Reduced Cortical Motor Potentials Underlie Reductions in Memory-Guided Reaching Performance

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We used the event-related potential (ERP) methodology to examine differences in neural processing between visually and memory-guided reaches. Consistent with previous findings (e.g., Westwood, Heath, & Roy, 2003), memory-guided reaches undershot veridical target location to a greater extent than their visually guided counterparts. Analysis of the ERP data revealed that memory-guided reaches were associated with reduced potentials over medial-frontal cortex at target presentation and following movement onset. Further, we found that the amplitudes of the potentials over medial-frontal cortex for visually and memory-guided reaches were significantly correlated with the peak accelerations and decelerations of the reaching movements. Our results suggest that memory-guided reaches are mediated by a motor plan that is generated while a target is visible, and then stored in memory until needed—a result counter to recent behavioral theories asserting that memory-guided reaches are planned just before movement onset via a stored, sensory-based target representation.

Keywords: motor control, memory guided, movement planning, ERP, EEG

Continuous visual input from the movement environment allows for the evocation of effective and efficient goal-directed reaching movements (i.e., visually guided reaching). The basis for this sensory-optimized response is thought to reflect the mediation of such actions by dedicated visuomotor networks residing in the posterior parietal cortex of the dorsal visual pathway. Notably, dorsal visual networks afford real time and metrical sensorimotor transformations related to limb and target position that optimize motor output(e.g., Binsted et al., 2007; Bridgeman et al., 1979; Desmurget et al., 1999; Goodale et al., 1986; Pisella et al., 2000; for a review see Goodale et al., 2004). In the absence of visual input (i.e., memory-guided actions), the real time properties of the dorsal visual pathway are disrupted

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(Westwood and Goodale, 2003) and the performer must rely on an alternate strategy to support movement planning and control processes.

It is, however, notable that in the absence of continuous limb and/or target information the motor system is able to maintain a marked degree of movement accuracy. One account for the reasonably accurate performance of memory-guided actions holds that a fully specified motor plan is structured at the time of target presentation and held in memory until the response is cued (the motor hypothesis: e.g., Ghafouri and Feldman, 2001; Henry and Rogers, 1960). A second account holds that memory-guided actions are planned via a stored sensory representation laid down and maintained by visuoperceptual networks residing in the inferotemporal cortex of the ventral visual pathway (the visual hypothesis: Heath et al., 2004a; Hu and Goodale, 2000; Westwood et al., 2003). Importantly, the sensory hypothesis states that stored target information is held in memory as a visual representation and is converted to a fully specified movement plan at the time of response cuing and not before. Stored target information has been shown to provide a temporally durable, representation to support motor output. However, actions based on stored target information are relatively less accurate and more variable than their visually guided counterparts and exhibit a systematic undershooting bias (Adamovich et al., 1999; Darling and Miller, 1993; Elliott and Madalena, 1987; Heath, 2005; Heath and Westwood, 2003; Heath et al., 2004b; McIntyre et al., 1997; Westwood et al., 2000, 2001, 2003). Seminal work by Elliott and Calvert (1990) tested the motor and sensory hypotheses by manipulating target uncertainty before visual occlusion of a movement target. The introduction of target uncertainty before the removal of target vision made it impossible for participants to generate a movement plan before movement onset. Importantly, Elliott and Calvert's results demonstrated that target uncertainty before target occlusion did not reduce the accuracy of memory-guided reaching movements—a finding that provided support for the sensory hypothesis.

Event-related brain potentials (ERP) provide a methodology for studying the neural mechanisms that underlie human reaching movements. For instance, early studies employing the ERP technique to study the neural mechanisms which underlie self-paced movements, reported the *bereitschaftspotenital* (BP) and *reafferente Potentiale* (RAP). The BP and RAP are commonly held to be two cortical motor ERP components associated with preparation and execution of self-paced movements, respectively. The BP is comprised of two primary subcomponents, the early BP which reflects premovement activity within supplementary motor area (Cui and Deecke, 1999a, 1999b; Praamstra et al., 1996) and the late BP which reflects premovement activity within lateral premotor area (Cui and Deecke, 1999a, 1999b; Shibasaki et al., 1980; Shibasaki and Hallett, 2006; Yazawa et al., 2000) and primary motor cortex (Gerloff et al., 1998; Shibasaki et al., 1980; Shibasaki and Hallett, 2006). In a similar fashion, the RAP is also comprised of early and late subcomponents which are thought to reflect motor activity within supplementary motor area, lateral premotor area, and primary motor cortex (Shibasaki et al., 1980), as well as the processing of kinaesthetic feedback (Shibasaki et al., 1980), and/or reafferent activity from motor areas (Cui and Deecke, 1999a, 1999b).

