrequent stop trails [36]. Findings of this latter study showed that the areas within the subthalamic nucleus (STN) and anterior striatum exhibited greater activations when stop signals were presented infrequently (unpredictable), whereas greater activations were observed in the caudate nucleus when stop signals followed a frequent (predictable) pattern. These findings suggest that initiation of movement is primarily mediated by neural networks within the cortical motor regions (e.g., DLPFC, SMA, and MPC), whereas movement inhibition is controlled by subcortical structures such as those in the basal ganglia network.

Although stimulus temporal predictability was shown to modulate neural activities after the movement initiation and inhibition, a number of studies have reported that neural activities prior to movement initiation [23,37–39] and inhibition [23] are also modulated in responses to temporally predictable vs. unpredictable sensory stimuli. Electroencephalography (EEG) recordings in humans have demonstrated that the pre-movement neural activities were elicited up to two seconds before the onset of motor response and were found to be stronger in scalp electrodes over the bilateral frontal areas [37]. In a follow-up work to our original study on temporal predictive mechanisms of speech and hand movement [24], we also examined the neural correlates of movement initiation in response to predictable and unpredictable stimuli using event-related potential (ERP) activities that were extracted from EEG signals recorded during the performed motor reaction time tasks [40]. In that study [40], we identified premotor ERP activities over the frontal and parietal areas, which were elicited 100 ms before speech and hand movement initiation and were significantly attenuated in response to temporally predictable compared with unpredictable sensory stimuli. Although the nature of such premotor neural activity attenuation is not fully understood, one possible interpretation of this effect is that the attenuation of premotor ERPs may be accounted for by modulation of neural processes that underlie predictive coding mechanisms during movement. For temporally predictable stimuli, the fixed timing interval between the prepare and go cues could potentially be more accurately extracted for driving motor commands compared to that for unpredictable stimuli with randomized timing intervals. Thus, the attenuation of ERP activities in response to temporally predictable stimuli may in fact represent a more accurately established predictive code for speech and hand movement in response to fixed timing intervals. In addition, we found that the amplitude of the premotor ERPs was negatively correlated with speech and hand motor reaction time during movement initiation, with a stronger correlation for temporally predictable stimuli. These findings indicated that the premotor ERPs are robust neurophysiological biomarkers of speech and hand motor reaction time and are modulated by stimulus temporal predictability.

Although previous studies have provided insights into the neural mechanisms of temporal information processing during movement initiation and inhibition, our understanding about these mechanisms has been limited by several factors. First, previous studies have primarily focused on examining the effects of temporal predictability on neural mechanism of movement initiation and inhibition and less is known about the mechanism of movement cessation during an ongoing motor action. Second, previous research has primarily focused on studying the neural correlates of movement initiation and inhibition after (but not before) the onset of motor responses, and therefore, it is unclear how