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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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, Nestrasil, & 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
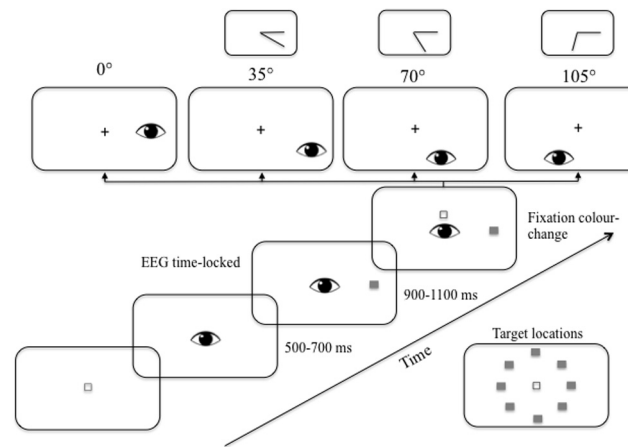
Fig. 1. Schematic of the sequence of visual events. A trial commenced when the fixation cross was presented and participants were required to achieve a stable fixation before proceeding. Once a stable fixation was achieved, a foreperiod began wherein one of the eight targets was presented. EEG data were 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 veridical 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., ± 1.5° 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

location that cued saccade onset.[2] Thus, and in keeping with our previous work involving the ERP correlates of VMR reaches, saccades were cued after target onset to dissociate the ERP components of movement planning (i.e., P300, CNV) from movement execution (i.e., the Bereitschaftspotential). For the standard and each angle of rotation task, six trials to each of the different target locations were completed within a block (i.e., 48 trials/block), and each block was repeated on three occasions (144 trials for each of the 0°, 35°, 70° and 105° tasks; i.e., 576 total experimental trials). The ordering of the different blocks was randomized. Because of the fixation stabilization criteria stated above, the interval between trials was not consistent (i.e., on some – but not all – trials participants achieved a stable gaze immediately following onset of the fixation stimulus); however, we estimate the average between-trial interval to be less than 5 s.

2.3. EEG recording

Participants were fitted with a 64-channel Ag/AgCl electrode cap. A standard 10–20 layout was used for electrode placement and Brain Vision Recorder software (Version 1.21, Brainproducts GmbH, Munich, Germany) and a ActiChamp Amplifier (Version 2, Brainproducts GmbH, Munich, Germany) was employed for data recording. For all electrodes, impedance levels were maintained below 20 kΩ, on average. Sampling of the EEG data was 500 Hz and we employed an antialiasing low-pass filter of 8 kHz.

2.4. Data analyses and dependent variables

Gaze position data were post-processed via the same procedures outlined in previous work by our group (e.g., Weiler, Hassall, Krigolson, & Heath, 2015). The onset of a saccade was marked when velocity and acceleration were greater than 30°/s and 8000°/s^2, respectively. In contrast, a velocity below 30°/s for 20 consecutive frames (i.e., 40 ms) marked saccade offset. Dependent variables for behavioural data included: reaction time (RT: time from movement cuing to saccade onset), movement time (MT: time from saccade onset to saccade offset), movement direction (MD: i.e., endpoint position) and the within-participant standard deviation of each of the aforementioned measures (i.e., $_V$RT, $_V$MT, $_V$MD). MD represented the angle between the required and achieved movement angle for each trial. For example, for the target presented at the 12 o'clock position MD values of 358° and 2° would denote endpoints 2° counter-clockwise and clockwise, respectively, to the location of the required response. Given the directional nature of endpoints, MD and vMD data were examined via circular statistics (Batschelet, 1981) using the CircStats toolbox for MATLAB (Berens, 2009).

