

COGNITIVE NEUROSCIENCE

Exploring the unknown: electrophysiological and behavioural measures of visuospatial learning

Brendan Quinlivan,^{1,2} John S. Butler,^{1,3} Abdur Raquib Ridwan,^{1,2} Ines Beiser,^{4,5} Laura Williams,^{4,5} Eavan McGovern,^{4,5} Sean O'Riordan,^{4,5} Michael Hutchinson^{4,5} and Richard B. Reilly^{1,2,6}

¹Trinity Centre for Bioengineering, Trinity College Dublin, 152–160 Pearse St, Dublin 2, Ireland

²School of Engineering, Trinity College Dublin, Dublin, Ireland

³School of Mathematical Sciences, Dublin Institute of Technology, Kevin St, Dublin, Ireland

⁴Department of Neurology, St Vincent's University Hospital, Dublin, Ireland

⁵School of Medicine, University College Dublin, Ireland

⁶School of Medicine, Trinity College Dublin, Dublin, Ireland

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Abstract

Visuospatial memory describes our ability to temporarily store and manipulate visual and spatial information and is employed for a wide variety of complex cognitive tasks. Here, a visuospatial learning task requiring fine motor control is employed to investigate visuospatial learning in a group of typically developing adults. Electrophysiological and behavioural data are collected during a target location task under two experimental conditions: Target Learning and Target Cued. Movement times (MTs) are employed as a behavioural metric of performance, while dynamic P3b amplitudes and power in the alpha band (approximately 10 Hz) are explored as electrophysiological metrics during visuospatial learning. Results demonstrate that task performance, as measured by MT, is highly correlated with P3b amplitude and alpha power at a consecutive trial level (trials 1–30). The current set of results, in conjunction with the existing literature, suggests that changes in P3b amplitude and alpha power could correspond to different aspects of the learning process. Here it is hypothesized that changes in P3b correspond to a diminishing inter-stimulus interval and reduced stimulus relevance, while the corresponding changes in alpha power represent an automation of response as habituation occurs in participants. The novel analysis presented in the current study demonstrates how gradual electrophysiological changes can be tracked during the visuospatial learning process under the current paradigm.

Introduction

Visuospatial memory is responsible for storing information about our environment and the spatial orientation of objects in that environment. Abnormal visuospatial processing has been observed in several clinical disorders, including autistic spectrum disorders (McGrath *et al.*, 2012, 2013), Parkinson's disease (Nantel *et al.*, 2012; Leek *et al.*, 2014) and schizophrenia (White *et al.*, 2011; Bourque *et al.*, 2013). The widespread nature of abnormal visuospatial processing creates a need for objective methods of assessment. The task (as adapted from Stafford *et al.*, 2012) and novel analysis presented in the current study may have utility for the investigation of visuospatial processing for these clinical cohorts.

In a recent study, Bednark *et al.* demonstrated a relationship between visuospatial learning and P3b amplitude (Bednark *et al.*, 2013). Bednark investigated visuospatial learning by comparing

behavioural movement times (MTs) and electroencephalogram (EEG) components acquired during a target location task consisting of 30 repetitions (Bednark *et al.*, 2013). In that study, trials 1–15 were grouped together, as were trials 16–30. In this fashion, Bednark *et al.* were able to show a relationship between P3b amplitude and MT across the first and second half of the task. The current study explores this relationship in greater detail by analysing behavioural and electrophysiological data at a consecutive trial level.

The P3b is a subcomponent of the P300 event-related potential (ERP); it is a positive component usually peaking in the time window of 300–500 ms post-stimulus. The P3b is most commonly observed in tasks that require an aspect of performance monitoring and where stimuli are relevant to task performance (Courchesne *et al.*, 1975; Polich, 2007). It has been observed that the amplitude of the P3b is modulated by factors such as stimulus relevance, stimulus occurrence probability (Duncan-Johnson & Donchin, 1977), stimulus complexity (Isreal *et al.*, 1980; Johnson, 1986) and inter-stimulus intervals (ISIs; Gonsalvez & Polich, 2002; Croft *et al.*, 2003; Polich, 2003; Steiner *et al.*, 2013, 2014). While there have

Correspondence: B. Quinlivan and Dr R. B. Reilly, ¹Trinity Centre for Bioengineering, as above.

E-mails: quinlivb@tcd.ie and reillyri@tcd.ie

been several studies that suggest a link between the P3b component and various types of learning (Lindin *et al.*, 2004; Jongsma *et al.*, 2006; Sailer *et al.*, 2010; Bednark *et al.*, 2013; Batterink *et al.*, 2015), it is a small subsection of these that explicitly link the P3b to visuospatial learning (Bednark *et al.*, 2013).

Changes of alpha oscillations (8–12 Hz) have been strongly linked to the cognitive state of participants. Power in the alpha band over occipital regions is generally observed to decrease during tasks requiring greater effort and attentional loads (Ergenoglu *et al.*, 2004; Bollimunta *et al.*, 2008; Snyder & Foxe, 2010). Increases in alpha power have been associated with decreased attentional demand and with improvements in learning-based tasks (Dockree *et al.*, 2007; Bays *et al.*, 2015). One interpretation of these characteristics is that increases in alpha power during repetitive tasks represent an aspect of automation of response from participants: as responses become automatic, less attention is required, which in turn leads to increased alpha power (Jensen & Mazaheri, 2010; Bays *et al.*, 2015). However, alpha power is also known to increase with time spent of repetitive tasks and is often accompanied by reduced performance (Foxe *et al.*, 2012), reflecting a decrease in concentration by participants. This confound implies that for increased alpha power to represent an increase in automation, behavioural performance must also remain consistent. This interpretation is only appropriate in tasks where habituation of response is possible, such as the current paradigm.

