



Motor timing and motor sequencing contribute differently to the preparation for voluntary movement

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ABSTRACT

Two crucial processes preceding voluntary action are determining the time for movement initiation and planning of the specific sequence of motor output. In this study we aimed to differentiate the neural activity related to motor timing and motor sequencing and to examine over what time periods they contribute to premovement activity during the readiness for voluntary action. Eighteen participants performed self-initiated voluntary finger movements in a readiness potential paradigm, both during EEG measurement and during fMRI. The finger movement task involved three conditions: (1) simple repetitive sequences; (2) increased demand on the sequencing of movement order; and (3) increased demand on the timing of movement initiation. Functional MRI and 64 channels EEG were conducted in two separate sessions. Motor timing and motor sequencing were found to involve different neural processes occurring at different times prior to movement initiation. Motor timing involved greater activation in lateral prefrontal regions over the earliest part of premovement activity, from 1200 ms before movement onset. Motor sequencing involved greater activation of dorsal premotor and parietal areas and was reflected in central and parietal scalp regions only over the later part of premovement activity, within 600 ms of movement onset. We suggest that different neural processes contribute to different aspects of the intended action over different time periods during the preparation for movement, and it is the coordinated activity of these multiple regions that is represented in premovement activity during the readiness for voluntary action.

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Introduction

The ability to plan and perform voluntary action is essential to express our intentions and manipulate the environment in relation to our own will. Every voluntary movement is preceded by brain activity aimed at preparing and executing the action. When movements are self-initiated, i.e. performed at our own will without any external cue, this brain activity can start up to 2 s before the execution of the movement. The activity appears in the EEG as a slow-rising negative potential that has been called Bereitschaftspotential or Readiness Potential (RP) (Deecke, 1969; Kornhuber and Deecke, 1965). Neuroimaging studies have shown involvement of a widespread higher-motor network in the preparation for action, including the supplementary motor area (SMA), premotor cortex, basal ganglia, inferior and superior parietal lobes, and prefrontal regions including the anterior cingulate (Ball et al., 1999; Cunnington et al., 2002, 2003; Deiber et al., 1999).

Premovement activity is suggested to involve two major components: an abstract level of movement preparation and intention to move followed by specific programming for movement execution. The former component is reflected in the early readiness potential and

premovement activity of regions including pre-SMA, prefrontal cortex, lateral premotor areas and parietal lobe. The latter component has been associated with the late readiness potential and activity of the primary motor cortex (M1) and SMA proper (Shibasaki and Hallett, 2006).

The function of the mesial motor areas (pre-SMA, SMA-proper and cingulate motor area) during preparation for movement and the specific cognitive or motor processes that contribute to the earliest component of premovement activity are unclear. Two crucial processes preceding voluntary action are determining when to initiate the action and determining the order of movements that are involved in the action. The former process we refer to in this study as motor timing and corresponds to the internal decision on when to perform a voluntary action (Deecke, 1996). It must be noted that the motor timing we examine here is the process of determining the appropriate time for movement initiation. This may be distinct from other forms of motor timing involved in rhythmic movement or coordinating the timing of sub-movements within a sequence (Bengtsson et al., 2005). The later process, motor sequencing, involves the planning of the specific sequence of motor output required to achieve the intended goal of the action. In this study, we examine the contribution of processes related to the timing of movement initiation and motor sequencing to premovement activity during the preparation and readiness for voluntary action.

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Previous studies have shown a role of the SMA in both the timing and the sequencing of movement. Neuroimaging studies show that there is a positive correlation between SMA activity and the ordinal complexity of a sequence of movements (Boecker et al., 1998; Sadato et al., 1996a). Moreover intracranial recordings in monkeys have shown that SMA activity is partly related to the selection of a specific sequence order (Shima and Tanji, 1998, 2000). Neuro-cognitive models of time estimation have pointed to the SMA and fronto-striatal circuits as the neuronal substrate of an internal clock that creates representation of time (Macar et al., 2004, 1999; Meck and Benson, 2002) on which mechanisms of movement initiation rely. Studies on motor timing show that premovement activity in the SMA is affected by rhythm complexity (Bengtsson et al., 2005; Chen et al., 2008; Dhamala et al., 2003; Lewis et al., 2004) and when maintaining movement rhythm in the absence of external cues (Rao et al., 1997).

Motor timing and motor sequencing, however, are also separable processes, as previous studies show that some brain regions have a preferential role in motor timing while others are more involved in motor sequencing.