Recently, studies using the ERP technique have examined the neural processes that underlie cued movements. For example, in one recent study Kirsch, Henni-

ghausen, and Rösler (2010) occluded the vision of participants (via blindfold) and had them complete one-dimensional reaching movements following an auditory cue via a table-mounted manipulandum until they were "stopped" at one of several predefined distances. Participants were then asked to accurately reproduce the movement distance following an audiotry cue after a brief delay period without the stopping mechanism in place. Kirsch and colleagues' ERP data revealed a negative potential that was maximal at movement onset for both the initial and the reproduced movements. The authors proposed that this early negativity was the initial part of the RAP—the motor potential (MP) (c.f., Brunia, 1988). Kirsch et al. (2010) also observed a subsequent negative potential which immediately preceded the deceleration phase of the reaching movements, a component which they termed the N4. From these results, Kirsch and colleagues (2010) proposed that the MP and N4—which were maximal over primary motor areas—reflected the programming of force and thus were directly related to acceleration changes during reaching movements. To the best of our knowledge, no study to date has used the ERP technique to examine differences in neural processing between visually and memory-guided reaching movements. Given Kirsch and colleagues (2010) results, it seems reasonable to assume that the behavioral differences typically observed when contrasting visually and memory-guided reaches (i.e., greater target undershooting) might be related to differences in cortical motor potentials such as the MP and N4.

   In the current study, participants completed reaches to visible and remembered target locations. We hypothesized that the performance differences that characterize visually and memory-guided movements would be reflected by differences in the cortical motor potentials during the reaching movements. Specifically, well-documented findings that memory-guided actions elicit a systematic pattern of endpoint undershooting (e.g., Heath and Westwood, 2003; Heath, 2005; Krigolson and Heath, 2004; Westwood et al., 2003) were predicted to be associated with reduced cortical motor potentials at or following movement onset. More specifically, we hypothesized that the amplitudes of the MP and/or N4 components would be reduced for memory-guided reaches relative to their visually guided counterparts. In addition, we sought to examine the ERP data for differences between visually and memory-guided reaching movements at target presentation. This research question was predicated on determining the nature of the information stored in memory and used to support memory-guided reaching movements. As mentioned above, the motor hypothesis states that a movement plan is generated when vision of the target is available and then stored in memory for later execution (e.g., Henry and Rogers, 1960). In contrast, the sensory hypothesis asserts that a sensory-based representation (specifically visual) is developed at the time of target presentation and is in held in memory for conversion to a motor plan at—and not before—response cuing (e.g., Elliott and Madalena, 1987; Heath et al., 2004b; Westwood and Goodale, 2003). In line with previous work demonstrating that the BP indexes movement planning within SMA (Cui and Deecke, 1999a) and work in monkey demonstrating activity in premotor areas following presentation of a movement target (Bauswein and Fromm, 1992), we predicted that if the motor hypothesis was true, then we might see differences in the ERP waveforms following target presentation indicative of differences. In other words, we predicted that if the motor hypothesis is true then we might expect differences in the ERP waveforms over motor regions of cortex

between visually and memory-guided reaches at the time of target presentation attributable to differences in motor planning at this time. Conversely, if the sensory hypothesis is true we predicted that there would be no differences in these ERP waveforms following target presentation.

Methods

Participants

Fifteen right-handed undergraduate students (8 male, 7 female) with no known neurological impairments and with normal or corrected-to-normal vision participated in the experiment. The participants provided informed consent approved by the Office of the Vice-President, Research, University of Victoria, and the study was conducted in accordance with the ethical standards prescribed in the original (1964) and subsequent revisions of the Declaration of Helsinki.

Apparatus and Procedure

Participants were seated comfortably in front of an aiming apparatus similar to that employed by Held and Gottlieb (1958). The apparatus consisted of a two-sided rectangular box (740 mm high, 960 mm wide, 600 mm deep) divided in half by a fully silvered mirror inclined at 20 degrees. A 17-inch computer monitor (LG 1750 SQ: 8 ms response rate; 1024×768 pixels) was placed upside down on the superior surface of the apparatus to project visual stimuli onto the surface of the mirror. A graphics tablet (WACOM Intuos 2, 300 mm $\times$ 450 mm, sampling rate: 125 Hz) was placed directly below the mirror such that movements made on the surface of the graphics tablet corresponded to movements of a cursor (5 by 5 mm red square) on the surface of the mirror. Notably, we used the cursor as a virtual representation of limb position because the mirror associated with our aiming apparatus prevented participants from directly viewing their limb.

Participants were instructed to complete reaching movements "as accurately as possible within the required time constraints" to one of two target locations in two experimental conditions: visually and memory-guided. The targets were 15 by 15 mm white squares located either 300 mm (i.e., the proximal target) or 320 mm (i.e., the distal target) along the horizontal axis to the right of a common start position (15 by 15 mm white square) located 155 mm to the left of participants midline and 150 mm from the front edge of the reaching apparatus. To minimize eye movements, participants were instructed to fixate on the target location once it appeared and to maintain this gaze location throughout a trial. At the start of each trial, participants moved their cursor into the start position after which time a 2000 ms preview period was provided wherein the start location, cursor, and one of the two targets was visible. During visually guided trials, an auditory tone signaled participants to initiate their reaching response at the end of the preview period. During memory-guided trials, the target location was occluded after the preview period and the auditory tone used to signal movement onset was provided following a 1,000 ms delay.

Participants were instructed to complete their reaching movement with a movement time between 400 and 700 ms, and trials following outside of the bandwidth

were placed back in the random trial sequence (see details below) and repeated. Participants completed 200 aiming trials which were arranged into four 50 trial blocks, two for each condition (visually guided, memory-guided). Trial blocks were randomized and participants were provided self-paced rest breaks between each block. For each block an equal number of trials was completed to the proximal and distal targets that were presented pseudo-randomly. Earlier work using the same experimental setup (e.g., Krigolson et al., 2008) demonstrated that 20 trials were sufficient to familiarize participants with the nature of the aiming apparatus and the movement time bandwidth. As such, in the present investigation participants were provided with 20 familiarization trials in advance of data collection, 10 in each visual condition. Following each familiarization trial participants were provided with feedback about their movement time to ensure that their movements were completed within the desired temporal limits.