This study confirms and extends the findings of Bednark and colleagues. In addition to investigating the P3b response, a novel analysis examines changes in alpha power during the learning process. P3b amplitudes and alpha power values were analysed at a consecutive trial level to study the dynamic time course of visuospatial learning across 30 consecutive trials. Correlation analysis was carried out to compare electrophysiological and behavioural metrics. Finally, correlation analysis was carried out at single participant level to test the reproducibility of the proposed electrophysiological metrics. It was hypothesized that the relationship between P3b amplitude and task performance is not an indication that P3b amplitude is reflecting visuospatial learning directly but may be driven by other well-documented properties of the P3b component.

Materials and methods

Participants/ethics

Eleven healthy adults participated in this study (25.3 ± 2.6 years, mean \pm SD). All participants were right-handed as revealed by self-report, and had normal or corrected to normal vision. Only male participants were included to account for gender imbalances in visuospatial processing (Roalf *et al.*, 2006). In accordance with the declaration of Helsinki, all participants gave their written informed consent to the study, which was approved by the Faculty Ethics Committee of the Faculty of Health Sciences at Trinity College Dublin.

The task

The task used in the current study was adapted from previous work by Stafford *et al.* (2012); Bednark *et al.* (2013). Participants were seated in a comfortable chair, 70 cm from a computer monitor in a dark and quiet room where they were asked to complete a behavioural experiment. Participants were presented with a black screen containing a white cursor (0.8° diameter, visual degrees), a grey cross-hair and in some conditions a grey annulus (Fig. 1).

Movement of the cursor within a bounded, square search space (10.8° width) was controlled using a Kensington Orbit Optical Trackball.

Prior to the experiment, participants were informed that their aim was to move the cursor into a circular target location (3.2° diameter) in the fastest and most accurate manner possible. Participants completed a shortened practice session to help familiarize them with the paradigm. Providing detailed instructions and practice sessions to the participants represents a departure from the protocol of Bednark *et al.*, but was introduced to eliminate unwanted learning effects in the opening blocks. The practice session consisted of 10 trials of each experimental condition with a single target location for each of the 10 trials. At the beginning of each trial, the cursor appeared at a new random starting position inside the search space. To complete a single trial, participants were required to manoeuvre the cursor into the target location. When the cursor entered the target location a green circular stimulus (1.1° diameter) was presented at the centre of the search space for 500 ms (Fig. 1). Each experimental block consisted of 30 trials. Within each block, the position of the target location remained consistent across all trials. At the beginning of each block, a new target location was randomly generated. The target location could be generated at any point inside the search space providing it was never placed at the centre of the search space or directly adjacent to a bounding wall. This stipulation helped to reduce learning of target location in relation to visible landmarks and encourage visuospatial learning of the search space.

Participants completed this task under two conditions: Target Learning (TL) and Target Cued (TC). In the TL condition the position of the target location was hidden and participants were expected to learn the new location over the course of each block. In the TC condition the target location was highlighted by a grey annulus. The TC condition was designed as a control condition where visuospatial learning would not occur but a motor response would still be present. Participants completed 10 experimental blocks for each condition in alternating order.

Data acquisition

Continuous EEG data, sampled at 512 Hz, were collected from 64 scalp and eight external active sintered Ag-AgCl electrodes using a BioSemi high-impedance recording system. Stimuli were generated and presented using Neurobehavioral Systems' Presentation software. Triggers were recorded at stimulus onset for offline EEG analysis. The international 10–20 electrode layout system was employed for recordings.

Data analysis

MT was defined as the time interval from the beginning of each trial to the point that the participant manoeuvred the cursor into the target location. Average MTs were calculated for all participants, and group average MTs were calculated across participants to allow for comparison with group average ERP data.

ERP analysis

EEG data were analysed using custom MATLAB R2013b scripts and EEGLAB (Delorme & Makeig, 2004). Data were first detrended by removing the line of best fit from each channel to correct for signal drift. The data were then filtered using a 4th order band-pass Butterworth filter with a pass band of 0.1–40 Hz. An external electrode on the nasion was employed to reject trials that contained