Brain Vision Analyzer 2 software (Version 2.1.1, Brainproducts, GmbH, Munich, Germany) was used for the offline post-processing of EEG data. Offline post-processing began by visually identifying any excessively noisy or faulty electrode channels and removing those channels. We then down-sampled the remaining EEG data to 250 Hz and re-referenced to the average mastoid electrodes and filtered with a passband of 0.1–30 Hz and employed a 60 Hz notch filter. EEG epochs that encompassed 1000 ms before and 2000 ms after each event of interest were extracted from the continuous EEG. Following this segmentation, we employed independent component analysis (ICA) to account for ocular artifacts (Delorme & Makeig, 2004; Luck, 2014). Data were then reconstructed after ICA, and we employed a spherical splines method to interpolate any removed channel. Next, shorter segments were defined from 200 ms before to 600 ms after target

presentation. A baseline correction procedure for all segments was based on a window that proceeded target onset by 200 ms. An artifact rejection algorithm identified and excluded segments with gradients more than 10 μV/ms and/or a 100 μV absolute within-segment voltage difference.

ERP waveforms were created by averaging epochs of the pre-processed data spanning from 200 ms before target onset to 600 ms after target onset from the continuous EEG data. This was done separately for each angle of rotation block. Based on our previous study of VMR reaches (Heath et al., 2015) we identified the N100, P300 and CNV as ERP components of interest. We examined for changes to: (1) the N100 at electrode Pz, (2) the P300 at electrode Pz, and (3) the CNV at electrode Cz. For statistical analyses, we computed for each ERP component the mean voltage for each participant $\pm$ x ms on the channel in which the difference between the grand average waveforms was maximal (x represents the widow required to identify the component width during visual inspection). In particular, the N100 represented the mean voltage $\pm$ 25 ms of the peak (162 ms) at channel Pz; the P300 represented the mean voltage $\pm$ 25 ms of the peak (321 ms) at channel Pz; and the CNV as the mean voltage $\pm$ 25 ms of the peak (525 ms) at channel Cz, and was done separately for each participant and experimental condition.

2.5. Statistical analyses

Trials with a RT shorter than 100 ms (Wenban-Smith & Findlay, 1991) or longer than 2.5 standard deviations above a participant- and angle of rotation-specific mean were excluded from further data analyses as were MD values greater than 2.5 standard deviations from a participant- and angle of rotation-specific mean. As indicated above, ICA was employed to eliminate EEG artifacts, and in line with Heath et al. (2015) trials were removed for gradient artifacts (10 μV/ms) and/or maximum to minimum restrictions −100 μV or greater change within a defined epoch. We analyzed only those trials involving valid RT, MD and EEG signals (range = 6–11% of an individual participant's trials were removed). A one-way repeated measures ANOVA (i.e., angle of rotation: 0°, 35°, 70° and 105°) was used to examine dependent variables and power polynomials were used to decompose significant main effects (i.e., trend analysis: see Pedhazur, 1997).[3]

3. Results

3.1. Behavioural data

RT and MT yielded grand means of 263 ms (SD = 61) and 68 ms (SD = 6), respectively, and neither variable elicited a significant effect, all $F(3,72) = 0.54$ and 1.98, respectively for RT and MT, ps = 0.54 and 0.12, $\eta_p^2 = 0.02$ and 0.06 (see left ordinates of Fig. 2a and b). Within-participants variability of RT and MT (i.e., $_V$RT and $_V$MT) were influenced by angle of rotation, all $F(3,72) = 11.26$ and 8.28, ps < 0.001, $\eta_p^2 = 0.32$ and 0.26. $_V$RT values increased linearly in relation to increasing angle of rotation (significant linear effect: $F(1,24) = 34.32$, p < .001), whereas $_V$MT increased from the 0° to 35° angle of rotation but did not reliably vary across the 35°, 70° or 105° angle of rotation (significant quadratic effect: $F(1,24) = 11.14$, p < .001) (see right ordinates of Fig. 2a and b).

Results for MD indicated a significant effect of angle of rotation, $F(3,72) > 1500$, p < .001, $\eta_p^2 = 0.99$, such that values increased in relation to the required rotation condition (only linear effect significant: $F(1,24) > 1500$, p < .001) (see left ordinate of Fig. 2c). Similarly, $_V$MD, $F(3,72) = 82.64$, p < .001, $\eta_p^2 = 0.77$, indicated that variability in movement direction increased linearly with increasing

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[2] In our group's VMR reaching study (Heath et al., 2015) an auditory imperative was used to signal movement onset, whereas the present work employed a fixation cross colour change. We were unaware of this distinction until a reviewer identified it, and we state no rationale for the different imperatives.