Behavioral Analysis

Cursor displacement data were filtered offline with a second-order dual-pass Butterworth filter using a low-pass cut-off frequency of 10 Hz. The displacement data were then differentiated using a three-point central finite difference algorithm to obtain instantaneous velocity data in the primary (horizontal) movement axis. The same algorithm was used to differentiate the velocity values to obtain instantaneous acceleration values at each sample. Movement onset was defined when the cursor velocity exceeded 50 mm/s for 100 ms, and movement offset was defined when cursor velocity fell below 50 mm/s for 100 ms. Dependent variables related to cursor displacement were: movement time (time between movement onset and offset), time after peak velocity (time between maximum velocity and movement offset), constant error (the signed error related to target under- and overshooting and represented as negative and positive valences, respectively) and its associated measure of endpoint variability (i.e., variable error). We also calculated the time of peak acceleration (the time from movement onset to the maximal positive acceleration) and peak deceleration (the time from movement onset to the maximal negative acceleration). To afford comparisons with the ERP data, we computed values for peak acceleration and peak deceleration by calculating the mean acceleration over a 100 ms window centered on the time points identified above for each participant as a function of experimental condition and target location.

Electrophysiological Analysis

The electroencephalogram (EEG) was recorded from 41 electrode locations using BrainVision Recorder software (Version 1.3, Brainproducts, GmbH, Munich, Germany). Electrodes in the following locations were mounted in a fitted cap and were referenced to a common ground: Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, FT9, FC5, FC1, FCz, FC2, FC6, FT10, T7, C3, Cz, C4, T8, TP9, CP5, CP1, CPz, CP2, CP6, TP10, P7, P3, Pz, P4, P8, PO7, POz, PO8, Oz. In addition, vertical and horizontal electrooculograms were recorded from electrodes placed above and below the right eye (Fp2, VEOG) and on the outer canthi of the left and right eyes (LHEOG, RHEOG), respectively. Electrodes were also placed on the left and right mastoid processes (LM, RM). Electrode impedances were kept below 10 kΩ at all times.

The EEG data were sampled at 250 Hz, amplified (Quick Amp, Brainproducts, GmbH, Munich, Germany) and filtered through a passband of 0.017 Hz—67.5 Hz (90 dB octave roll off).

Following data collection, the EEG data were filtered through a (0.1 Hz—25 Hz passband) phase shift free Butterworth filter and rereferenced to a mean mastoid reference. Ocular artifacts were corrected using the algorithm described by Gratton et al. (1983). Trials in which the change in voltage at any channel exceeded 35 uVs per sampling point were also discarded. Less than 10% of the ERP data were discarded for each participant. All ERP waveforms were baseline corrected using a 200 ms epoch immediately before target preview. For each experimental condition (visually guided, memory-guided), ERP epochs were extracted from the continuous EEG and averaged with respect to target preview (200 ms before to 600 ms after) and movement onset (300 ms before to 700 ms after) for each participant and electrode channel. For a statistical examination of the ERP data, we calculated the mean voltage for a 100 ms window centered on peaks of interest (see below) for each participant, electrode channel, and experimental condition.

Behavioral and ERP data (for channels of interest) were submitted to 2 (experimental condition: visually guided, memory-guided) by 2 (target displacement: proximal, distal) repeated-measures ANOVAs. Significant interactions were decomposed via paired samples *t* tests. All statistical tests were evaluated at an alpha level of 0.05. Mean error terms reflect the within subject standard deviations (Loftus and Masson, 1994; Masson and Loftus, 2003). For movement time between subject standard deviation values are also provided to afford an assessment of between subject variability.

Results

Behavioral Results

Temporal Measures of Reach Trajectories.   An analysis of movement time did not yield a main effect for experimental condition ($p > .05$)(Figure 1a); however, this variable did produce a main effect for target displacement, $F(1,14) = 54.90$, $p < .001$, and an interaction between experimental condition and target displacement, $F(1,14) = 7.01$, $p = .018$ (Figure 1a). Specifically, movement times increased reliably as a function of increasing target displacement for memory-guided (proximal = 550 ms *SD* 8 ms [BSD 31 ms]; distal = 565 ms *SD* 8 ms [BSD 30 ms]) ($t(14) = 5.79$, $p < .001$) but not visually guided reaches (proximal = 542 ms *SD* 8 ms [BSD 39 ms]; distal = 545 ms *SD* 8 ms [BSD 40 ms])($t(14) = 1.20$, $p = .250$). In terms of time after peak velocity, results showed that the deceleration phase of visually guided reaches (274 ms *SD* 8 ms) was reliably longer than memory-guided counterparts (254 ms *SD* 8 ms), $F(1,14) = 12.11$, $p = .004$ (Figure 1b).