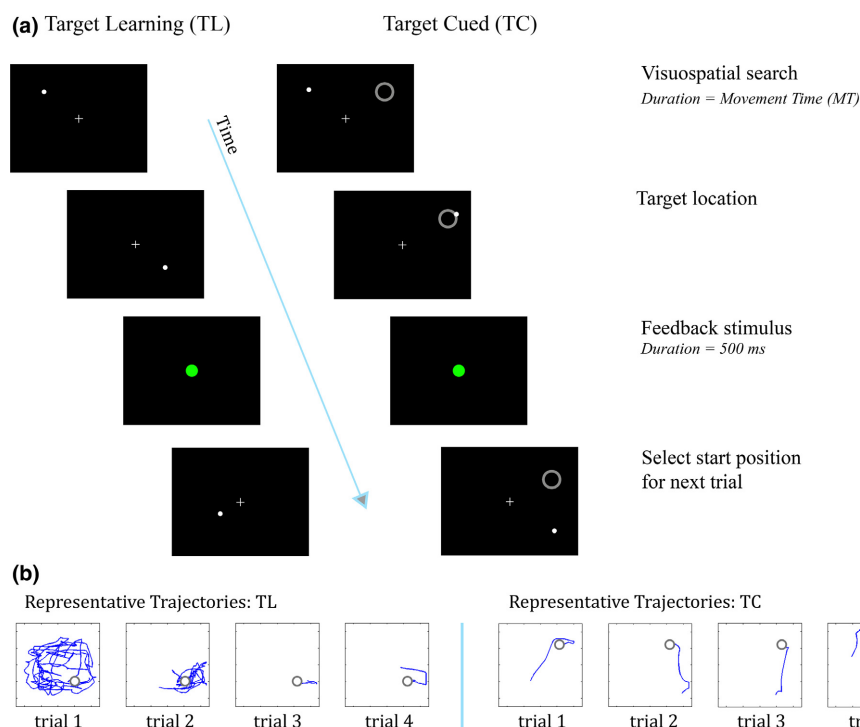


FIG. 1. Sample frames from the Target Learning (TL) and Target Cued (TC) conditions of the visuospatial learning paradigm (a). The figure illustrates the progression from the start of a single trial to the location of the target and finally the presentation of the 500-ms feedback stimulus. Representative trajectories for each condition, for trials 1–4, are displayed in (b). The blue line represents the trajectories of the cursor, and the grey annulus represents the target location. MT, movement time.

eye blinks; any channel that contained a voltage greater than $\pm 80 \mu\text{V}$ was also rejected. Trials that consisted of more than 10% bad channels were excluded from further analysis. In trials where the number of bad channels was fewer than 10%, those bad channels were interpolated using four nearest 'good' neighbours, as described in Butler *et al.* (2011). Average reference was employed during analysis by re-referencing the data to the average of all channels (Michel *et al.*, 2004; Nunez & Srinivasan, 2006); a 80-ms pre-stimulus window was used as the baseline period. Average ERPs to feedback stimulus onset were calculated for a 600-ms window for each trial. Individual ERPs were calculated across all blocks for the TL and TC experimental conditions for each trial. Group average ERPs were calculated across all participants. P3b amplitudes were calculated for each trial at group mean level by taking the mean value of the ERP waveform over the time interval 310–390 ms post-stimulus (Leue & Beauducel, 2015). This time window was selected to include the peak of the P3b component across all trials. This analysis was carried out over nine central electrodes of interest (FC1, FC2, FCz, CP1, CP2, CPz, C1, C2, Cz), and the mean of these was taken as the P3b amplitude for a given trial.

Spectral analysis

Power in the alpha band was estimated using a 500-ms time window prior to target location and the presentation of the feedback stimulus. This time window was selected to provide electrophysiological data during participant response. Given that alpha oscillations are not stimulus locked, it was necessary to calculate alpha power at a single trial level. To calculate the power in the 8–12 Hz spectral band, the Fourier Transform of the 500-ms window was calculated and the average power across the specified band was estimated. The

alpha power of a single trial was calculated as the mean power in the 8–12 Hz frequency band. Electrodes of interest (CP3, CP1, CPz, P5, P3, P1, Pz, P2, PO3, POz, O1, Oz) were used to calculate alpha power, where the topography showed alpha power to be most prominent. Group average alpha power was then calculated by generating the mean across blocks and participants.

Statistical analysis

Variance analysis

MTs were submitted to a two-way ANOVA to compare the mean differences between the TL and TC conditions. The independent variables used for this analysis were condition (level = 2, TL and TC) and trial (level = 30, trials 1–30); the dependent variable was MT. In a follow-up analysis, MTs from the TL and TC conditions were submitted to a one-way ANOVA to determine if significant differences existed due to trial number. The independent variable for this test was trial (level = 30, trials 1–30), and the dependent variable was MT. This analysis was carried out to explore how the performance of participants varied over trials and across conditions. P3b amplitude data and alpha power data were submitted to identical two-way and one-way ANOVA analysis. The aim of this analysis was to determine the significance of the observed changes in P3b amplitude and power in the alpha band across trials and condition. A Greenhouse–Geisser correction was applied to all analysis of variance carried out here.

Due to the unique exploratory nature of trial 1 in the TL condition, it was hypothesized that results from this trial could strongly influence the ANOVA analysis. For this reason all ANOVAs were performed twice, with and without inclusion of trial 1.

Correlation analysis

Correlation analysis was carried out on P3b and MT data at the group mean level to explore the relationship between P3b amplitude and task performance in both the TL and TC experimental conditions across the 30 trials of the block. Alpha power was also compared against MT to determine the statistical relationship between these metrics. Finally, correlation analysis of alpha power and P3b amplitude data was carried out to determine if these distinct electrophysiological parameters were statistically related. Correlations were calculated using the grand average values to test for correlation over the 30 trials of the experimental block.

As with the ANOVA, all correlation tests were carried out twice, once with inclusion of trial 1 and once without. A significance level of 0.015 was selected to account for multiple comparisons of the MT variable (Bonferroni correction).

In order to test the reproducibility of the results at single participant level, single participant MT, P3b amplitude and alpha rhythm power averages were calculated and submitted to the same correlation analysis as outlined for the grand average data above. Single participant correlations were calculated using the average across blocks for all trials. All reproducibility analysis was carried out with exclusion of trial 1. As with the group mean correlations, a significance level of 0.015 was selected to account for multiple comparisons.