[3] Power-polynomials (i.e., trend analyses) were used to decompose significant effects of angle of rotation. As indicated by Pedhazur (1997), trend analyses are tantamount to a test of the means and can be used to quantify whether differences between continuous variables are monotonic or non-monotonic.
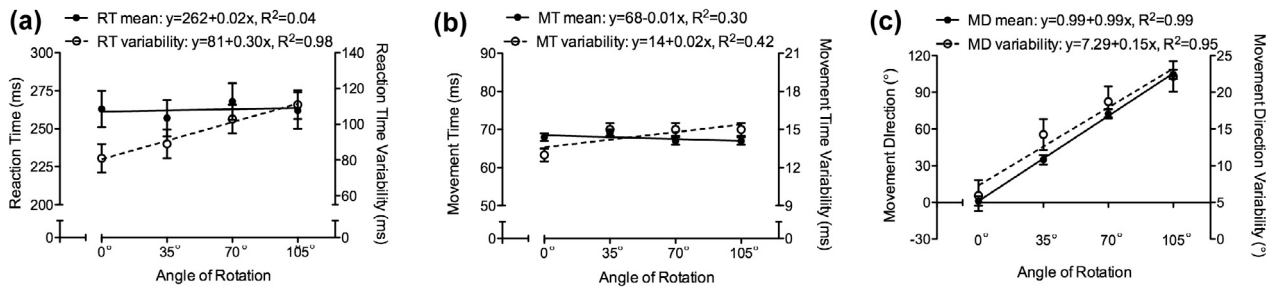
Fig. 2. Solid circle symbols plotted against the left ordinate represent mean reaction time (2a), movement time (2b) and movement direction (2c) for the standard task (i.e., 0°) and each angle of rotation task (i.e., 35°, 70°, and 105°). The open circle symbols plotted against the right ordinate represent corollary mean within-participant standard deviation (i.e., participant-specific trial-to-trial variability). Linear regression lines and equations are presented for each panel. The mean-squared error term for the angle of rotation was used to compute the 95% within-participant confidence interval (Loftus & Masson, 1994).

angle of rotation (only linear effect significant: $F_{(1,24)} = 173.21$ p $< .001$) (see right ordinate of Fig. 2c). Moreover, we sought to determine whether angle of rotation differentially influenced systematic endpoint bias. To that end, MD values for individual angle of rotation conditions were contrasted to their veridical target location (i.e., 0°, 35°, 70° and 105°) via single-sample t-tests. Results showed that values did not reliably differ from their veridical location (all $t_{(24)} < 1.66$, ps > 0.10). Thus, a systematic under- or over-rotation bias did not characterize any of the angles of rotation.

3.2. ERP data: the N100, P300 and CNV

Figs. 3a and 4a present the grand averaged waveforms for channels Pz and Cz, respectively, and demonstrate that the N100 (at channel Pz) yielded a significant effect for angle of rotation, $F_{(3,72)} = 9.64$, $p < .001$, $\eta_p^2 = 0.28$. The mean voltage for the N100 was more negative for the 0° than the 35° angle of rotation and then plateaued (significant quadratic effect: $F_{(1,24)} = 12.01$, p $< .001$) (Fig. 5). The mean voltages for the P300 (i.e., channel Pz; Fig. 3c) and CNV (i.e., channel Cz; Fig. 4c) elicited significant effects for angle of rotation, Fs $(3,72) = 10.50$ and 4.30, ps < 0.01, $\eta_p^2 = 0.30$ and 0.17. The P300 amplitude was more positive for the 0° than the 35° angle of rotation but did not reliably vary across the 35° to 105° angles of rotation (significant quadratic effect: $F_{(1,24)} = 7.43$, p $< .02$). In turn, the CNV amplitude was systematically modulated by the angle of rotation such that the component became less negative with increasing angle of rotation (only linear effect significant: $F_{(1,24)} = 6.72$, p $< .02$).