Spatial Measures of Reach Trajectories.   Visually guided reaches were more accurate (1 mm *SD* 7 mm) than memory-guided counterparts, which were characterized by a reliable pattern of undershooting (-16 mm *SD* 7 mm), $F(1,14) = 5.92$, $p = .029$. In addition, reaches to the proximal target (-4 mm *SD* 1 mm) undershot target location less than reaches to the distal target (-12 mm *SD* 1 mm), $F(1,14) = 39.79$, $p < .001$ (see Figure 1c), a result possibly attributal to a range
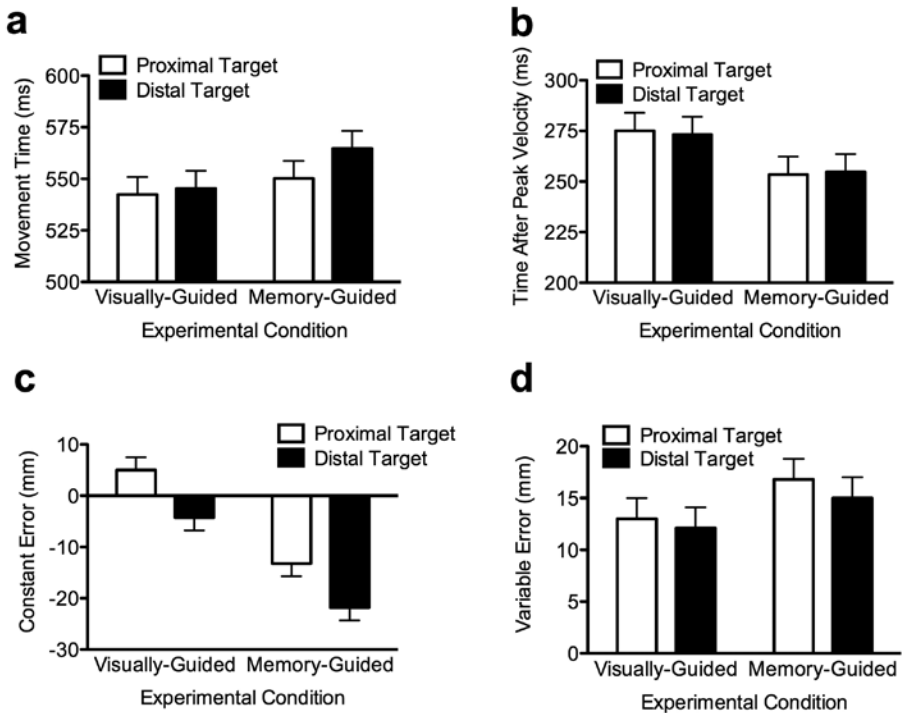
Figure 1 — (a) Movement time (ms) as a function of experimental condition and target displacement (mm). (b) Time after peak velocity (ms) as a function of experimental condition and target displacement. (c) Constant error (mm) as a function of experimental condition and target displacement. (d) Variable error (mm) as a function of experimental condition and target displacement. All error bars reflect the within subject standard error of the mean (c.f., Loftus & Masson, 1994; Masson & Loftus, 2003).

effect (see Pepper and Herman, 1970). In terms of variable error, endpoints for visually guided reaches (11 mm *SD* 1 mm) were more stable than memory-guided ones (14 mm *SD* 1 mm), F(1,14) = 16.98, *p* < .001, and endpoint variability for the proximal (13 mm *SD* 1 mm) target was increased in comparison with the distal target (12 mm *SD* 1 mm), F(1,14) = 16.66, *p* < .001 (see Figure 1d).

Acceleration and Deceleration of Reaches.   Results for peak acceleration and deceleration elicited main effects for experimental condition, Fs(1,14) = 36.53 and 13.44, respectively for peak acceleration and deceleration, ps < 0.001, and target displacement, Fs(1,14) = 50.60 and 23.05, respectively for peak acceleration deceleration, ps < 0.001, as well as their interaction, Fs(1,14) = 12.22 and 5.89, respectively for peak acceleration and deceleration ps < 0.05. For peak acceleration, we found the magnitude to increase for both visually and memory-guided reaches with increasing target displacement (see Figure 2) (ts(14) = 9.06 and 4.25, respectively for visually and memory guided conditions, ps < 0.001), hence our