Results

Behavioural

The behavioural measure of performance employed in this study was MT, the time taken for the participant to move the cursor into the target location in each trial. Figure 2a shows the group average MTs for both the TL and TC tasks. Figure 2b shows group average MTs with exclusion of trial 1. A steep increase in performance is observed over the first five trials of the TL task; MTs remain consistent over the remaining 25 trials. MTs remain consistent across the TL task with no obvious learning effect. A 2 (condition: TL, TC) \times 30 (trial: 1–30) repeated-measures ANOVA was conducted on MTs, and demonstrated a main effect of condition ($F_{1,10} = 75.7$,

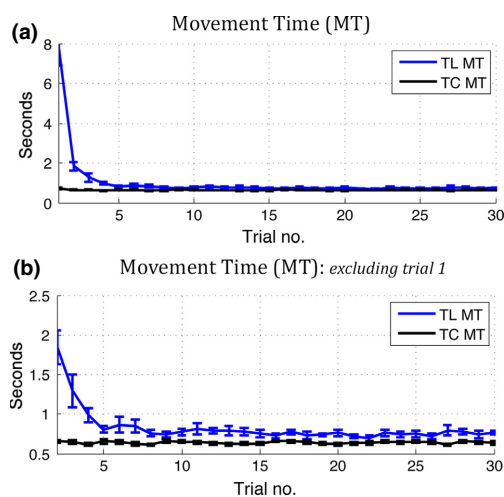


FIG. 2. (a) The group average movement times (MTs) for the Target Learning (TL; blue) and Target Cued (TC; grey) conditions plotted against all trials, 1–30. Error bars represent the standard error across participants. (b) The same MTs with exclusion of trial 1. Exclusion of trial 1 is incorporated to accommodate the unique exploratory nature of the first trial in the TL condition.

$P < 0.001$), a main effect of trial ($F_{1,3,12.9} = 51.8$, $P < 0.001$) and an interaction effect ($F_{1,3,13.1} = 49.8$, $P < 0.001$). This main effect of condition shows MTs are slower in the TL condition. Planned comparisons demonstrated significant differences between trials for the TL condition ($F_{1,3,12.9} = 51.2$, $P < 0.001$), but not for the TC condition ($F_{3,7,37.2} = 1.8$, $P = 0.15$). Exclusion of trial 1 from the MT ANOVA analysis did not alter the significance of the results (Table 1). These results demonstrate that participants become progressively faster at the task in the TL condition over trials but not in the TC condition. A summary of repeated-measures ANOVA and planned comparison analysis is displayed in Table 1.

Electrophysiological

ERP results

Figure 3a depicts the group average ERPs for the TL condition, and Fig. 3b shows the corresponding ERPs for the TC condition. There was no visible change in P3b amplitude after the 5th trial in either condition, therefore trials 6–30 are plotted as a mean curve with standard error displayed. The topographical distribution of the P3b component for both experimental conditions was calculated over an 80-ms window from 310 to 390 ms post-stimulus onset. Group average topographical distributions for the first five trials of each condition are displayed (Fig. 3c). P3b amplitude was calculated for each of the consecutive 30 trials for the TL and TC condition, as described in the Materials and methods. These P3b amplitudes and corresponding standard errors were plotted for each condition to illustrate the observed change in P3b amplitude over the experimental block (Fig. 3d). The 2 (condition: TL, TC) \times 30 (trial: 1–30) repeated-measures ANOVA on the P3b amplitudes showed a significant effect of condition ($F_{1,10} = 35.5$, $P < 0.001$), a significant effect of trial ($F_{7,2,72.1} = 6.1$, $P < 0.001$) and a significant interaction of condition by trial ($F_{6,1,61.2} = 7.7$, $P < 0.001$). This main effect of condition shows that P3b amplitude is larger in the TL condition. Planned within-condition one-way repeated-measures comparisons demonstrated significant differences between trials for the TL condition ($F_{6,4,63.8} = 12.5$, $P < 0.001$), but not for the TC condition ($F_{5,9,59.4} = 0.7$, $P = 0.63$). Exclusion of trial 1 from the P3b amplitude ANOVA analysis did not alter the significance of the results (Table 1). This analysis demonstrates that P3b amplitude decreases over trials in the TL condition but remains consistently non-existent in the TC condition.

Spectral results

In both the TL and TC conditions, an increasing trend in alpha power is observed over the course of the experimental block (Fig. 4a and b). A 2 (condition: TL and TC) \times 30 (trial: 1–30) repeated-measures ANOVA revealed a significant effect of condition ($F_{1,10} = 5.1$, $P < 0.05$) and a significant effect of trial ($F_{4,7,47.2} = 7.5$, $P < 0.001$), with no interaction effect ($F_{5,5,54.6} = 1.5$, $P = 0.187$). This main effect of condition represents the fact that alpha power is larger in the TC condition than in the TL condition, this is likely due to the lower attentional level required in the cued condition. This result may be influenced by the fact that alpha power appears to increase to its peak value earlier in the TC condition, as can be observed in Fig. 4; however, this is not statistically supported as no interaction of condition and trial was present. Planned one-way ANOVA comparisons showed a significant effect of trial in both the TL condition ($F_{5,1,51.3} = 4.3$, $P < 0.05$) and TC condition ($F_{4,8,47.8} = 5.6$, $P < 0.001$). These results indicate that alpha power increases with trial number in both

