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Visuomotor mental rotation of a saccade: The contingent negative variation scales to the angle of rotation

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ABSTRACT

The visuomotor mental rotation (VMR) of a saccade requires a response to a region of space that is dissociated from a stimulus by a pre-specified angle, and work has shown a monotonic increase in reaction times as a function of increasing oblique angles of rotation. These results have been taken as evidence of a continuous process of rotation and have generated competing hypotheses. One hypothesis asserts that rotation is mediated via frontoparietal structures, whereas a second states that a continuous shift in the activity of direction-specific neurons in the superior colliculus (SC) supports rotation. Research to date, however, has not examined the neural mechanisms underlying VMR saccades and both hypotheses therefore remain untested. The present study measured the behavioural data and event-related brain potentials (ERP) of standard (i.e., 0° of rotation) and VMR saccades involving 35°, 70° and 105° of rotation. Behavioural results showed that participants adhered to task-based rotation demands and ERP findings showed that the amplitude of the contingent negative variation (CNV) linearly decreased with increasing angle of rotation. The cortical generators of the CNV are linked to frontoparietal structures supporting movement preparation. Although our ERP design does not allow us to exclude a possible role of the SC in the rotation of a VMR saccade, they do demonstrate that such actions are supported by a continuous and cortically based rotation process.

1. Introduction

The speed at which the brain transforms visual images provides a measure of mental chronometry and is aptly demonstrated in Shepard and Metzler's (1971) mental rotation (MR) task. Shepard and Metzler measured the speed of perceptual reports related to whether pairs of 3D perspective line drawings presented at different orientations (i.e., angles from 0° to 180°) were the same or different. Results showed that reaction times (RT) increased linearly with an increase in the angle of rotation required to align the stimulus pair (for rotation of letters see Cooper & Shepard, 1973). Accordingly, Shepard and Metzler asserted a continuous mental rotation process wherein one item in the stimulus pair is rotated until it matches the other. Moreover, electroencephalographic (EEG) studies of the MR task have consistently shown that the amplitude of the P300 event-related brain potential (ERP) linearly decreases (i.e., becomes more negative) as a function of increasing angle of rotation (Heil, 2002; Milivojevic, Hamm, & Corballis, 2009; Peronnet & Farah, 1989; Wijers, Otten, Feenstra, Mulder, & Mulder, 1989) – a

result interpreted to reflect a direct neural correlate of mental rotation.

The visuomotor mental rotation (VMR) task is the motor analogue of the MR task. Most of the work in this area has examined reaching responses directed to a location that is different from a visual target stimulus by a pre-specified angle. The VMR literature has shown that RT increases with increasing *oblique* angles of rotation (Georgopoulos & Massey, 1987; Heath, Hassall, MacLean, & Krigolson, 2015; Neely & Heath, 2010, 2011; Pellizzer & Georgopoulos, 1993).¹ In addition, single-cell recordings in non-human primates have shown that VMR reaches are associated with an analogue rotation of directionally tuned neurons in the primary motor cortex (M1) (Georgopoulos, Lurito, Petrides, Schwartz, & Massey, 1989). As well, a recent study by our group provided an initial examination of the ERP correlates of VMR reaches in human participants (Heath et al., 2015). Notably, and unlike the MR literature, Heath et al., showed that the P300 did not systematically vary with angle of rotation; rather, the amplitude of the contingent negative variation (CNV) became more positive with increasing angle of rotation. The CNV is a late occurring waveform source

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¹ Our group has previously shown that VMR reaches produce RTs that increase with increasing oblique angles. 90° and 180° of rotation do not produce a monotonic rise in RT – a result attributed to perceptual familiarity with cardinal angles and the evocation of a motor response that does not require a continuous rotation process (Neely & Heath, 2010).

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localized to visuomotor and motor structures (i.e., M1, premotor areas, parietal cortex) (Lamarche, Louvel, Buser, & Rektor, 1995) and exhibits a sustained negativity during response preparation. Accordingly, the early and late stages of the component have been tied to the orienting properties of a target stimulus and the cognitive and visuomotor properties supporting response preparation (Bares, Nestrail, & Rektor, 2007; Brunia, 1988; Zaepffel & Brochier, 2012). As such, Georgopoulos and colleagues' work in combination with our group's ERP findings suggest that a conjoint visuomotor – and not an explicit visual or motor – rotation supports VMR reaches.

The present investigation examined the combined behavioural data and ERP components of VMR saccades. The motivation for our investigation was twofold. First, reaches and saccades are mediated via dissociable visuomotor transformations (i.e., head-to-shoulder centred versus retinocentric; for extensive review see Flanders, Helms Tillery, & Soechting, 1992) and it is therefore unclear whether effector-dependent – or independent – rotation processes support VMR reaches and saccades. Second, we are aware of two previous behavioural studies (de'Sperati, 1999; Fischer, Deubel, Wohlschläger, & Schneider, 1999) examining VMR saccades, and each showed a linear increase in RT commensurate with VMR reaches. The authors linked their behavioural findings to distinct neural mechanisms. de'Sperati proposed that the frontal eye field (FEF), supplementary eye field (SEF) and parietal regions represent the neural structures supporting VMR saccades – a conclusion derived from single-cell and ablation studies in non-human primates reporting that the aforementioned structures support the directional tuning of saccades. As such, de'Sperati proposed that VMR saccades are subserved via an analogue and cortically based rotation akin to their reaching counterparts. In contrast, Fischer et al., proposed that a continuous shift in neuron activity from the target location to the intended saccade goal location within the intermediate layers of the superior colliculus (SC) supports VMR saccades. To our knowledge, no work has provided a direct or indirect test of either hypothesis. Hence, we examined the behavioural data and ERP correlates of a standard saccade (i.e., 0°; standard task) and those involving VMR angles of 35°, 75° and 105° (i.e., the same angles used by Heath et al., 2015). If saccades are mediated via a cortically based rotation (i.e., de'Sperati, 1999) akin to explicit perceptual reports (i.e., the MR task), or VMR reaches, then the P300 or CNV amplitude should, respectively, demonstrate a systematic modulation with angle of rotation. In contrast, if neither the P300 nor CNV – nor any other identifiable ERP component – demonstrate a systematic modulation then results would provide *indirect* evidence supporting Fischer et al.'s hypothesis that rotation occurs within the motor maps of the SC.