post hoc decomposition did not reveal the nature of the experimental condition by target displacement interaction. However, examination of experimental means suggested that the nature of the interaction was rooted in a target displacement magnitude effect. For that reason, we computed target displacement difference scores for peak acceleration (far target—near target) separately for visually and memory-guided conditions and observed that difference scores in the former (303 mm/ms^2 *SD* 54 mm/ms^2) were larger than the latter (106 mm/ms^2 *SD* 54 mm/ms^2), t(14) = 5.74, *p* < .001. In terms of peak deceleration, visually guided reaches scaled to target displacement such that values for the proximal target (-3162 mm/ms^2 *SD* 107 mm/ms^2) were less than the distal target (-3554 mm/ms^2 *SD* 107 mm/ms^2), (t(14) = 5.56, *p* < .001). In contrast, memory-guided reaches did not scale to target displacement (proximal target = -2786 mm/ms^2 *SD* 10 mm/ms^2; distal target = -2896 mm/ms^2 *SD* 107 mm/ms^2), (t(14) = 1.28, *p* = .220). As with the effect of
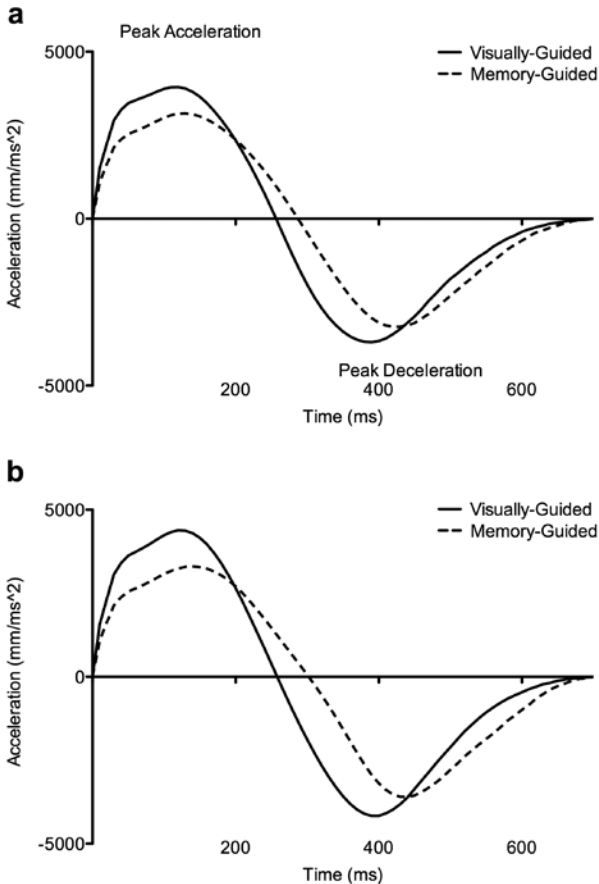

Figure 2 — Acceleration profile for reaches to the proximal (a) and distal (b) target in the visually and memory-guided conditions.

target displacement on constant error, the impact of target displacement on peak acceleration and deceleration may reflect a range effect (Pepper and Herman, 1970).

Electroencephalographic Results

Potentials Evoked by Target Presentation.   Visual inspection of the ERP waveforms averaged with respect to target presentation revealed a difference between visually and memory-guided reaches 250–400 ms posttarget that was maximal at electrode FCz (Figure 3). Subsequent statistical analysis affirmed this difference, $F(1,14) = 16.77$, $p = .001$ (visually guided 0.1 uV *SD* 0.4 uV; memory-guided 1.8 uV *SD* 0.4 uV). In addition, examination of Figure 4 shows the
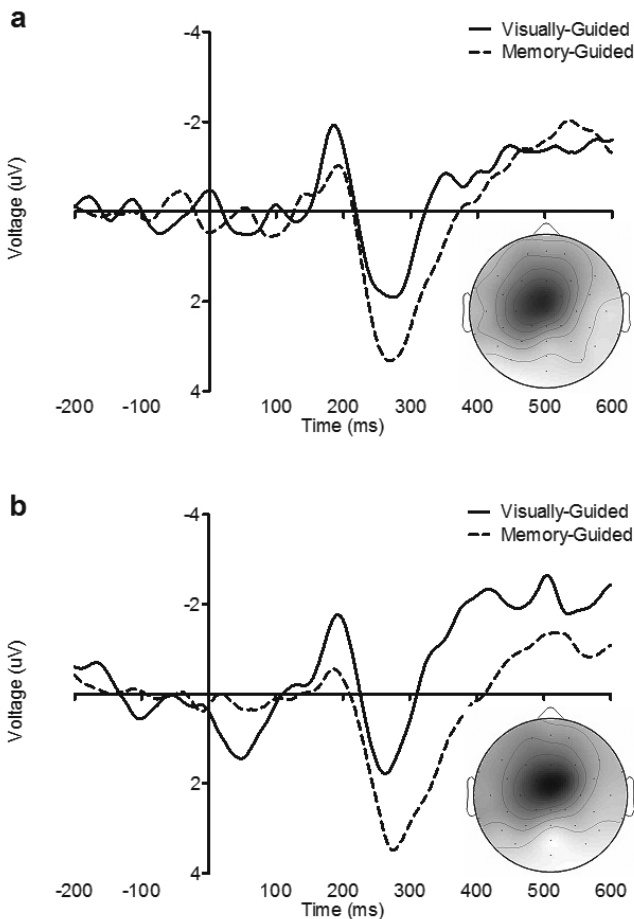
Figure 3 — Grand average ERP waveforms locked to target presentation for the proximal (a) and (b) distal targets in the visually and memory-guided conditions. The topography map reflects the scalp distribution of the maximal peak difference between the visually and memory-guided waveforms.

relationships between peak acceleration/deceleration and the mean amplitudes of the potentials we observed at target presentation for visually and memory-guided reaches. From this figure it can be seen that the mean amplitudes of the potentials during this time frame (i.e., 250–400 ms) were significantly correlated with peak acceleration ($r = -0.28, p = .028$) and peak deceleration ($r = .29, p = .024$) (Figure 4).