TABLE 1. Summary of all repeated-measures ANOVA and planned comparison analysis for MTs, P3b amplitude and alpha power

		df	<i>F</i>	<i>P</i>	df	<i>F</i> ex. 1	<i>P</i> ex. 1
MT							
Two-way ANOVA	Condition	1, 10	75.7	< 0.001	1, 10	34.1	< 0.001
	Trial	1.3, 12.9	51.8	< 0.001	2.4, 24.2	11.2	< 0.001
	Condition × Trial	1.3, 13.1	49.8	< 0.001	2.5, 25.1	10.7	< 0.001
P3b							
Two-way ANOVA	Condition	1, 10	35.5	< 0.001	1, 10	31.6	< 0.001
	Trial	7.2, 72.1	6.1	< 0.001	7, 70.3	2.8	< 0.05
	Condition × Trial	6.1, 61.2	7.7	< 0.001	5.7, 56.8	4	< 0.005
Alpha power							
Two-way ANOVA	Condition	1, 10	5.1	< 0.05	1, 10	5.2	< 0.05
	Trial	4.7, 47.2	7.5	< 0.001	4.9, 48.9	6.2	< 0.001
	Condition × Trial	5.5, 54.6	1.5	0.187	5.4, 53.9	1.5	0.187
Planned Comp.							
(Trials) TC	Trials	5.9, 59.4	0.7	0.63	5.9, 59.4	0.7	0.85
	Trials	6.4, 63.8	12.5	< 0.001	6.2, 62.1	5.9	< 0.001
Planned Comp.							
(Trials) TL	Trials	5.1, 51.3	4.3	< 0.05	5, 50	2.9	< 0.05
	Trials	4.8, 47.8	5.6	< 0.001	4.9, 49.2	5.1	< 0.001

F- and *P*-values are reported for all analyses carried out with the inclusion of trial 1 and with the exclusion of trial 1 (ex. 1). All main and interaction effects are reported, as are degrees of freedom (df). Greenhouse–Geisser corrected. MT, movement time; TC, Target Cued; TL, Target Learning.

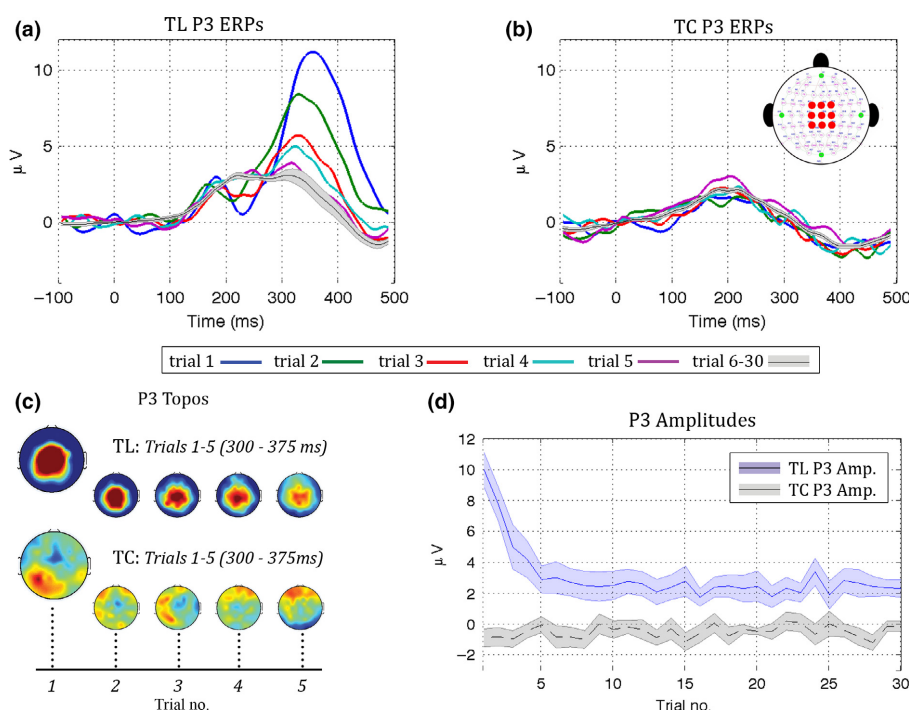


FIG. 3. (a and b) The group average P3b responses for the Target Learning (TL) and Target Cued (TC) conditions, respectively. In both cases no change in amplitude was present after the 5th trial, for this reason the curves corresponding to trials 6–30 were plotted as a single mean with standard error indicated. (c) A topographical distribution of the P3b component for the first five trials of the TL and TC conditions. This distribution was calculated over an 80-ms window from 310 to 390 ms post-stimulus onset. (d) The group average P3b amplitudes across all trials for the TL (blue) and TC (grey) conditions, shaded areas represent standard error. ERP, event-related potential.

the TL and TC conditions. Exclusion of trial 1 from the alpha power ANOVA analysis did not alter the significance of these results (Table 1).

Correlation

Correlation analysis of P3b amplitude and MT showed a significant relationship in the TL condition ($R = 0.85$, $P < 0.001$) with no

significant relationship in the TC condition ($P = 0.828$). The correlation in the TL condition maintained with exclusion of trial 1 ($R = 0.95$, $P < 0.001$) while, again, no relationship was observed in the TC condition ($P = 0.14$). The positive correlation of P3b and MT in the TL task indicates that the amplitude of the P3b decreases with the reduction in MT. This relationship is not observed in the TC condition.

