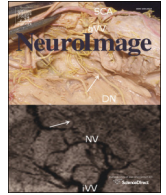




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Dissociable neural representations of wrist motor coordinate frames in human motor cortices

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ABSTRACT

There is a growing interest in how the brain transforms body part positioning in the extrinsic environment into an intrinsic coordinate frame during motor control. To explore the human brain areas representing intrinsic and extrinsic coordinate frames, this fMRI study examined neural representation of motor cortices while human participants performed isometric wrist flexions and extensions in different forearm postures, thereby applying the same wrist actions (representing the intrinsic coordinate frame) to different movement directions (representing the extrinsic coordinate frame). Using sparse logistic regression, critical voxels involving pattern information that specifically discriminates wrist action (flexion vs. extension) and movement direction (upward vs. downward) were identified within the primary motor and premotor cortices. Analyses of classifier weights further identified contributions of the primary motor cortex to the intrinsic coordinate frame and the ventral and dorsal premotor cortex and supplementary motor area proper to the extrinsic coordinate frame. These results are consistent with existing findings using non-human primates and demonstrate the distributed representations of independent coordinate frames in the human brain.

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Introduction

The brain allows for skillful manipulation of the body to interact with the external environment. This sophisticated and flexible operation involves transformations between coordinate frames of the internal body and external environment, possibly computed in distributed brain regions. The intrinsic coordinate frame is body- and/or muscle-centered, whereas the extrinsic coordinate frame refers to points outside the body. However, it is still unclear how these two coordinate frames are represented in the brain.

Extensive studies using monkeys have shown that the primary motor cortex (M1) and the premotor cortex (PM) are important in coding coordinate frames. M1 has been found to represent not only the intrinsic coordinate frame, through parameters such as muscle tension (Cheney et al., 1985; Donoghue et al., 1992; Evarts, 1968; Kakei et al.,

1999) and joint angle (Scott and Kalaska, 1995), but also the extrinsic coordinate frame in the form of movement direction (Georgopoulos et al., 1986; Kakei et al., 1999). The ventral and dorsal regions of PM (PMv and PMd) have been found to be associated with the extrinsic coordinate frame. PMv codes the direction of action (Kakei et al., 2001), whereas PMd codes motor preparation (Kurata, 1993) and the relative position of targets for reaching (Pesaran et al., 2006). The supplementary motor area (SMA) is also included in the medial portion of PM. To our knowledge, no previous studies have examined the neural representation of distinct coordinate frames in SMA. However, the roles of the anatomically subdivided areas, pre-SMA and SMA proper, seem to be relatively different. Evidence for these areas suggests that pre-SMA activates in relation to visual cues (Matsuzaka et al., 1992) or new motor plans (Shima et al., 1991), whereas SMA proper activates in relation to somatosensory stimuli (Matsuzaka et al., 1992).

These observations are further extended by human functional magnetic resonance imaging (fMRI), transcranial magnetic stimulation (TMS), and positron emission tomography (PET) studies. M1 has been found to be involved in both the intrinsic and extrinsic coordinate frames (Alaerts et al., 2009; Eisenberg et al., 2010; Toxopeus et al.,

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2011). A TMS study showed that movement observation leads to highly muscle-specific resonating activity in M1, indicating representation of the intrinsic coordinate (Alaerts et al., 2009). Conversely, fMRI studies using a “center-out task” showed that M1 encodes direction of movement, i.e., the extrinsic coordinate frame (Eisenberg et al., 2010; Toxopeus et al., 2011). TMS studies have shown the involvement of PMd in motor preparation (Davare et al., 2006) and action prediction (Duque et al., 2012; Stadler et al., 2012), and TMS and PET studies have indicated a role for PMv in motor imagery, motor preparation, and grip force prediction (Dafotakis et al., 2008; Davare et al., 2009; Stephan et al., 1995). Although evidence of non-primary motor areas in the human cortex have not shown complete homology with those in monkeys, findings from both species suggest that PMd and PMv may be involved primarily in the extrinsic coordinate frame, because motor preparation and action prediction likely require position information of the body parts in external space.

Studies using PET or regional cerebral blood flow measurement found activation in pre-SMA for externally cued or unfamiliar movement tasks and in SMA proper for self-paced or familiar tasks (Deiber et al., 1991; Grafton et al., 1992; Jenkins et al., 1994; Jenkins et al., 2000; Playford et al., 1992). These findings may suggest that SMA proper is more strongly associated with direct motor control than pre-SMA.

Though electrophysiological studies have been performed to examine the neural representations of motor coordinate frames in monkeys (Kakei et al., 1999, 2001), performing similar studies in humans poses practical challenges. fMRI offers an attractive solution because it is a non-invasive approach and can be used to examine M1 and PM regions in their entirety, a capability impossible for electrophysiological methods

focusing on microscopic areas. In order to extract such mutually transformed coordinate representations using fMRI data, increased analysis power is likely needed to detect experimental manipulations. Multivariate pattern analysis (MVPA) is a machine learning technique that can be applied to fMRI data, and its utility has become increasingly apparent due to its high sensitivity to experimental manipulation and areal dissociations (Kriegeskorte, 2011; Mourao-Miranda et al., 2005). Notably, it detects fine-grained pattern differences not found in regional-average activation by conventional univariate analyses and discovers novel neural mechanisms (Kamitani and Tong, 2005; Kriegeskorte, 2011; Miyawaki et al., 2008; Mur et al., 2009). MVPA may, thus, be suitable to dissociate neural representations of the intrinsic and extrinsic coordinate frames.