Within Movement Cortical Motor Potentials.   Visual inspection of the ERP waveforms averaged with respect to movement onset revealed two peaks, one at 50 ms (the MP) and one at 300 ms (the N4) which occurred before peak acceleration (100 ms) and peak deceleration (400 ms), respectively (Figure 5). Statistical analysis of ERP waveforms revealed that at 50 ms, ($F(1,14) = 11.79, p = .004$), and at 300 ms, ($F(1,14) = 13,52, p = .002$), the peak potentials were more negative for visually guided as opposed to memory-guided reaches (peak acceleration: -9.5 uV *SD* 0.7 uV versus -7.1 uV *SD* 0.7 uV; peak deceleration: -10.6 uV *SD* 1.2 uV versus -6.3 uV *SD* 1.2 uV). An examination of the relationship between these
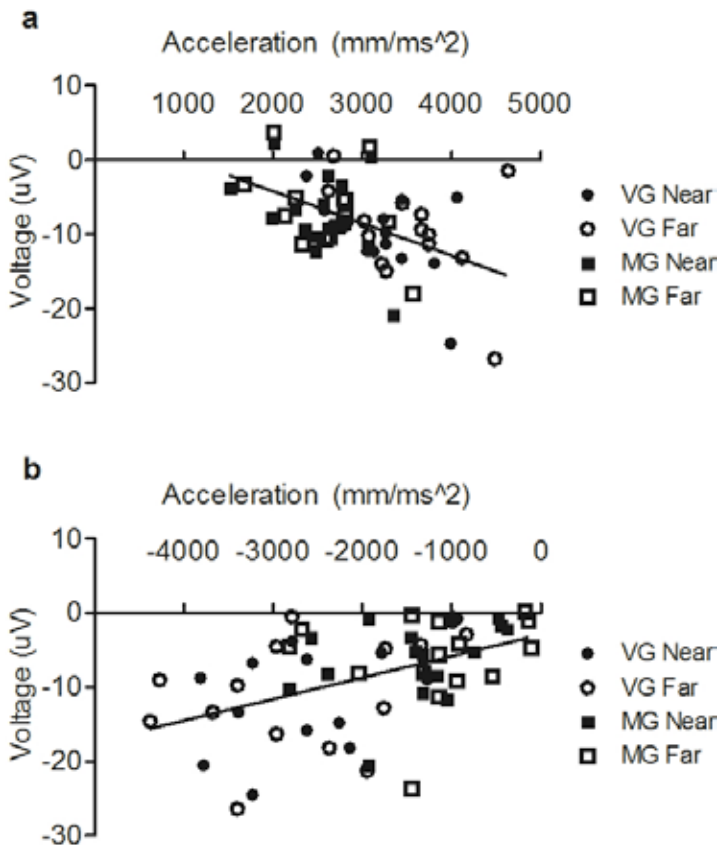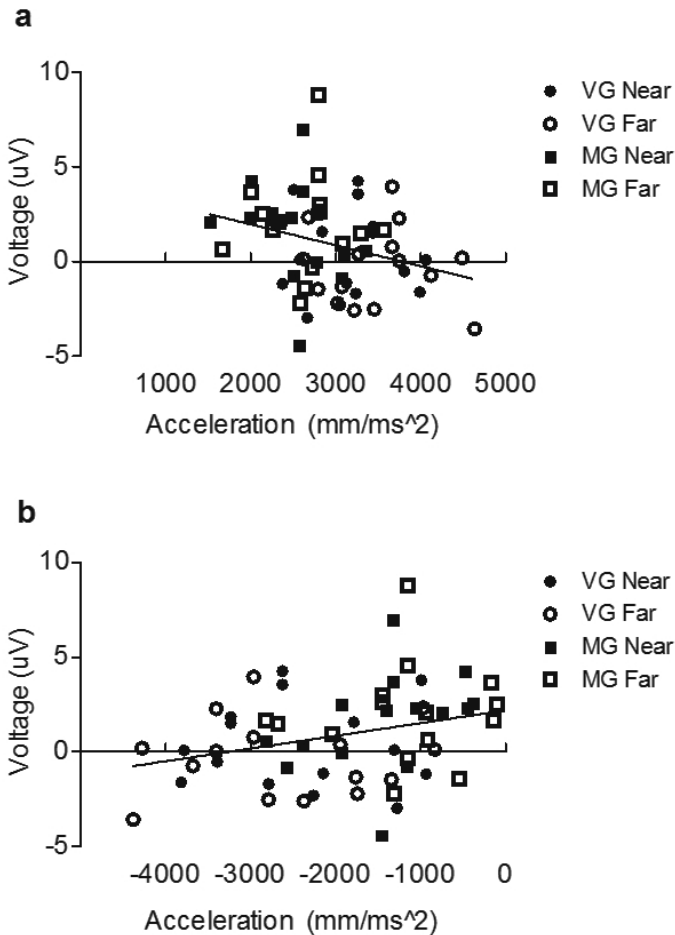

Figure 4 — Correlations between (a) peak acceleration and the motor planning potentials and (b) peak deceleration and the motor planning potentials.