Alpha power was tested against MT to determine if it had any relationship with participant performance during the task. A

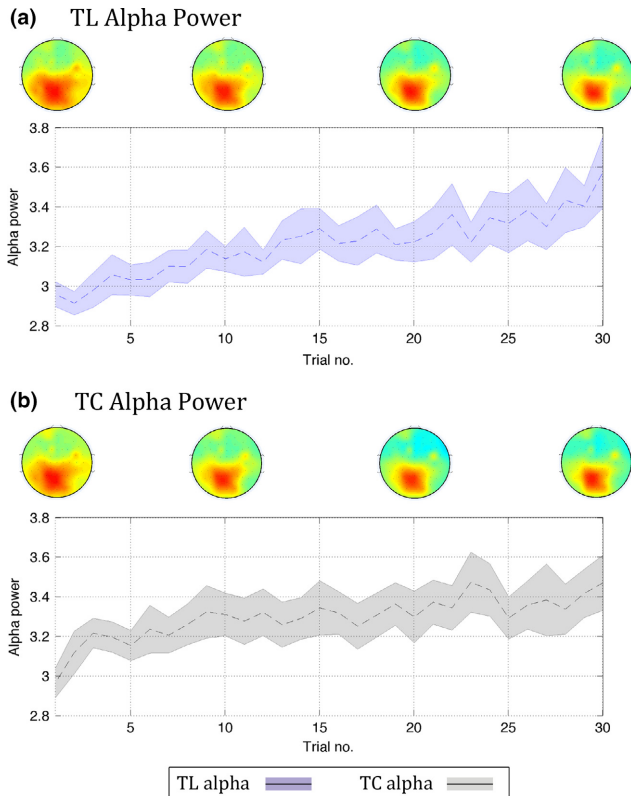


FIG. 4. (a and b) Alpha power plotted against trial number for the Target Learning (TL) and Target Cued (TC) experimental conditions, shaded areas represent standard error. A topographical plot of alpha power has been included for trials 1, 10, 20 and 30. These plots highlight the increase in alpha power that occurs in both experimental conditions. The topographical plots also indicate that alpha power becomes more focal over the course of the experiment.

relationship was observed between alpha power and MT for the TL experimental condition ($R = -0.47$, $P < 0.015$), while no significant relationship was seen in the TC condition ($P = 0.14$). Exclusion of the first trial did not alter the significance of the results (Table 2). This negative correlation in the TL condition indicates that alpha power increases with improvement in task performance as measured by decreasing MTs.

To probe the relationship between P3b amplitude and alpha power, a correlation analysis was carried out. At group mean level, the correlation analysis showed a significant relationship between these distinct electrophysiological parameters ($R = -0.67$, $P < 0.001$) in the TL experimental condition. No relationship was observed in the TC condition ($P = 0.15$). Exclusion of the first trial did not alter the significance of the results. A summary of these results is displayed in Table 2 and illustrated in Fig. 5.

To test the reproducibility of P3b amplitude and alpha power, correlations were calculated at single participant level. The corresponding P -values are summarized in Table 3. A significant relationship was observed between MT and P3b amplitude in eight of the 11 participants in the TL condition, the remaining participants showed no relationship between MT and P3b amplitude. In the TC condition, no significant relationship was observed between MT and P3b amplitude. This result shows that the relationship between P3b amplitude and MT is highly reproducible at single participant level. A significant relationship between MT and alpha power was observed in six participants in the TL condition. In the TC condition

TABLE 2. A summary of correlation analysis results for TL and TC experimental conditions

	TL	TC	TL ex. 1st trial	TC ex. 1st trial
MT vs. P3b	$R = 0.85$ $P < 0.001^{**}$	$R = 0.04$ $P = 0.828$	$R = 0.95$ $P < 0.001^{**}$	$R = 0.29$ $P = 0.14$
MT vs. Alpha	$R = -0.47$ $P < 0.015^{*}$	$R = -0.45$ $P = 0.14$	$R = -0.63$ $P < 0.001^{**}$	$R = 0.015$ $P = 0.937$
P3b vs. Alpha	$R = -0.64$ $P < 0.001^{**}$	$R = 0.27$ $P = 0.15$	$R = -0.60$ $P < 0.001^{**}$	$R = 0.197$ $P = 0.305$

Analysis was carried out for both experimental conditions with inclusion and exclusion of the first trial. Correlations between MT and P3b amplitude, MT and alpha power, and P3b amplitude and alpha power are included. R - and P -values are reported ($*P < 0.015$, $**P < 0.001$). MT, movement time; TC, Target Cued; TL, Target Learning.

there was only one significant relationship across participants. Finally, the reproducibility of the relationship between P3b amplitude and alpha power was tested. It was observed in the TL condition that this result was significant in two participants only. In the TC condition, one significant relationship was observed. This result would suggest that the relationship between P3b and alpha is not highly reproducible at the single participant level.

Discussion

The current study is an investigation of electrophysiological and behavioural measures collected during visuospatial learning in a motor search task. Given the results and the existing literature, it is hypothesized that the observed changes in task performance, as measured by MT, are influenced through a combination of visuospatial learning and automation of response. Furthermore, it is suggested that the observed changes in P3b amplitude primarily reflect a decreasing MT, rather than visuospatial learning directly.

Behavioural

MT was employed as a behavioural metric of task performance (Stafford *et al.*, 2012; Bednark *et al.*, 2013; Thirkettle *et al.*, 2013). Results show a significant decrease in MT across the first five trials in the TL condition, no such change is visible in the TC. In the TL condition, MTs decrease to a low plateau, although they still remain slower than that of the TC condition. It is hypothesized that the observed change in MT in the TL condition primarily represents the process of visuospatial learning; however, there may also be a secondary effect on performance due to automation of response. It is possible that the use of more sensitive metrics would allow these effects to be distinguished.

Electrophysiological

The P3b has long been associated with the process of decision making (Sutton *et al.*, 1965; Hillyard *et al.*, 1971). Recent studies continue to demonstrate how our understanding of these components can continue to evolve through the development of specific and well-designed experimental protocols (O'Connell *et al.*, 2012; Kelly & O'Connell, 2013; Twomey *et al.*, 2015). Bednark *et al.* demonstrated that both MT and the amplitude of the P3b component decreased between the first and second half of this 30-trial experiment (Bednark *et al.*, 2013). In the current study, P3b amplitude was analysed at consecutive trial level across all 30 trials.