2. Methods

2.1. Participants

Twenty-five individuals (17 female, age range = 18–34 years) participated in this study. All participants were identified as being right-handed as per the Waterloo Handedness Questionnaire, had normal or corrected-to-normal vision, and reported not having any neurological or psychiatric disorder. We conducted this work as per the Declaration of Helsinki, and prior to data collection participants signed consent forms approved by the local research ethics board.

2.2. Procedures and apparatus

Participants sat at a normal table top with their head placed in a head-chin rest. A 27-inch LCD monitor (27CW, Hewlett Packard, Palo Alto, CA; 1920 by 1080 pixels; viewing surface of 598 mm and 397 mm width and height, respectively; 60 Hz and 16 ms response rate) located 790 mm from the participant and centred on their midline was used to present visual stimuli on a black background. Stimuli included a white fixation square (0.8° by 0.8°) positioned at the monitor's centre, and

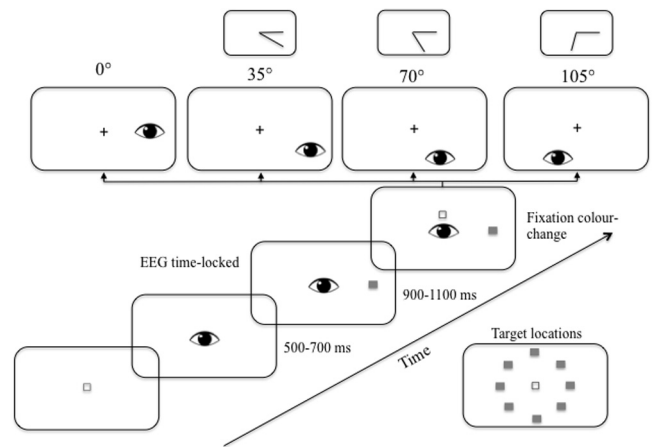


Fig. 1. Schematic of the sequence of visual events. A trial commenced when the fixation cross was presented and participants were required to achieve a stable fixation before proceeding. Once a stable fixation was achieved, a foreperiod began wherein one of the eight targets was presented. EEG data were synchronized to target onset and both fixation and target remained visible until saccade offset. From 900 to 1100 ms after target onset a fixation cross colour change cued participants to a saccade to the vertical target location (standard task: 0°) or VMR-based angles of rotation of 35°, 70° and 105°. The line drawing associated with each VMR condition are presented as smaller panels above the numerical label for each angle of rotation.

grey target squares (0.7° by 0.7°) positioned at 45° increments about an imaginary concentric circle surrounding the fixation (see inset panel of Fig. 1). The distance from fixation to a target stimulus was 6.0°. Monocular gaze position data of participants' right eye were captured via an EyeLink II (SR Research, Mississauga, ON, Canada) sampling at 500 Hz. Prior to data acquisition a nine-point calibration was performed and confirmed via an immediate recalibration. The calibration was accepted only if each point in the calibration matrix showed less than 1° of error. MATLAB (8.6.0: The Math Works, Natick, MA, USA) and the Psychophysics Toolbox extensions (ver 3.0, see Brainard, 1997) controlled all computer, and visual events.

In advance of data collection, a general instruction screen was presented to participants and indicated that they would saccade to the location of a target (i.e., 0°: standard task) or complete VMR responses to a location that deviated from the target by 35°, 70° and 105°. The instruction screen emphasized that the standard and each VMR task would be completed in separate blocks. In addition, the general instruction screen indicated that VMR responses were to be completed in a clockwise rotation (Heath et al., 2015; Neely & Heath, 2010, 2011; see also Georgopoulos & Massey, 1987). After the general instruction screen, a block-specific instruction screen was presented. For example, the block-specific instruction screen for the 70° VMR task stated: “*In this block of trials you will complete eye movements (i.e., saccades) to a location that is deviated 70° to the target stimulus (and in a clockwise direction). The line drawing below presents an angle of 70°. Please complete your response as quickly and accurately as possible.*” Fig. 1 presents the line drawing associated with each VMR condition. Line drawings were a pictorial representation of the required angle with the origin centred on the monitor. When the participant determined that they were familiar with the task the instruction screen was removed. Ten practice trials for each angle of instruction were completed prior to data collection.

A trial began with onset of the fixation location. Once participants achieved a stable fixation (i.e., $\pm 1.5^\circ$ for 400 ms) a 500–700 ms foreperiod was introduced (i.e., to baseline EEG data) after which time one of the eight targets was presented. The EEG data were time-locked to target onset and both fixation and target remained visible until saccade offset (see kinematic definition of saccade offset below). Following target presentation, a delay between 900 and 1100 ms was introduced and was followed by a white-to-green colour-change of the fixation

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