potentials and peak acceleration/deceleration revealed that the mean amplitude of the potential at 50 ms was significantly correlated with peak acceleration ($r = -0.48, p < .001$) and the mean amplitude of the potential at 300 ms was significantly correlated with peak deceleration ($r = .47, p < .001$)(Figure 6). No effects were observed for target displacement, nor was an interaction between experimental condition and target displacement observed (p's > 0.05).
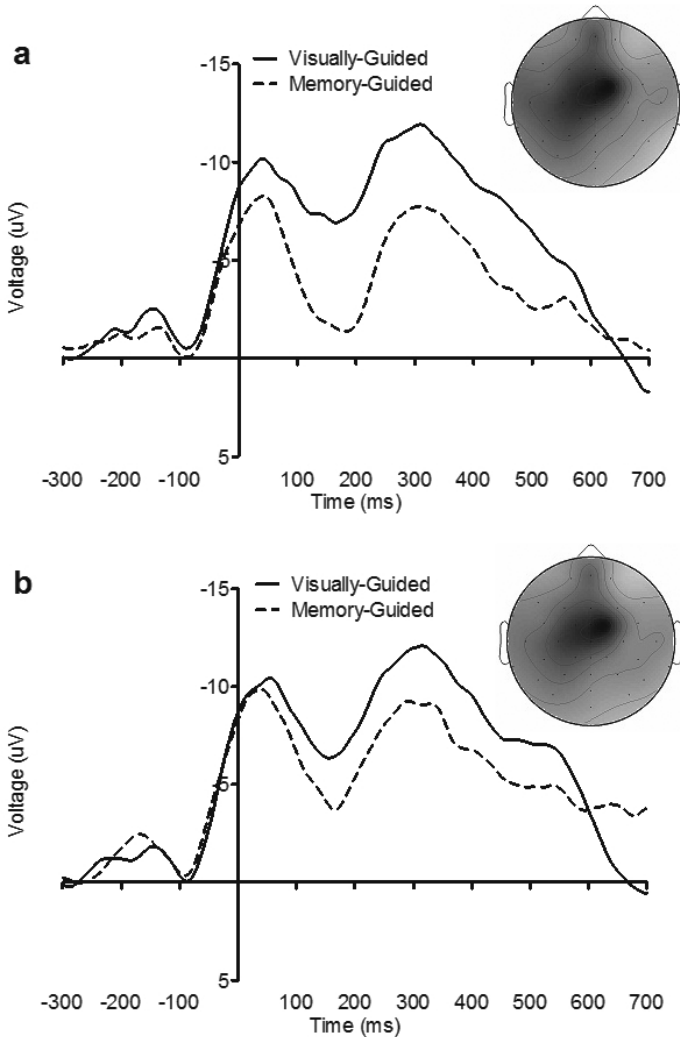
Figure 5 — Grand average ERP waveforms locked to movement onset for proximal (a) and distal (b) targets in the visually and memory-guided conditions. The topography map reflects the scalp distribution of the maximal peak difference between the visually and memory-guided waveforms.

Figure 6 — Correlations between (a) peak acceleration and the early within movement motor potentials and (b) peak deceleration and the late within movement motor potentials.

Discussion

Spatial and Temporal Parameters of Visually and Memory-Guided Reaches

In the current study we found that endpoints for memory-guided reaches were more variable and exhibited a marked pattern of target undershooting in comparison with their visually guided counterparts—a finding in line with previous work (e.g., Westwood et al., 2003). Notably, the between-condition differences we observed cannot be attributed to a speed-accuracy trade-off (Fitts, 1954) given the comparable movement times of visually and memory-guided reaches. Rather,

the fact that the deceleration phase of reach trajectories was longer in the visually guided as compared with memory-guided condition suggests that reaches in the latter condition depended on a mode of control whereby movement accuracy was achieved via online limb adjustments (e.g., Chua and Elliott, 1993; Crossman and Goodeve, 1983; Keele, 1968; Woodworth, 1899). In turn, the shorter deceleration times associated with memory-guided reaches, in combination with their less accurate and more variable endpoints, is directly in line with earlier behavioral studies showing that such actions are planned primarily in advance of movement onset (i.e., offline): a mode of control wherein few –if any- feedback-based corrections are implemented to the unfolding trajectory (cf. Binsted and Heath, 2005; Elliott et al., 1999; Heath, 2005; Heath et al., 2004b; Schmidt et al., 1979).

As we addressed above, the distinct performance characteristics of visually and memory-guided reaches are thought to reflect differences in movement planning and control. In the case of visually guided responses, it has been proposed that while such actions are planned to some extent in advance of movement onset, movement accuracy is ensured by dedicated visuomotor networks residing in the posterior parietal cortex of the dorsal visual pathway that allow for rapid online adjustments to an ongoing movement (see Goodale et al., 2004 for review). In contrast, convergent evidence indicates that the removal of target vision disrupts the online control of action. As such, memory-guided responses are executed via a motor plan generated primarily in advance of movement onset. The motor plan that subserves memory-guided actions is thought to either be generated at the time of target presentation and held in memory for subsequent use (the motor hypothesis) or generated just before movement onset via a stored sensory representation (the sensory hypothesis). Importantly, both hypotheses hold that time-dependent motor or visual decay renders memory-guided actions to be less accurate and more variable than visually guided counterparts (Heath et al., 2004b; McIntyre et al., 1998; Lemay and Proteau, 2001; Westwood et al., 2001, 2003).

Evidence for Differences in Movement Planning at Target Presentation

We observed a difference in the ERP waveforms for visually and memory-guided reaches at target presentation. More specifically, we found a difference in the ERP waveforms between visually and memory-guided reaches that was maximal over medial-frontal cortex 250–400 ms following target presentation (or 1600–1750 ms before movement onset/target occlusion). We also found that the amplitudes of the ERP potentials for visually and memory-guided reaches during this window were correlated with peak acceleration and peak deceleration. Recall, that participants were aware of the experimental condition at the time of target presentation. This represents a salient issue because previous work has shown that knowledge of the availability of upcoming sensory information influences how participants structure their response. For instance, when vision is known to be available participants structure their response online to take advantage of visual feedback, whereas if vision is to be occluded participants structure their response primarily in advance of movement onset with the response unfolding without online corrections (Elliott and Allard, 1985; Jakobson and Goodale, 1991; Khan et al., 2003; Heath et al., 2006; Zelaznik et al., 1983).