In a separate ANOVA model, we examined N100, P300 and CNV amplitudes only for the 35°, 70° and 105° conditions to examine the ERP components of VMR saccades independent of a response with a direct sensorimotor transformation (i.e., the 0° condition). N100 and P300 amplitudes did not produce significant effects, Fs$(2,48) < 1.0$,

ps > 0.80, all $\eta_p^2 < 0.02$. The CNV produced a significant effect, $F_{(2,48)} = 3.34$, p $< .05$, $\eta_p^2 = 0.14$: the component's amplitude became less negative as a function of an increased angle of rotation (only linear effect significant: $F_{(1,24)} = 4.28$, p $< .05$). These additional analyses further demonstrate that the CNV – but not the N100 or P300 – scaled to the angle of rotation.

4. Discussion

This study sought to determine whether an ERP component systematically scales to the angle of rotation in a VMR saccade task. This objective was derived from competing – but untested – hypotheses forwarded by de'Sperati (1999) and Fischer et al. (1999). de'Sperati proposed that frontoparietal structures support the continuous rotation of VMR saccades, whereas Fischer et al. proposed that the rotation is supported by a continuous directional shift of motor-related neurons in the intermediate layers of the SC. As such, we measured the behavioural data and ERP characteristics of standard saccades (i.e., 0°) and those involving angles of rotation of 35°, 70° and 105°.

4.1. Behavioural measures of standard and VMR saccades

The results for movement direction (i.e., MD) demonstrate that saccades scaled to the different VMR angles of rotation, and that standard and VMR tasks did not yield a systematic rotation bias (i.e., under- or over-rotation) – a result indicating that participants adhered to task-based rotation demands. In turn, the variability of movement direction increased monotonically with increasing angle of rotation (i.e., $_v$MD). The less variable endpoints for the standard task is expected and is in line with the view that spatial overlap between stimulus and response (SR) results in a motor response that is mediated via absolute target location information (for review see Goodale, 2011). In turn, the
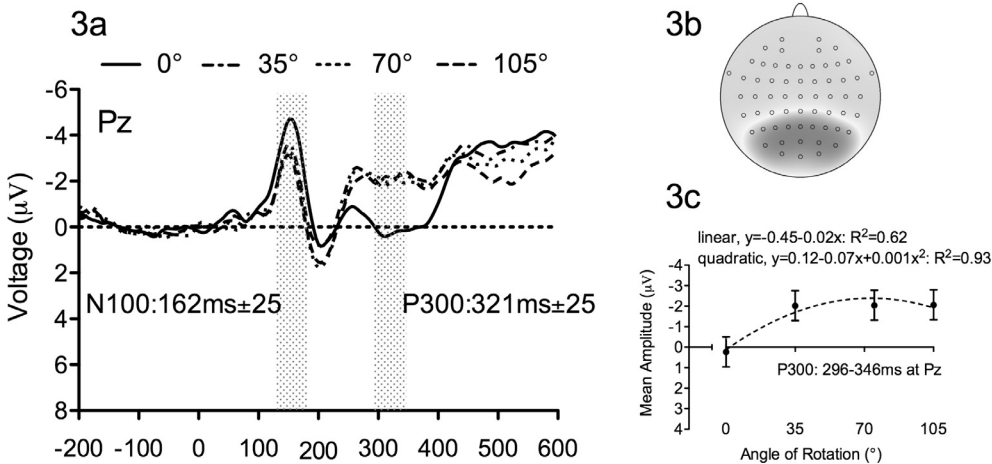
Fig. 3. Panel 3a presents grand-average event-related brain potential waveforms (μV) for electrode Pz when synchronized to target presentation for the standard task (i.e., 0°) and each angle of rotation task (i.e., 35°, 70°, and 105°). The panel has 'windowed' the time wherein waveforms were maximally different for the N100 and P300 (i.e., the hatched light grey rectangles). Panel 3b shows a representative scalp topography for the P300. Panel 3c shows mean voltages for the P300 at Pz and reports the linear and quadratic polynomials. Hierarchical analysis indicated a quadratic component produced a significant increase in explained variance (p $< .001$) and is represented by the hatched line in the panel. Error bars per Fig. 2.
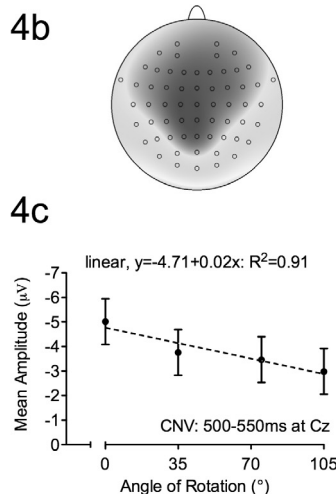
4a