In this fMRI study, we directly addressed these issues by applying a novel approach to the representation of wrist action (intrinsic) and movement direction (extrinsic). During fMRI acquisition, healthy human participants performed isometric wrist flexion and extension tasks (Fig. 1) in different forearm postures, allowing independent manipulation of the intrinsic and extrinsic coordinate frames. In order to identify brain areas associated with the respective coordinate frames, two binary classifiers were trained based on sparse logistic regression (SLR) (Yamashita et al., 2008), a type of MVPA, for discriminating voxel pattern information for flexion vs. extension (FvE) movements and upward vs. downward (UvD) movements. Taking advantage of SLR, which can train high-dimensional classifiers without prior dimension reduction, binary classifier weight values for M1 and PM regions were examined to identify brain areas associated with the intrinsic and extrinsic coordinate frames.

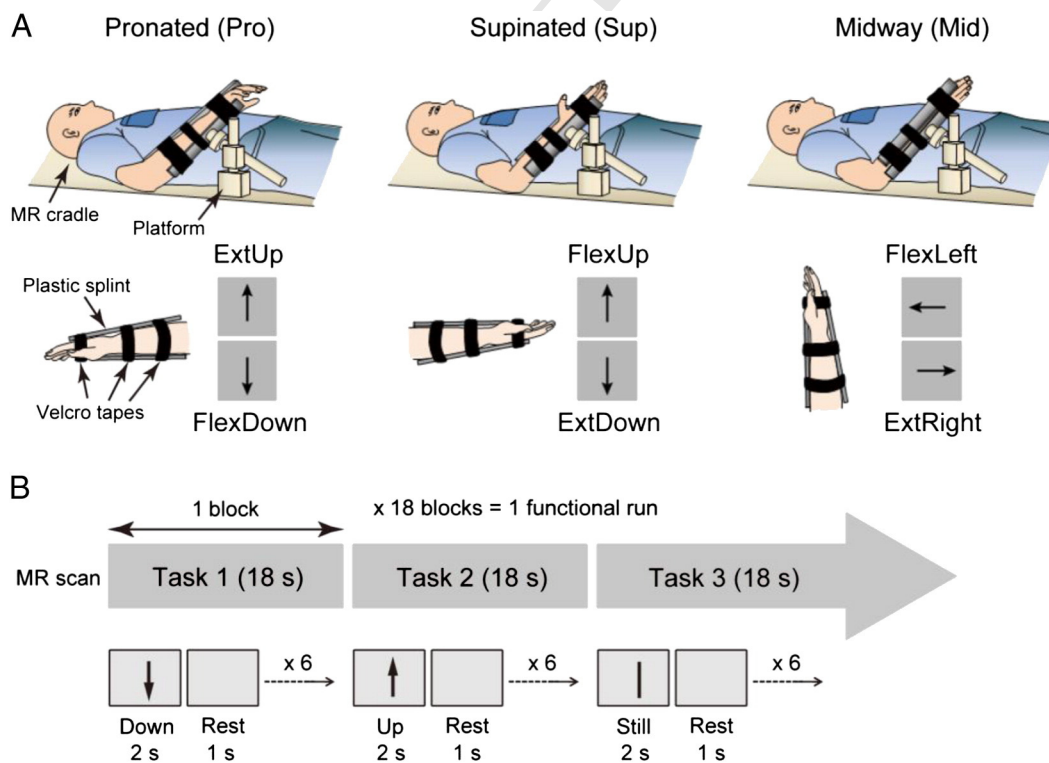


Fig. 1. (A) Schematic of participant postures and relation between movement directions and tasks according to visual instructions in three different wrist postures. The MRI-compatible fixation apparatus consists of splints, Velcro tape, titanium screws, and a plastic platform. [Left panel] Pronated posture (Pro). An upward force exertion was equivalent to an extension task and cued with an up arrow (ExtUp), whereas a downward force exertion was equivalent to a flexion task and cued with a down arrow (FlexDown). [Middle panel] Supinated posture (Sup). An upward force exertion was equivalent to a flexion task and cued with an up arrow (FlexUp), whereas a downward force exertion was equivalent to an extension task and cued with a down arrow (ExtDown). [Right panel] Midway posture between Pro and Sup (Mid). A left or right arrow was used for visual instruction in this posture. A leftward force exertion was equivalent to a flexion task and cued with a left arrow (FlexLeft), whereas a rightward force exertion was equivalent to an extension task and cued with a right arrow (ExtRight). (B) Block design for the fMRI experiment. Execution tasks (Flex and Ext) were instructed with up and down arrows (in Pro and Sup) or left and right arrows (in Mid) inside a gray box, and a no-force task (Still) was instructed with a vertical bar (in Pro and Sup) or a horizontal bar (in Mid).

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