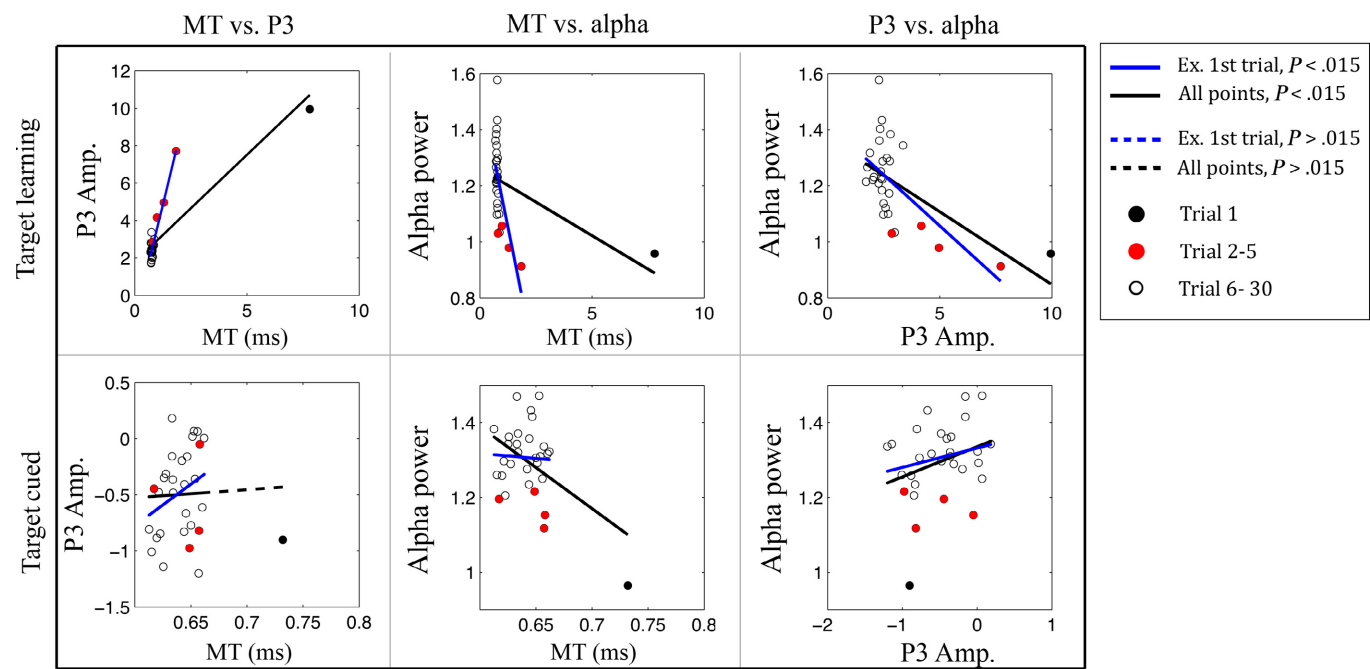


FIG. 5. Scatter plots with line of best fit to illustrate all correlation analyses that were carried out at the group mean level. Blue lines represent the fit with exclusion of data from trial 1; black lines illustrate the fit with all data points. Solid lines represent statistically significant correlations; dashed lines are used to indicate where no correlation was observed. The first trial on each plot is highlighted as a solid black point, trials 2–5 are indicated as a solid red point, and all other trials are represented by a black annulus. MT, movement time; TC, Target Cued; TL, Target Learning.

TABLE 3. A summary of the single participant reproducibility analysis for TL and TC conditions

	Significant ($P < 0.015$)	Non-significant
TL: MT vs. P3b	8	3
TL: MT vs. alpha	6	5
TL: P3b vs. alpha	2	9
TC: MT vs. P3b	0	11
TC: MT vs. alpha	1	10
TC: P3b vs. alpha	1	10

Significance has been defined as a P -value less than 0.015. The number of participants with significant and non-significant correlations between MT and P3b amplitude, MT and alpha power, and P3b amplitude and alpha power are reported. MT, movement time; TC, Target Cued; TL, Target Learning.

This novel analytic approach facilitated a deeper investigation into the relationship between visuospatial learning and P3b amplitude. The current results reveal a strong relationship between P3b amplitude and MT in the TL condition, which is highly consistent with the results presented by Bednark and colleagues. An important property of the P3b component is that its amplitude is modulated by ISIs (Gonzalez & Polich, 2002; Croft *et al.*, 2003; Polich, 2003; Steiner *et al.*, 2013, 2014). Given that MT directly equates to ISI in this task, it is possible that the observed decrease in P3b amplitude is an effect of the decreasing MT (and ISI). If the change in P3b amplitude is an effect of ISI then this change could only be considered a secondary effect of visuospatial learning rather than a direct measure. Bednark *et al.* addressed this concern through inclusion of a third condition in which cursor movement did not elicit a stimulus but ISI was matched to the TL condition, i.e. movement \neq outcome. In this condition, no relationship was observed between P3b amplitude and MT. This result could suggest that the change in P3b

is not a factor of ISI; however, it could also result from lowered participant engagement during a task where one's responses are meaningless and stimulus relevance has therefore been removed.