—— 0°   – – 35°   ···· 70°   – ·· 105°

Cz

CNV:525ms±25

4b

4c

linear, y=-4.71+0.02x: R²=0.91

CNV: 500-550ms at Cz

Fig. 4. Panel 4a presents grand-average event-related brain potential waveforms (μV) for electrode Cz when synchronized to the presentation of the target for the standard task (i.e., 0°) and each angle of rotation task (i.e., 35°, 70°, and 105°). The panel has 'windowed' the time wherein waveforms were maximally different for the CNV component (i.e., the hatched light grey rectangle). Panel 4b shows a representative scalp topography for the CNV. Panel 4c shows mean voltages for the CNV at Cz. Only the linear polynomial accounted for a statistically reliable effect and is represented by the hatched lines (i.e., higher-order polynomials: all $F_{(1,24)} < 1$). Error bars per Fig. 2.

Pz

linear, y=--3.33+0.01x: R²=0.81
quadratic, y=-3.52-0.03x+0.001x²: R²=0.92

N100: 137 - 187 ms at Pz

Fig. 5. Mean voltages (μV) for the N100 component for electrode Pz when synchronized to target onset for the standard task (i.e., 0°) and each angle of rotation task (i.e., 35°, 70°, and 105°). The figure reports the linear and quadratic regression polynomials. Hierarchical analysis indicated a quadratic component produced a significant increase in explained variance (p < .001) and is represen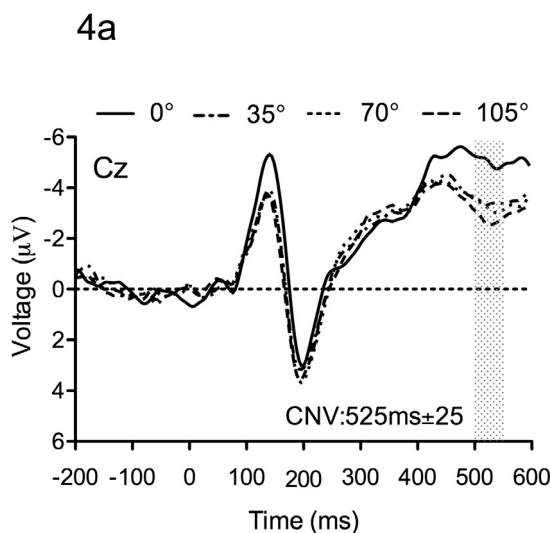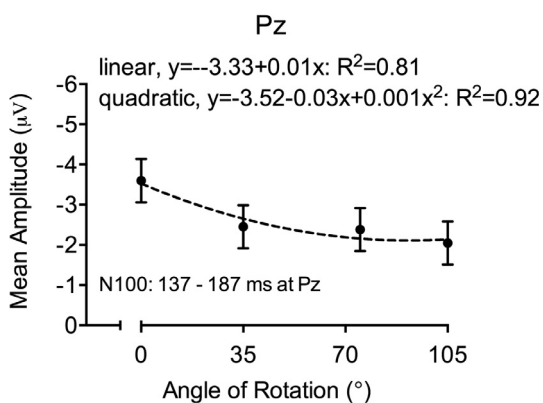ted by the hatched line in the panel. Error bars per Fig. 2. Further, the grand average waveforms associated with this component across each angle of rotation can be found in Fig. 3a.