Numerous studies highlight the crucial role of a fronto-parietal circuit in movement sequencing (Bengtsson et al., 2004; Catalan et al., 1998; Rushworth et al., 2001a, b, 1997, c; Sadato et al., 1996b). Rushworth et al. (2001b) studied the effects of motor attention to movement sequencing, showing enhanced activity in the cingulate motor area, dorsal lateral premotor area and intraparietal sulcus when participants specifically attended to sequencing movements. Moreover, sequence preparation is disrupted by stimulation of the parietal cortex by transcranial magnetic stimulation (Rushworth et al., 2001a) and patients with parietal damage show deficits in using advance information for movement sequencing (Rushworth et al., 1997). Bengtsson and co-workers suggested that the posterior parietal area may process trajectories of movements, while the lateral frontal area and the inferior parietal area may be involved in creating abstract representation of sequences of elements (Bengtsson et al., 2004). Therefore ordering movements in sequence seems to rely on a neural circuit involving frontal and parietal areas.

Other studies show that attention to motor timing and decision on when to move specifically involve activity of the right dorsolateral prefrontal cortex (DLPFC) (Lewis and Miall, 2003, 2006). In a recent time processing model (Lewis and Miall, 2003), SMA and DLPFC have been referred to as key structures for time processing. In this model both these areas are involved in time management but they play different roles. During automatic time processing, SMA may act as an internal clock to create a representation of time intervals. Under cognitively controlled time processing an auxiliary internal clock may also be activated in the right prefrontal cortex. This model is in line with evidence of DLPFC involvement in non-routine decision making on the timing of movements (Jahanshahi and Frith, 1998; Jahanshahi et al., 1995; Jenkins et al., 2000).

In this study, we compared in the same paradigm the process of ordering movements in a sequence with the process of timing for movement initiation and the decision on “when to move.” We aimed to differentiate the pattern of neural activity related to each process and to examine when these different processes contribute to neural activity prior to movement initiation. We employed a self-paced movement task in which we separately manipulated motor timing and motor sequencing. We compared a condition of simple repetitive sequences with two conditions of high processing demand related to movement timing and sequencing respectively. In one, we increased demand on movement sequencing by alternating trial-by-trial between two complex finger sequences. In the other, demand on motor timing was increased by alternating trial-by-trial between two different time intervals between sequences. We used ERPs to identify the critical time periods during movement preparation for processes related to the timing of movement initiation and those related to sequencing of movement order. We also used fMRI to identify the

brain areas involved in these two processes. In this way we were able to investigate both when and where motor timing and motor sequencing contribute to the preparation for voluntary action.

Method

Participants

Eighteen young healthy volunteers (7 females and 11 males; mean age: 25.5 ± 2.85 years) participated in the experiment and gave their informed consent. All subjects were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Data of one participant was excluded from EEG analyses due to technical problems during the EEG recording.

Task

Participants were asked to perform fast self-paced sequences of six consecutive movements and to interpose intervals of several seconds between sequences (Fig. 1). The sequences were executed with four fingers of the right hand (2–index, 3–middle, 4–ring, 5–small finger) by pressing four keys, one for each finger, on a response keypad.

As shown in Fig. 1, the specific sequences to perform and the timing or temporal range required for the initiation of each sequence were manipulated across conditions in order to independently vary task difficulty for movement sequencing and timing. There were three conditions.

Simple (Si): The sequence to be performed involved only adjacent finger movements (2–3–4–5–4–3) in a scale sequence. Participants were required to initiate movements within a relatively large time range, from 5 to 12 s after the end of the previous sequence. Therefore the task was relatively simple and repetitive and without strict timing demand.

Timing (Ti): Participants performed simple scale sequences (2–3–4–5–4–3); however, they were required to initiate each sequence within two narrow time ranges alternating between trials, from 3 to 6 s and from 7 to 10 s after the end of the previous sequence. This required participants to attend closely to movement timing, to initiate movements within the correct time ranges and alternate initiation times between trials. To control for timing strategies, participants were explicitly asked to avoid counting seconds or estimating time based on rhythmic activity (i.e., subvocalization, tapping and breathing).

Sequencing (Se): Participants performed two different complex sequences, alternating between trials. Both sequences involved non-adjacent finger movements: 2–4–3–5–3–4 and 2–5–3–4–3–5. However, the timing of initiation followed the simple condition in which participants initiated movements within a relatively large time range, from 5 to 12 s following the end of the previous sequence. This required participants to attend closely to the sequencing of movements, to perform the correct complex sequences alternating between trials.

In this way, the demand on motor timing and motor timing precision were higher in Timing condition than in Simple and Sequencing conditions. Conversely, the complexity of movement sequences and demand on processing of sequencing order were higher in Sequencing than in Simple and Timing. Crucially, because both the Timing and the Sequencing conditions involve alternating between complex patterns trial-by-trial, both should involve similar working memory demands. Direct comparisons between Timing and Sequencing conditions should therefore not be confounded by differences in cognitive or working memory demands.

We conducted pilot testing in which we varied the width of the temporal ranges for movement initiation and the order of the movements within sequences so that subjective task difficulty, as evaluated by 12 young healthy volunteers, was approximately

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