P3b amplitude is also modulated by stimulus relevance for a wide range of visual and auditory tasks (Sawaki & Katayama, 2006; Briggs & Martin, 2009). This property of the P3b may also have a role in the observed correlation. It is plausible that stimulus relevance is higher during the early stages of learning, and decreases as the target location is learned and feedback is no longer required. This decrease in stimulus relevance during visuospatial learning could explain why a decrease in P3b amplitude is observed over the early trials of the TL condition. This mechanism would also explain why the TC condition failed to elicit a P3b: as the participant always knows the target location, the feedback stimulus is not relevant to task completion and would therefore not be expected to produce a P3b response.

Whether the change in P3b amplitude in the TL condition is a factor of ISI, decreasing stimulus relevance or a combination of the two, it has utility as an electrophysiological metric of task performance rather than a direct measure of visuospatial learning. While it is possible that the P3b component is reflecting visuospatial learning independently of ISI in the current task, the strength of the correlation observed here and the extensive literature on this point (Gonzalez & Polich, 2002; Croft *et al.*, 2003; Polich, 2003; Steiner *et al.*, 2013, 2014) reduce the plausibility of this hypothesis.

In both the TL and TC conditions of this study, a significant increase in alpha power was observed across trials. Increases in alpha power during repetitive visual tasks can be explained by two distinct mechanisms. Some studies suggest that increases in alpha power reflect a level in automation during repetitive tasks where it is possible for the participant to learn the required response (Jensen & Mazaheri, 2010; Bays *et al.*, 2015). In such studies, increases in alpha power have been observed to correlate with improvements in

performance. On the other hand, when habituation of response is not possible, alpha power has been observed to increase with time-on-task and has been seen to correlate with reduced performance (Foxe *et al.*, 2012). In both cases, it seems that alpha power tends to increase as attention levels decrease. As habituation of response is possible in the current paradigm and performance is not observed to decrease with increases in alpha, it is plausible that the increase observed here represents a level of automation of response and a reduced attention load over the experimental block. Alpha power has also been observed to undergo event-related desynchronization in the time window of 400–700 ms post-stimulus presentation (Klimesch *et al.*, 2007; Makin *et al.*, 2014; Wright *et al.*, 2015). Given that the 500-ms pre-stimulus time window employed in the current study will overlap with this 400–700-ms time window from the previous trial in some cases, it is possible that the observed increases in alpha power could be impacted by a reduced level of event-related desynchronization.

The fact that this result is present in both experimental conditions would suggest that this automation occurs in both the TL and TC conditions. For this hypothesis to be accurate, differences observed between the TL and TC conditions for MT and P3b amplitude data must be explained by a process other than automation of response. This agrees with the previous hypothesis that those changes were a result of improved task performance, which was suggested are primarily driven by visuospatial learning with automation of response as a smaller secondary factor. One limitation to this theory is that no correlation is observed between alpha power and MT in the TC condition, as would be expected under the given hypothesis. This may be explained by a lack of sensitivity of the performance metric MT.

Correlation analysis

The correlation analysis for the TL condition revealed a significant relationship between alpha power and MT, and between P3b amplitude and MT. No such relationship was observed in the TC condition. These results support the view that MT reflects an overall measurement of performance, which is affected by changes in visuospatial learning and automation of response. Furthermore, the results of the correlation analysis reveal that this change in alpha power is strongly related to the observed change in P3b amplitude in the TL condition at the group mean level. Given the hypothesis that the changes in P3b are driven by changes in MT, this correlation likely reflects the alpha MT correlation rather than a separate relationship between P3b and alpha power. The results of the single participant correlation analysis reveal that the relationships between P3b amplitude and MT and alpha power and MT are both highly reproducible. The relationship between P3b and alpha was not robust at this level, supporting the view that the correlation at group level was not meaningful. These results support the group average correlations, and suggest that the current paradigm and proposed metrics have utility for research at a single participant level.

Concluding remarks

The task presented here has many qualities that make it suitable for the study of visuospatial learning; it is repeatable without a learning effect, it provides an objective measure of performance, it is intuitive and engaging for participants, and it is scalable in difficulty (Stafford *et al.*, 2012). These qualities make it suitable for deployment in movement disorder studies such as Parkinson's disease or dystonia where participants have varying levels of motor control.

The novel analysis presented here highlights how P3b amplitudes and alpha power can be assessed at a consecutive trial level, and demonstrates the versatility of such tasks in visuospatial learning research.

In the current study, it has been demonstrated that performance in this visuospatial learning task, as measured by MT, is highly correlated with both alpha power and P3b amplitude at a consecutive trial level. It is hypothesized here that the relationship between MT and P3b amplitude is driven by factors such as ISI and stimulus novelty rather than being a direct reflection of visuospatial learning. The hypothesis that alpha power could reflect an increasing level of automation in the given task is supported by the correlation between alpha power and MT in the TL condition, but is hindered by the lack of correlation in the TC condition. It is possible that the use of a more sensitive behavioural measure would allow for more definitive conclusions on this point, but further research is required to fully address this question. The analysis carried out here has shown that the data collected in this paradigm are robust enough to be analysed at a consecutive trial level. This novel analytic approach has allowed for a deeper understanding of the relationships between MT, P3b amplitudes and alpha power, and has informed the hypotheses presented in the current work. Another important implication of this work is that the analysis presented by Bednark *et al.* (2013) could likely be carried out with less data, allowing for shorter recording sessions in clinical populations. This work has also demonstrated that this analysis is highly reproducible at a single participant level. This gives the current paradigm further utility in clinical populations where inter-participant variability may be inflated, and group mean analysis may not be appropriate.

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Abbreviations

EEG, electroencephalogram; ERP, event-related potential; ISI, inter-stimulus interval; MT, movement time; TC, Target Cued; TL, Target Learning.

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