monotonic rise in movement direction variability with increasing angle of rotation is in line with VMR reaching studies (Heath et al., 2015; Neely & Heath, 2010, 2011) and supports the contention that SR decoupling renders a systematic increase in the neural noise (Meyer, Abrams, Kornblum, Wright, & Smith, 1988; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979) associated with a visuomotor transformation. Moreover, that variability in saccade RT (i.e., $_V$RT) increased with angle of rotation provides convergent evidence that increasing the angular disparity between SR systematically increases the noise in transforming a target's visual coordinates into a motor response.

In most of the VMR literature target onset provides the cue to complete an instructed reach or saccade, and results have consistently shown that RT increases linearly with increasing oblique angles of rotation (for saccades see de'Sperati, 1999; Fischer et al., 1999; for reaches see Georgopoulos & Massey, 1987; Neely & Heath, 2010, 2011). In the present investigation, participants were cued to complete their saccade 900–1100 ms after target presentation to disentangle the ERP components of movement planning (i.e., the P300 and CNV) and movement execution (i.e., the Bereitschaftspotential). Given this methodology, RTs in the present investigation did not reliably vary with angle of rotation. One explanation for this result is that participants completed their VMR transformation during the time between target presentation and response cuing. Such an explanation would

therefore support the assertion that the time between target presentation and response cuing served as the 'window' to examine the ERP correlates associated with the visual, motor, or visuomotor rotation supporting VMR saccades. A second explanation is that the VMR process was only partially completed in the aforementioned window. This explanation is based on the fact that RT variability systematically increased with angle of rotation. As stated previously however, we believe that the increase in RT variability (and associated increase in movement direction variability) reflects neural noise associated with SR decoupling. Regardless of the explanation, the present behavioural data demonstrate that participants adhered to task demands and that the period between target presentation and response cuing served as an appropriate window to examine the constituent ERP correlates of VMR saccades.

A notable difference between our group's previous VMR reaching study (Heath et al., 2015) and the present work is that the former reported a systematic increase in RT with increasing angle of rotation. In accounting for this discrepancy. Heath et al.'s VMR reaching task required that participants maintain fixation throughout their response; that is, the task did not permit for a concurrent saccade. This represents a salient difference because separate cortical mechanisms and RTs are associated with planning simultaneous eye and limb movements versus a selective eye or limb movement (e.g., Fischer & Rogal, 1986; van Donkelaar, 1997). For example, Mushiake, Fujii, and Tanji (1996) reported that supplementary eye field neurons are involved in signaling whether a motor task is oculomotor or a combined saccade and reaching response, whereas frontal eye field neurons are primarily related to oculomotor control. Further, the accumulation of neural activity for saccades and reaching movements is distinct (Pouget et al., 2011), and thus may account for why Heath et al. – but not the current VMR saccade study – observed a reliable increase in RT with increasing angle of rotation.

4.2. ERP measures of standard and VMR saccades

4.2.1. The N100

The visual N100 has been reported to produce a peak amplitude 150–200 ms following exogenous visual stimulus presentation and is maximal at inferoposterior and anterosuperior electrode sites. The component has been source-localized to extrastriate visual areas (for review see Hopfinger, Luck, & Hillyard, 2004) and its amplitude is modulated when a directionally valid precue precedes a lateralized target (Mangun & Hillyard, 1991), and is larger for a choice than a simple-RT task (Vogel & Luck, 2000; see also Mangun & Hillyard, 1991). Accordingly, the N100 has been interpreted to reflect an early