We believe the difference in the ERP waveforms between visually and memory-guided reaches at target presentation reflect task-based differences in movement planning within areas of cortex such as supplementary motor area. Although source analysis is not a strength of the ERP technique (Luck, 2005), previous research has localized early cortical motor potentials to the supplementary motor area (e.g., Shibasaki et al., 1980; Shibasaki and Hallett, 2006) and as such, a parsimonious interpretation of our results is that differences observed at the time of target presentation also originate from this area of cortex. Moreover, the fact that we observed differences in the ERP waveforms between visually and memory-guided reaches shortly after target presentation (and well in advance of movement onset) suggests that such actions are subject to different movement planning—a result which supports the motor hypothesis of memory-guided reaching (Ghafouri and Feldman, 2001, Henry and Rogers, 1960). Indeed, given that we observed conditional differences in the ERP waveforms shortly after target presentation, our data suggest that memory-guided reaches are executed via a movement plan that is generated at target presentation and then held in memory for later use. Further, given that we found a relationship between the amplitude of the potentials at this time and peak acceleration/deceleration, our data suggest the greater target undershooting we observed in the memory-guided condition is due to the implementation of a motor plan that is programmed with less overall force (as indexed by the reduced potentials we observed in the memory-guided condition, see below), and that this reduction in force translates to reduced accelerations during reaching movements (i.e., Kirsch et al., 2010)—and thus an overall shorter movement.

Premovement and within Movement Cortical Motor Potentials

Immediately before movement onset we observed potentials that shared similarities with the cortical motor potentials observed during the performance of simple self-paced finger movements (i.e., the BP: Cui and Deecke, 1999a, 1999b; Shibasaki et al., 1980; Shibasaki and Hallett, 2006). With that said, we found no differences between the ERP waveforms for visually and memory-guided reaches immediately before movement onset (i.e., the BP). However, during the reaching movements, we observed potentials similar to those reported by Kirsch and colleagues (2010)—an early negativity (the MP) that peaked shortly after movement onset and a later negativity (the N4) that peaked approximately 300 ms after movement onset that did exhibit conditional differences. Importantly, our results revealed that the MP and N4 were smaller for memory-guided, as opposed to visually guided, reaching movements. It is also noteworthy that the scaling of MP and N4 potentials across reaching conditions related to the scaling of reaching endpoints: Memory-guided reaches produced smaller MP and N4 potentials than did visually guided ones, and further, reach endpoints in the latter condition significantly undershot the veridical target locations. Further, as with previous work (e.g., Kirsch et al., 2010), we found that the MP immediately preceded peak acceleration and that the N4 immediately preceded peak deceleration. Supporting a possible relationship between the cortical motor potentials and acceleration, we found that the amplitudes of the MP were correlated with peak accelerations and the amplitudes of the N4 were correlated with peak decelerations. As with the results we observed for the potentials at target presentation, these data suggest that the greater target undershooting in the

memory-guided condition is due to a reduction in the within movement cortical motor potentials in this condition. Again, we propose that the reduced cortical motor potentials in the memory-guided condition reflect the implementation of a motor plan programmed with less force, which results in smaller overall accelerations and thus greater target undershooting.

Previous research suggests that within-movement cortical motor potentials can be attributed to motor activity in supplementary motor area, lateral premotor area, and primary motor cortex (Shibasaki et al., 1980) and is dependent on the processing of kinaesthetic feedback and/or reafferent activity from other motor areas (Cui and Deecke, 1999a, 1999b; Shibasaki et al., 1980; Shibasaki and Hallett, 2006). In line with the recent work by Kirsch and colleagues (2010), we believe the MP and N4 observed for visually and memory-guided originate from the aforementioned premotor and motor regions of cortex and are related to the force output of reaching movements. As stated above, we propose that the reduced amplitudes of the MP and N4 that we observed for memory-guided reaches reflect reduced activity within supplementary motor area that results in reduced force production and thus reduced accelerations (and therefore target undershooting). We believe these results support the motor hypothesis (Henry and Rogers, 1960) and suggest that memory-guided reaching movements rely on a movement plan generated at the time of target presentation. Further, our data suggest that during memory-guided reaching a more conservative movement plan is adopted (c.f., Elliott et al., 1999) which is observable here as a reduction in the potentials observed at target presentation, and later potential during the reaching movements—the MP, and the N4. The adoption of a more conservative motor plan ultimately leads to a reduction in the amount of force applied during the movement and thus the target undershooting characteristic of memory-guided reaching movements.

Conclusions

We observed reduced potentials for memory-guided reaches relative to visually guided reaches at target presentation and within reaching movements (the MP and N4)—results which suggest that the behavioral differences typically observed when contrasting these types of reaches (i.e., greater target undershooting) stem from differences in movement planning. Supporting this, we also demonstrated that the amplitudes of the potentials at these time points were correlated with peak acceleration and peak deceleration. As such, our results are counter to recent work which suggests that memory-guided reaches are executed via a motor plan which is generated just before movement onset from a stored and sensory-based target. Instead, our data suggests that memory-guided movements rely on a motor plan generated when vision of the target is available and held in memory until the time of response initiation.

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