and sensory-based focusing and discrimination of visuo-spatial attentional mechanisms (Luck, Woodman, & Vogel, 2000). In a previous study our group reported that the N100 amplitude for a standard reaching task was greater (i.e., more negative) than VMR reaches (i.e., 35°, 75° and 105°), and that each VMR task produced comparable amplitudes (Heath et al., 2015). The present finding mirror those associated with VMR reaches in that N100 amplitudes were larger for standard than each VMR saccade task (which did not reliably differ).[4] That the N100 was larger for the standard task – but did not reliably vary across the VMR angles of rotation – indicates that the analogue rotation associated with VMR saccades (and reaches) cannot be attributed to visuo-spatial attentional mechanisms within early visual pathways. Instead, that the N100 amplitude is larger for a standard task provides evidence of increased attentional gain and discrimination for a response with direct (i.e., standard) – compared to indirect (i.e., each VMR angle of rotation studied here) – SR mapping.

4.2.2. The P300

The P300 is a parietal-central positive deflection with a peak amplitude 250–500 ms post stimulus onset (for review see Polich, 2007). A consistent finding from the MR literature is that with an increased magnitude of rotation the P300 amplitude becomes more negative (Heil, 2002; Milivojevic et al., 2009; Peronnet & Farah, 1989; Wijers et al., 1989). Wijers et al. suggested that the decrease in the P300 amplitude reflects a slow parietal negativity wave imposed on the concurrent P300, and that such a finding provides direct psychophysiological evidence of a *visual* rotation in occipital and parietal areas. The present study found that the P300 peak amplitude was within its documented latency window and was maximal at parietal electrode site Pz. Notably, and in line with a previous VMR reaching study (Heath et al., 2015), the P300 amplitude for the standard saccade task was greater (i.e., more positive) than any of the VMR tasks (which did not reliably differ). Of course, VMR saccade and reaching tasks differ from a MR task in that the former mandates that the visual coordinates of a target be transformed into an appropriate motor command (Flanders et al., 1992), and are influenced by the need to constrain both the speed and accuracy of movement planning processes to ensure an accurate response (Fitts, 1954). Such constraints are not imposed in an MR task wherein participants are required to perceptually align two stimulus pairs (Shepard & Metzler, 1971). Thus, it is perhaps not surprising that the ERP signature of a VMR task is distinct from that reported in the MR literature. As such, the present results are consistent with saccade and reaching studies showing that the P300 is sensitive to developing a task-set necessary to support SR decoupling (Heath, Bell, Holroyd, & Krigolson, 2012; Kang, Diraddo, Logan, & Woodman, 2014; Krigolson, Holroyd, Van Gyn, & Heath, 2008; Weiler et al., 2015). For example, Krigolson et al. (2008) reported that the P300 amplitude in a goal-directed reaching task increased in relation to an unexpected 'jump' in target location and proposed that the finding reflects the updating of an internal task-set (for review of P300 and context-updating hypothesis see Donchin & Coles, 1988). Given these findings, we conclude that the difference in P300 amplitude between the standard and each angle of rotation task used here underlies the cognitive demands of instantiating a general task-set for SR decoupling and does not reflect a systematic visual, motor or visuomotor rotation of a response vector.

4.2.3. The CNV

The CNV is characterized by a sustained negative deflection in the EEG that occurs in the time leading up to movement initiation, and the component's late wave is maximal over central electrode sites (Walter,

Cooper, Aldridge, McCallum, & Winter, 1964). The component has been linked to the cognitive and visuomotor properties of movement planning and is strongly influenced by movement-related variables including direction (Brunia, 1988; Jentzsch, Leuthold, & Ridderinkhof, 2004; Ulrich, Leuthold, & Sommer, 1998; Zaepffel & Brochier, 2012). A previous study by our group showed that the CNV amplitude systematically decreased (i.e., became more positive) with increasing angle of rotation (Heath et al., 2015) – a result that was taken as evidence that a VMR reach entails a visuomotor rotation. The present saccade study similarly shows that the CNV amplitude monotonically decreased with increasing angle of rotation. We believe that such a finding is important for at least three reasons. First, the cortical regions linked to the generation of the CNV (primary motor cortex, supplementary motor area, premotor area, parietal cortex) (Bares et al., 2007; Lamarche et al., 1995) are associated with the visuomotor transformations of standard and non-standard tasks (Connolly, Goodale, Desouza, Menon, & Vilis, 2000; Moon et al., 2007; Zhang & Barash, 2000). Although source localization is not a strength of the ERP paradigm, our results showing that the CNV had a more central-parietal topography potentially highlights a visuomotor – as opposed to purely visual or motor – rotation process. Indeed, the fact that our group has observed CNV scaling across reaches *and* saccades evinces that VMR tasks are mediated via an effector-independent visual-to-motor transformation process. Second, that the CNV – and not the P300 – scaled to the angle of rotation for VMR saccades indicates that the electrophysiological correlates of the task are distinct from the perception-based rotation properties characterizing the MR task (i.e., the P300). In other words, the present findings demonstrate the visuomotor demands of the VMR task are dissociable from the perception-oriented rotation processes of the MR task. Third, and perhaps most germane to the present work, results support de'Sperati's (1999) contention that VMR saccades are mediated cortically via an extensive frontoparietal network. If VMR saccades were *selectively* mediated via a continuous shift of SC neuron activity then we would not expect to observe an ERP component systematically modulated by angle of rotation. Moreover, the present findings are consistent with neuroimaging work in humans and electrophysiological studies in non-human primates showing that a frontoparietal network (e.g., frontal eye field, supplementary eye field, intraparietal cortex) supports the decision and selection processes guiding saccades (Bruce & Goldberg, 1985; Chen et al., 2016; Johnston, Lomber, & Everling, 2016; Zhang & Barash, 2000; for review see Schall & Thompson, 1999). In further support of this view, recent studies using combined prefrontal cortex deactivation and neural recordings of the SC in monkeys demonstrates that the former provides direct and excitatory inputs to the SC that relate to the goals – or task-set – of an oculomotor response (Johnston, Koval, Lomber, & Everling, 2014; for review see Everling & Johnston, 2013). In other words, there is convergent evidence to suggest that the high-level task demands associated with VMR saccades are mediated cortically and subsequently relayed to saccade-related neurons in the SC.

As a final point, we note that some work has shown that task complexity and cognitive arousal influence CNV amplitude (Nagai et al., 2004; Tecce, Savignano-Bowman, & Meinbresse, 1976). As such, it could be argued that CNV amplitude scaled in relation to the cognitive demands associated with the different angles of rotation. It is, however, important to note that previous work linking cognitive demands/arousal to the CNV amplitude entailed measuring autonomic arousal associated with perception-based visual processes (i.e., letter recall). In turn, work examining the relationship between oculo- and motor responses has shown that the CNV amplitude is most strongly linked to the visuomotor properties associated with movement preparation (Brunia, 1988; Jentzsch et al., 2004; Ulrich et al., 1998; Zaepffel & Brochier, 2012). We therefore believe that a visual-to-motor – as opposed to a cognitive demands/arousal – explanation provides the most parsimonious account for the present CNV findings.

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[4] Heath et al. (2015) reported that the maximal difference in the N100 amplitude occured at the average of occipital electrode sites O1 and O2. In the present investigation, the N100 did not produce a significant linear effect of angle of rotation at the average of O1 and O2 (significant linear effect: $F(1,24) = 2.82$, $p = .09$, $\eta_p^2 = 0.08$).

5. Conclusions

The movement direction data outlined above coupled with VMR saccade studies reporting that RT increases in relation to the magnitude of the required angle of rotation (de'Sperati, 1999; Fischer et al., 1999) provide strong behavioural support for asserting that the task is mediated via a continuous rotation process. Moreover, results showing CNV amplitude scaling to the angle of rotation evinces a psychophysiological marker for the onset of visuomotor rotation. Of course, we recognize that the current ERP study cannot rule out a possible role of the SC in the rotation of a saccade (i.e., Fischer et al., 1999); however, the present results provide first demonstration supporting de'Sperati's contention that a continuous and cortically based rotation process supports VMR saccades.

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